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GEOGRAPHICAL DIFFERENTIATION IN ARCTIC ANATIDAE AS A RESULT OF ISOLATION DURING THE LAST GLACIAL

by

P. L. PLOEGER

Zoological Museum, University of Amsterdam

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1. Introduction

1.1. AIM

The aim of this study is to consider the present distribution pattern and geographical variation of arctic swans, geese and ducks in relation to the physical-geographical situation of their breeding ranges during the Last Glacial. As these birds breed in tundras of whatever type the problem can be put as follows: Where did tundras occur in the holarctic region during the Last Glacial? Reconstruction of the former distribution of tundras may be considered to indicate the localization of potential breeding grounds and the possible geographical isolation of geographical forms of the species during the Last Glacial.

1.2. PROBLEMS

In this study I have confined myself to the last glaciation as this is the only Pleistocene glacial period of which the effects are still to be seen in the present distribution of present geographical forms. Fortunately it is also the best known of the glacial periods. In some instances it was necessary to make a tentative reconstruction of the whole Pleistocene history prior to the Last Glacial.

Though further data are required radiocarbon datings made so far have proved that the Wisconsin glaciation in North America, the Würm glaciation in the Alps and the Weichselian glaciation in NW Europe were synchronous. Probably the same applies to their stadials and interstadials. In dealing with problems related to the Last Glacial the name *Weichselian* will be used for palearctic, *Wisconsin* for nearctic conditions.

The main lines of the extension of the inland ice sheets in the Northern Hemisphere during the Last Glacial are fairly well known and generally accepted. There is much controversy with regard to the maximum extension of the inland ice sheets in the coastal regions of W and N Norway, Iceland and Greenland. Many scientists strongly advocate the possibility of ice-free refuge areas existing in these regions throughout the Last Glacial.

In North America the question of the northern limit of the Wisconsin Laurentide ice sheet in the Canadian Arctic Archipelago has only recently been settled.

In Europe and Asia extensive tundra areas certainly existed. But in North America the Cordilleran and Laurentide ice sheets only left tundras in the unglaciated regions of Alaska and probably in the emerged Bering Sea areas. Whether tundras occurred north and south of the Laurentide ice sheet is an important controversial issue.

Answering these questions may help to solve some zoogeographical problems relating to the recent history of arctic birds. Therefore, the problem of the extension of glaciated and unglaciated areas in these regions has been studied thoroughly and dealt with at length in the Physiographical Part of this study, whereas areas which certainly were unglaciated and offered refuge breeding grounds, are only briefly mentioned.

The present breeding ranges of non-exclusively-marine arctic birds can be arranged according to the following groups:

(a) Distribution continuously or discontinuously circumpolar (23 species):

Gavia stellata
Anser albifrons
Branta bernicla
Clangula hyemalis
Somateria spectabilis
Falco rusticolus
Lagopus mutus
Charadrius hiaticula
Arenaria interpres
Calidris alba
Calidris canutus
Calidris maritima
Calidris alpina
Phalaropus fulicarius
Phalaropus lobatus
Stercorarius parasiticus
Stercorarius longicaudus
Xema sabini
Sterna paradisaea
Nyctea scandiaca
Calcarius lapponicus
Plectrophenax nivalis
Carduelis hornemanni

(b) Distribution nearly circumpolar with a gap in the North Atlantic area (8 species):

Gavia adamsii
Gavia arctica
Cygnus columbianus
Buteo lagopus
Lagopus lagopus
Pluvialis squatarola
Stercorarius pomarinus
Eremophila alpestris

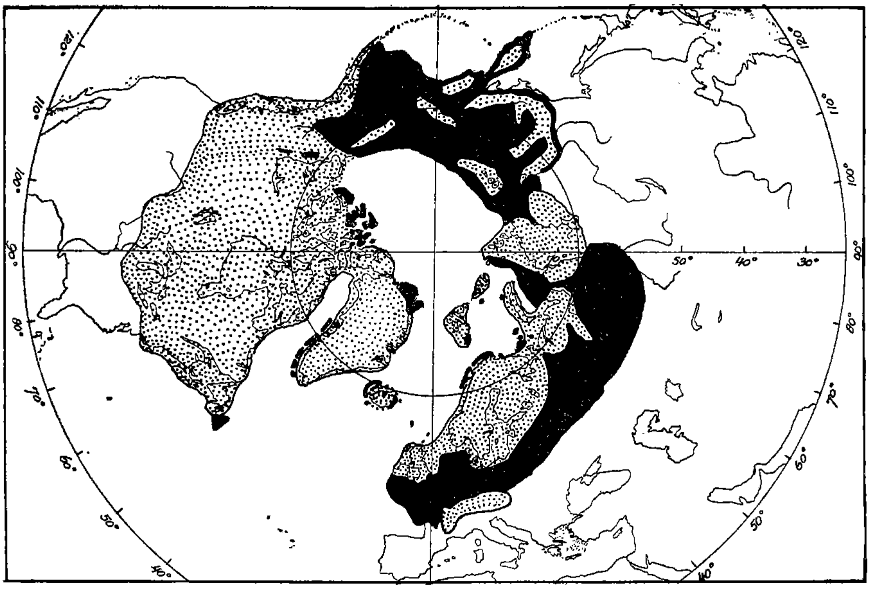

FIGURE 1a. Ice sheets and tundras during the Last Glacial. *Stippled areas* = maximum extent of ice sheets during the Last Glacial (Small and southern mountain glaciations not shown). *Black areas* = potential Last-Glacial tundra breeding grounds for arctic birds.

(c) Distribution confined to North America (10 species):

Gavia immer
Anser rossii
Branta canadensis
Numenius borealis
Limosa haemastica
Calidris fuscicollis
Calidris bairdii
Calidris pusilla
Micropalama himantopos
Tryngites subruficollis

(d) Distribution confined to Eurasia (9 species):

Anser fabalis
Branta ruficollis
Limosa lapponica
Calidris minuta
Calidris ruficollis
Calidris temminckii
Calidris acuminata
Calidris ferruginea
Anthus cervinus

(e) Distribution confined to Bering Sea area (5 species):

Anser canagicus
Polysticta stelleri
Somateria fischeri
Calidris mauri
Eurynorhynchus pygmeum

(f) Distribution in Eurasia and North America, with the Bering Sea area in the centre of the distribution range (4 species):

Anser caerulescens
Pluvialis dominica
Limnodromus scolopaceus
Calidris melanotos

(g) Distribution in North Atlantic area only (2 species):

Branta leucopsis
Pagophila eburnea

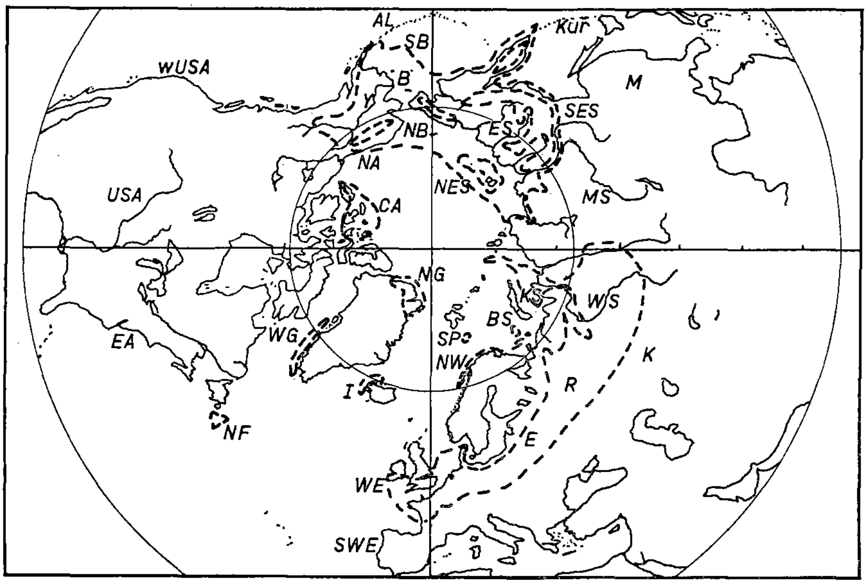

FIGURE 1b. Location of the potential Last-Glacial breeding grounds for arctic birds. For *abbreviations* see Paragraph 1.6.

(h) Distribution with considerable disjunctions (2 species):

Histrionicus histrionicus *Bucephala islandica*

Together they comprise 64 of the total number of 76 arctic species. These distribution patterns suggest the influence of the Last Glacial. Many of the circumpolar arctic birds have well-developed geographical forms. Assuming these forms to have evolved through geographical isolation, the present distribution of the geographical forms can be considered to indicate the location of the isolation during the Last Glacial. In some cases the former isolation no longer exists. Wherever once-isolated forms meet, the populations, if recognizable at all, form zones of secondary intergradation and the resulting geographical variation is at best a stepped cline.

Geographically isolated populations of the same species form separated gene pools. Gene mutations within the populations alter the total gene content and may lead to morphological differentiation, even if the ecoclimatological circumstances in the isolated areas are completely identical. However, in the majority of cases geographically isolated regions do differ in ecoclimatological aspects. These differences affect the result of selection pressure and therefore subsequently lead to differentiation between the populations.

In the following study relating to the Last Glacial attention is paid to geographical isolation only, without taking into account possible ecoclimatological differences between isolated areas. This could not be done, as even the knowledge of present ecoclimatological differences within the extensive breeding ranges of arctic birds is negligable.

1.3. Methods

After the distribution and the extension of tundras during the Last Glacial have been located (Fig. 1a and 1b), they will be considered as the palaeogeographical basis for delimiting the potential glacial breeding areas of arctic birds. An equally important step is to indicate which areas certainly could not have formed glacial breeding grounds. In some cases a number of alternatives for Last-Glacial potential breeding ranges exist. When this occurs, present-day subspecific differentiation has been used to indicate which alternative is the most probable. I am aware, however, that in these cases I am reversing the method generally applied in this paper, by which I try to find the Last-Glacial breeding ranges and to explain the subspecific differentiation on the basis of physiographical data.

The theoretical Last-Glacial breeding ranges thus found must provide the geographical basis for the processes of geographical differentiation and species formation of the arctic species of swans, geese and ducks studied.

1.4. Assumptions

The following assumptions have been made:

(1) During the Last Glacial the arctic breeding birds had the same or similar ecological preferences as they have to-day.
(2) The family tie and migration behaviour were the same as they are at present.

1.5. Definitions

An *arctic bird species* is here defined as a species which at present regularly breeds in a more or less extensive area within the Arctic. Its breeding range may extend beyond the Arctic, but only into the Sub-arctic or the most northerly parts of the boreal zone or corresponding mountains habitats (Johansen 1958: 87).

The *Arctic* is the area on the northern hemisphere beyond the July-isotherms of 10° C. (Fig. 2).

The *tundra* is here defined as a treeless landscape with a perennial frozen subsoil and a flora consisting of many species with arctic or arctic-alpine distribution.

Any periglacial treeless vegetation is not necessarily a tundra. It may lack a permafrost, a dominating arctic character of the flora, and may have the warmest month above 10° C. The treeless character may be due to other factors than those essential in the present Arctic, e.g. edaphic factors, arid or semi-arid conditions, and slow reimmigration of trees after the retreat of the ice. These facts must be stressed here, as especially the presence of a permafrost causes wet and marshy conditions in large

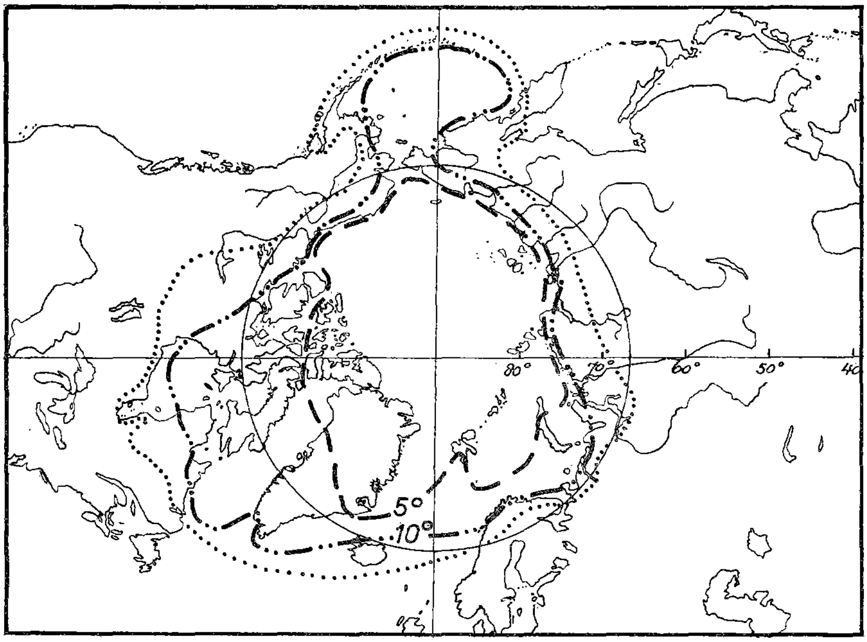

FIGURE 2. Present limits of arctic and subarctic regions.
— — — = 5° C isotherm of warmest month: southern limit of High-arctic.
—··—·· = 10° C isotherm of warmest month: southern limit of Low-arctic.
.... = southern limit of subarctic region (JOHANSEN 1963).

tundra areas. These tundra swamps provide suitable breeding and feeding habitats for the swans, geese and ducks dealt with in this study.

The *High-arctic* has the mean July temperature below 5° C (Fig. 2). This is the zone of the lichen and moss tundra, and of snow and ice. It is part of the ET and the complete EF climate of KÖPPEN.

The *Low-arctic* lies between the July-isotherms of 5° C and 10° C (Fig. 2). This is the zone of lichen and moss tundra and of the scrub tundra. It is part of the ET climate of KÖPPEN.

The term *Pan-arctic* applies to the Low- and High-arctic together.

The *Sub-arctic* is the transitional zone between the arctic and boreal zones. This is the wooded tundra zone, birch zone, or Hudsonian life-zone.

The *boreal* zone is the zone with an average July temperature above 10° C and an average temperature of the coldest month below —3° C. This is the boreal, mainly coniferous, forest zone, or the Canadian life-zone. It has the D-climates of KÖPPEN.

1.6. Abbreviations

Throughout the text of the Zoogeographical Part the following abbreviations have been used (Fig. 1b):

AL	— Aleutians
B	— shelf area in Bering Sea and adjacent ice-free areas
BS	— shelf area in Barents Sea
CA	— north-western Canadian Arctic Archipelago
E	— area immediately south and south-east of the Scandinavian inland ice
ES	— East Siberia
I	— shelf area off Iceland
K	— Kazakstan
KS	— shelf area in Karo Sea
KUR	— Kuril Islands
M	— Manchuria
MS	— Middle Siberia
NA	— shelf area off northern Alaska
NB	— shelf area north of Bering Strait
NES	— shelf area off north-eastern Siberia
NF	— Newfoundland Bank
NG	— north-east Greenland
R	— Russia
SB	— south coast of Bering Sea shelf area
SES	— southern East Siberia
SP	— Spitsbergen Bank
SWE	— south-west Europe
USA	— area in the USA south of the inland ice
WE	— North Sea area (western Europe)
WG	— shelf area off W. Greenland
WS	— West Siberia
WUSA	— Pacific coastal area south of Cordilleran ice sheet
Y	— Alaska-Yukon area

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A. PHYSICAL-GEOGRAPHICAL PART

2. Greenland

It is generally assumed that the Greenland ice sheet had a greater extension during the Last Glacial than at present.

2.1. EVIDENCE OF ICE-FREE AREAS

There is evidence that some areas remained ice-free throughout the Last Glacial.

2.1.1. *Geological and geomorphological evidence*

KOCH (1928, 1961) found large terminal moraines with a height of over hundred metres, across the northern part of Peary Land. North of this moraine no traces of a former ice cover have ever been found. It is concluded that this area never was glaciated during the Pleistocene (KOCH 1928).

So far no conclusive evidence for ice-free areas during glacial times in other districts of Greenland has been published. Nevertheless, many scientists have emphasized the possibilities of unglaciated areas. They based their opinions on geomorphological, palynological and phytogeographical evidence, and on present climatological circumstances.

Based mainly on geomorphological data two types of ice-free areas have been distinguished:

(a) areas at low altitude protected against the inland ice by high mountains flanked by deep fjords, through which the outlet-glaciers from the inland ice sheet drained quickly

(b) high mountains peaks projecting through the inland ice as true nunataks

Conditions mentioned under (a) possibly existed in:

Jameson Land, 70°20′N (NORDENSKJOLD 1909), Blosseville Coast of the former Knud Rasmussens Land, c. 70°-67°30′N, e.g. Cape Daussy, 68°43′N (BÖCHER 1956), Angmagssalik Island and the small islands south and east of it (BÖCHER 1956: 10-11), Arsuk-Frederikshaab region (BÖCHER 1956), Godthaab Fjord region (BÖCHER 1956), Region between Sukkertoppen and Holsteinsborg, c. 66°32′N, Parts of Disco Island (SALISBURY 1896; GELTING 1941), Middle Eddefuglö, c. 74°N, 57°37′W (PATERSON 1951).

Conditions mentioned under (b) possibly existed in:

Dronning Louise Land, a.o. in a large range on Koldewey Island, c. 76°43′N — 76° 10′N (KOCH & WEGENER 1930), Liverpool Land, c. 71°N — 70°30′N (ROBERTS 1935), several islands in the northern part of Melville Bay, e.g. Devil's Thumb, c. 74°50′N, 57°40′W (KOCH 1928), Cape York district, e.g. Conical Rock, c. 76°8′N, 68°27′W (KOCH 1928).

According to KOCH (1961) the highest parts of Greenland were never completely covered by ice during the Pleistocene.

2.1.2. *Palynological evidence*

IVERSEN (1952-1953) made palynological investigations of lake sediments in Tungmeralik, a large valley in W Greenland (c. 64°20′ N, 51°50′ W) in the Godthaab Fjord area. The sediments must have been deposited immediately after the retreat of the inland ice. In the oldest layer Iversen found only pollen of herbs, including those of 16 hardy species. Eight of these are found at present in the same area, on nunataks up to a height of 1250-1500 m. Eleven of these species at present also occur in the northernmost parts of Greenland, north of 80° N lat.

The occurrence of these higharctic species immediately after the retreat of the ice strongly suggests that they survived the Last Glacial somewhere in close vicinity to the ice margin. The more so, as apparently these species are not better adapted to long distance dispersal than are *Salix glauca* and *Betula nana*, which do not appear in the pollendiagram before zone 2, thousands of years after the retreat of the ice (Iversen 1952-1953).

Four of these 16 species have been reported as food plants of present breeding birds in Greenland (Salomonsen 1950; Witherby *et. al.* 1952; Porsild 1955):

Plant species	Breeding birds in Greenland reported to have fed on these plants
Oxyria digyna	*Branta bernicla*
	Branta leucopsis
	Anser caerulescens
	Anser fabalis brachyrhynchus
Cerastium alpinum	*Branta bernicla*
Dryas integrifolia	*Branta bernicla*
	Anser fabalis brachyrhynchus
Empetrum hermaphroditum	*Branta bernicla*
	Anser caerulescens
	Lagopus mutus

In the same layer of lake sediment in Tungmeralik Iversen (1952-53) found 17 relatively thermophilous plant species besides the hardy plants mentioned earlier. According to Iversen it is very unlikely that these species survived the Wisconsin time in W Greenland. Instead, they must have immigrated shortly after the retreat of the ice. The dispersal mechanisms of these plants agree with this view:

(a) Spread by air currents over large distances: Spores of Cryptogams: 4 species
(b) Spread on drifting ice by ocean currents: Seeds and plants of 3 species of Spermatophyta.
(c) Spread epizoically and endozoically: Small seeds attached to the feet of waterbirds: *Hippuris vulgaris*, *Myriophyllum exalbescens*, *Potamogeton filiformis*, *Potamogeton* sp., *Montia lamprosperma*, *Triglochin palustre*, *Plantago maritima*, *Lomatogonium rotatum*.
(d) Small seeds transported endozoically by birds: *Rumex acetosella*
(e) Plant species with uncertain means of dispersal: *Thalictrum alpinum*

Among the birds at present breeding in W and N Greenland *Anser albifrons flavirostris* and *Branta bernicla hrota* have their present winter quarters in the British Isles, especially in Ireland. Their migration routes lead from Ireland across the Atlantic to S Greenland, or via Iceland to E Greenland (Angmagssalik) from where they go on to the west coast across the Greenland ice sheet, or in the case of *Anser albifrons flavirostris*, around Cape Farwell (Salomonsen 1950, 1958). Iversen therefore believes that the seeds of the water and marsh plants mentioned above have been taken to Greenland by geese.

Nine of these ten species of plants have a present distribution area and ecological range (Hegi 1906; Bonnier & Douin 1934; Hultén 1958; Polu-

NIN 1959) that do not exclude their presence in western Europe during the Late-Glacial. As for *Lomatogonium rotatum*, at present not occurring in W Europe, it is unlikely that it actually occurred in W Europe during the Late-Glacial. This species probably immigrated to W Greenland from the North American mainland. In this connection it is important to note that part of the populations of *Branta bernicla* at present breeding in N Greenland, have their wintering grounds on the eastcoast of the United States. In spring these birds fly across Strait Davis to W Greenland and then along this coast to the far north. The annual *Lomatogonium rotatum* prefers wet clayey soil and it produces a profusion of small seeds, which, together with clay particles easily adhere to the feet of geese and waders (IVERSEN 1952-1953: 98). Hence, immigration of *Lomatogonium* from eastern North America by means of migrating *Branta bernicla* is not unlikely.

If geese had imported the seeds of most of these species of plants immediately after the retreat of the ice in W Greenland, it is likely that these birds had their breeding grounds nearby. If they had not nested in W Greenland during, or, at least, immediately after the local retreat of the inland ice, their breeding places should be localized somewhere along their present migration routes: in Iceland, or along the eastcoast of North America. In Western Europe lowarctic conditions prevailed, unsuitable for *Branta bernicla*, but assumed to have offered refuge breeding grounds to lowarctic *A. albifrons* (*flavirostris*) (see 8 and 19.2.).

As during Older Dryas time arctic conditions still prevailed in W Europe, it is not likely that *Anser albifrons* was compelled to shift its breeding grounds to W Greenland.

The northern part of the North American eastcoast was ice-covered during the maximum of the Last Glacial and in the southern part boreal conditions prevailed (see 12). Therefore, the only possibilities for refuge breeding grounds for *Branta bernicla* were on the emerged shelf areas of W Greenland (see 2.2.) and W Iceland (see 5.2.). Though *Branta bernicla* (*hrota*) may have bred in W Iceland there would have been no cause to induce it to shift its breeding area suddenly to the westcoast of Greenland when climatic amelioration began during the Cary substage (= Older Dryas) or earlier. This species may also have bred in W Greenland during the Last Glacial. It could have transported seeds of water and marsh plants both from its North American and W European wintering grounds throughout the Last Glacial. As far as thermophilous plants are concerned seeds could not germ until the climatic amelioration of the Late-Glacial. By this time the rising sea-level possibly compelled *Branta bernicla* to shift its breeding grounds from the shelf areas of W Greenland to areas on the mainland of Greenland. Here areas newly freed from inland ice offered possibilities both for the growth of plants and the breeding of *Branta bernicla*.

Conclusion. There is palynological evidence that some higharctic plants survived in refuge areas in the Godthaab Fjord region during the Last Glacial. If birds imported seeds of plants during Older Dryas time, these birds will have bred in W Greenland already before that time.

2.1.3. *Phytogeographical evidence*

According to some botanists at least part of the present-day Greenlandic plant species may have survived in Greenland during the Last Glacial (Böcher 1938, 1956; Böcher *et. al.* 1959; Dahl 1950; Gelting 1934, 1941; Hultén 1937; Polunin 1959; Savile 1961; Sörensen 1945, 1953). Their conclusions are mainly based on the present distribution patterns of these species. These distribution patterns can be arranged according to the following characteristics:

(a) Disjunct distribution areas within Greenland.
(b) Restriction of distribution of one species to one isolated area in Greenland.
(c) Restriction of distribution of several species to one and the same area.
(d) Concentration of a relatively large number of other plant species in the area referred to sub (b) and (c).
(e) Occurrence of endemic species and subspecies in isolated areas referred to sub (b) and (c).
(f) Occurrence of one or more distribution centres within the progressive equiformal areas of Hultén (1937) in N Greenland.

On basis of the distribution patterns of plant species it has been suggested that the following areas in Greenland remained ice-free during the Wisconsin glacial period:

Peary Land, N Greenland (Hultén 1937; Gelting 1941; Sörensen 1953; Savile 1961), Clavering Island and Wollaston Forland (Gelting 1934), E Greenland (Gelting 1941), Liverpoolland (Brian 1935; Gelting 1941), numerous areas along the southeast coast (Böcher 1938), coastal regions in SW Greenland (Gelting 1941), Söndre Strömfjord (Böcher 1950), W Greenland (Gelting 1941; Sörensen 1953), Thule District (Sörensen 1953).

Discussion. Areas supposed to have been ice-free for geological and geomorphological reasons, harbouring at the same time a number of rare and isolated plant species, were probably refuge areas in which these plants have survived uninterruptedly from the beginning of the Wisconsin period. Unfortunately, our knowledge of the distribution of the rarer plant species in the less accessible parts of Greenland being as yet inadequate, it is still rather premature to draw far reaching conclusions. Moreover, the spreading capacities of these plants seem to have been underestimated. It has been impossible so far to ascertain in what way many plant species crossed large geographical barriers as, for example, the Atlantic Ocean, Davis Strait, and the Greenlandic ice-cap. Botanists who are convinced that some plant species survived the Last Glacial somewhere in Greenland, still have to deal with the problem how these species managed to reach Greenland before the Wisconsin. Some botanists have tried to solve this problem by means of Wegener's theory of continental drift. According to Sörensen (1953) the migration of some Wisconsin glacial survivors from Europe to Greenland must have occurred shortly before the Wisconsin, as the present populations of the species in Greenland and western Europe do not differ specifically. SÖRENSEN suggested that these species had spread across landbridges between W Europe and Greenland during the Last Interglacial, before the drifting apart of the northern parts of the European and American continents. But this theory clashes with the general opinion among geologists that, if the American and European continents ever drifted apart, this must certainly have happened long before the Pleistocene.

In the middle ages numerous plant seeds must have been imported by Danes transporting hay from Norway and Iceland to Greenland. In the studies about the history of the flora of Greenland this fact has been taken into account as far as possible. Travelling eskimoes may also have transported seeds along the coasts of Greenland (SÖRENSEN 1953). In addition, migratory birds probably also imported plants from W Europe. When on their spring migration comparatively large numbers of birds first arrive in southeast Greenland (SALOMONSEN 1950). Some of these migratory birds are certainly able to make a nonstop flight across the Atlantic Ocean from W Europe to S or SE Greenland, e.g. *Anser albifrons flavirostris*, *Branta bernicla hrota*, *Branta leucopsis*, *Anser fabalis brachyrhynchus*. Birds habitually preen thoroughly before starting a long distance flight and will thus remove seeds attached to their feathers. But they do not clean their feet and if they have been feeding on clayey soil, some clay with, possibly, some seeds may cling to their feet, and thus be taken to Greenland in a nonstop flight.

Gaps in the distribution pattern of plant species may also be caused by unfavourable lithological circumstances. So far, too little is known about the ecology of the plants of Greenland for me to say whether lithology ever played a role in causing disjunctions and if so, where.

SÖRENSEN (1941) showed that there were great disparities between microclimates of sites at short distances, owing to differences in lithology, exposure, water saturation of the soil, and type of vegetation. The vegetation type, in this connection, may have been both a result and a cause (SÖRENSEN 1941; SCHIMPER & VON FABER 1935). Concentration of large numbers of plant species on southern mountain slopes, may therefore have resulted either from a favourable microclimate, caused by southern exposure and dry slopes, or else by favourable lithological circumstances. Examples of the latter, according to BÖCHER (1956), are some of the mountain slopes on Angmagssalik Island.

Disjunctions of distribution and concentrations in isolated areas may also have resulted from the wide distribution of plants during the post-

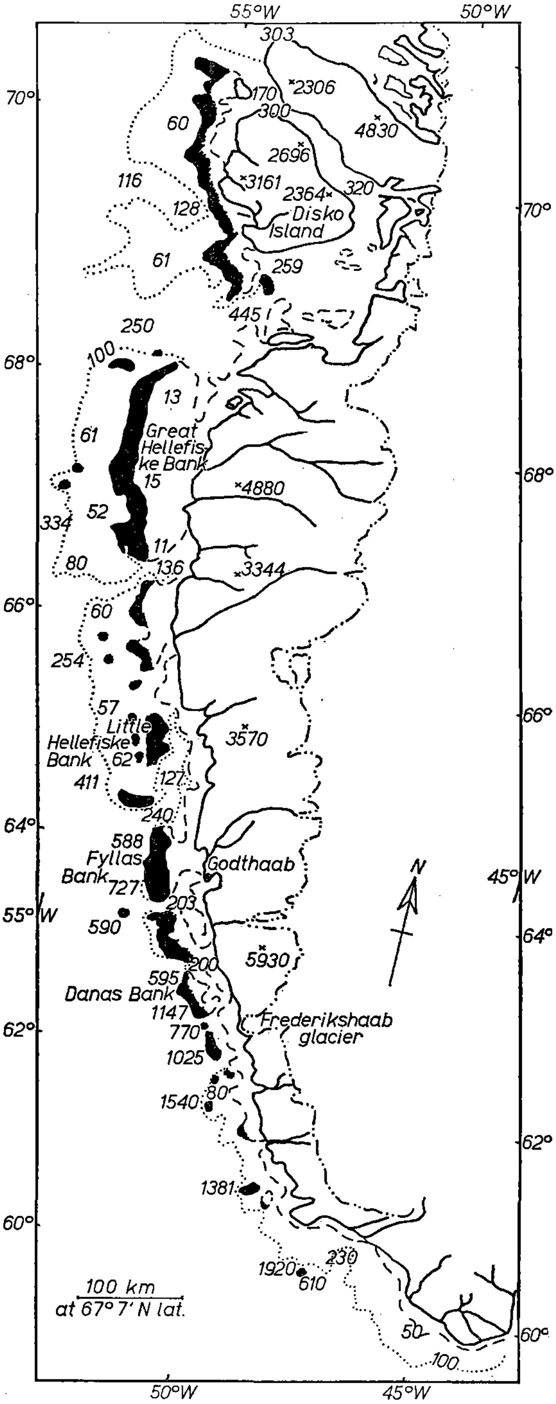

FIGURE 3. Explanation on opposite page.

glacial hypsithermal interval and the restriction to isolated favourable sites when the climate deteriorated afterwards.

Conclusion. Phytogeographical data do not supply conclusive evidence as to ice-free areas; they do not contradict the assumption of ice-free refuge areas in Peary Land and in the Godthaab Fjord region; they may even indicate that more refuge areas for plants existed.

2.2. POSSIBLY ICE-FREE AREAS ON THE SHELF

Numerous areas on the emerged continental shelf along the coast of W Greenland between 60° N lat. and 71° N lat. may have been protected against being covered by inland ice, in the same way as referred to under (a) in paragraph 2.1.1. The most important areas are (Fig. 3):

(1) The continental shelf along the west coast of Disco Island (long c. 210 km, wide 20-50 km), protected against inland ice by the Disco Island Mountains up to 2696 feet high, flanked by fjords to the south, 126 — 445 fathoms deep, to the north, 170 — 300 fathoms deep. In my opinion the central part of this shelf area cannot possibly have been overrun by inland ice. Glaciers originating from the mountains of Disco Island may have covered this shelf in some areas, but still the greater part may have been ice-free.

(2) Great Hellefiske Bank (c. 66°30′N lat. — 68°10′N lat.) long c. 180 km, wide 70 km, protected against inland ice by mainland mountains up to 4880 feet. West of this bank there are four small shelf areas less than 90 metres deep, about 100 km from the present coast line, not far from deep water (400 fathoms) further west. In this area the present inland ice border is about 180 km from the coast line. North of the bank the present sea depth is from 250 to 314 fathoms. On the south side there is a sound, c. 20 km wide, with a depth of 130 — 176 fathoms.

(3) Fyllas Bank off Godthaab District, c. 63°30′N lat. — 64°20′N lat., long 72 km, wide 40 km, protected against inland ice by mainland mountains up to 5930 feet. North of this bank the depth of the broad sound is 156 — 283 fathoms. On the south side there is a sound of about 20 km width with a depth of 106 — 203 fathoms. Immediately west of this the sea reaches the considerable depth of 546 — 727 fathoms.

(4) Fiskernae Bank, immediately south of the former, long 40 km, wide 30 km, bordered on the south side by a 200 fathom sound.

(5) Danas Bank, approximately 25 km south of the Fiskernae Bank, long 45 km, wide from 10 — 27 km, bordered on three sides by sounds of 100 — 255 fathoms and on the west side by a very large depth, 595 — 1147 fathoms.

South of Danas Bank the shelf areas less than 90 metres deep form only a very narrow strip, but still there are seven isolated shallow shelf areas, 18-54 km from the present coast and all fringing very deep water on the west side, from 770 to 1920 fathoms. Inland ice reaching thus far could easily discharge into the deep sea, hence the islands may have remained ice-free during the Last Glacial.

Though no isobasen can be drawn, it is assumed that the shelf areas were not very much pressed down by the weight of the neighbouring inland ice sheet,

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FIGURE 3. Southern West Greenland. *Black areas* = Present shelf areas of less than 50 fathoms depth, which were possibly ice-free land during the maximum of the Last Glacial. Depth in fathoms, height in feet. —··—·· = present border of inland ice. — — — = 50 fathom isobath. .... = 100 fathom isobath.

as the Greenlandic situation can be compared with that of the Last Glacial along the Norwegian coast.

It must be stressed that the regions (1), (2), (3) and (5) coincide with the W Greenland areas mentioned on page 11 under (a) and that regions (3) and (4) coincide with the Godthaab Fjord area where palynological evidence suggested ice-free areas in the neighbourhood (Iversen 1952-1953).

Conclusion. It is tentatively concluded that along a 1130 km stretch of the W Greenland coast south of 71° N lat., large emerged shelf areas remained unglaciated during the Last Glacial.

Table 1

Present summer temperatures in Greenland

Weather Bureau U.S.A., Dept. of Commerce 1943, *World Meteorol. Organization* 1962, *Meteorol. Office, London* 1964, 1965.

	Monthly average			Monthly average of daily max. temperatures		
	June	July	Aug.	June	July	Aug.
Upernavik	1,7	5,0	5,0	5,5	8,9	8,3
Jacobshavn	4,4	7,7	6,7	7,7	10,5	10,0
Egedesminde	3,7	6,4	6,1	—	—	—
Godthaab	4,4	6,7	6,1	8,3	11,1	10,5
Ivigtut	7,7	10,0	8,3	12,2	13,8	12,8
Jörgen Brönlunds Fjord	2,6	6,2	3,7	4,9	8,9	5,9
Nord	0,4	3,9	1,6	2,9	6,8	3,9
Danmarkshavn	1,1	3,5	2,3	4,0	8,5	6,0
Cap Tobin	-0,4	2,5	2,7	—	—	—
Angmagssalik	5,6	7,3	6,6	10,0	12,2	11,1

2.3. Present and Last-Glacial summer temperatures

In W Greenland at the same latitude as the presumed ice free shelf areas the average temperatures for July range from 6,4° to 10° C (Table 1). Even if summer mean temperatures during the maximum of the Last Glacial decreased with 6° C a moderate plant and animal life could persist, certainly in southern W Greenland.

At Jörgen Brönlands Fjord weather station in NE Greenland, the northernmost weather station but one, relatively high average July temperatures have been recorded. Though the number of years of record is admittedly small, these temperatures need not be exceptional. During 35 of 102 days of observation daily maximum temperatures were above 10° C, during 8 even above 15° C. The absolute maximum was 18° C in August 1948 (Fristrup 1952). Krinsley (1960) reports from Centrum Sö (80°10′ N, 22° W; 98 m above present sea level, 40 km from the border of the inland ice) an annual precipitation of 10-15 mm, mean daily air temperatures in July from 12° to 14° C and an absolute maximum in July of 16° C.

Over NE Greenland there is a strong tendency for high pressure to persist in all seasons (METEOROLOGICAL OFFICE 1964, 1965). This causes high frequency of westerly winds. These winds lost their moisture content on the windward side of the Greenland ice sheet. To the northeast of the inland ice the winds descend and grow warmer dynamically, thus becoming *föhn*-like in character. Along the coast of NE Greenland much fog has been reported in summer, but in the interior bright summer conditions prevail. As a rule there is a temperature inversion at about 600-800 m, causing and maintaining calm weather starting in the last week of June onwards and throughout July. As the snow has already disappeared the incoming radiation can be fully used to heat the land and the surface layers of the air, resulting in relatively high temperatures (KOCH 1928).

In summary, at present NE Greenland has probably the most continental climate of all ice-free areas in Greenland, with a prevalence of bright weather inland, which, at least in some places, gives rise to relatively high summer temperatures. It is, perhaps, the extremely small precipitation that most seriously restricts the plant-growth here, though it is compensated by snowdrifts. In sheltered places at 82° N latitude excellent grazing has been found for the herds of muskoxen (WEATHER BUREAU U.S.A. 1943).

Valuable micro-climatological data have been supplied by SØRENSEN (1941). SØRENSEN studied temperature relations and phenology of the Northeast Greenland flowering plants. The area of investigation comprised the land between 71°10′ N lat. and 79°30′ N lat. The mean air temperatures of July are: Scoresby Sund 4,5° C; Myggbukta 3,7° C and in Danmark Havn 4,4° C. The mean annual precipitation in these places was 317 mm, 78 mm and 146 mm, respectively.

The principal results of SØRENSEN's temperature observations are (SØRENSEN 1941: 238, 239):

(a) The diurnal mean temperature of the soil surface intersects the 0° C-line in spring three to four weeks before the mean temperature of the air.

(b) During an essential part of the vegetation period the mean values of the soil surface temperatures lie 5° to 7° C above the mean value of the air temperatures.

(c) During a period of about two months the minimum temperatures of the air hardly ever fell below zero.

(d) Observations at Eskimonaes have shown that by the time the mean temperature of the air definitely passes the 0° C-line in spring, the soil has thawed to a depth of about half a metre.

(e) From Ella Ø (72°50′ N lat.) an observation series has been given from an early snow-free warm ecosystem occurring in the summer-warm inner fjord area during a hot summer. From this series it appears among other things that during the period ranging from June 7 1932 till August 22 1932 the diurnal maximum temperature of the soil on 53 days was over 30° C.

These series of temperature observations are an approximate measure of the temperature conditions in which a number of the East Greenland plant communities actually live. *They are not exceptional cases.* SØRENSEN (1941) warns not to overestimate the extreme temperature values of a soil surface, *i.e.* not to take them as an ecological factor in the phanerogamic vegetation, for the plant organism itself is not limited to a two-dimensional plane and the presence of any vegetation precludes the most extreme surface temperatures.

From the foregoing it may tentatively be concluded that, even if we assume a drop in mean air temperature of 6° C during the maximum of the Last Glacial, summer temperatures in NE Greenland may have been favourable enough to sustain a moderate plant and animal life.

A large frequency of anticyclonic air-circulation may be assumed by deduction. This circulation system must have resulted in a large frequency of *föhn*-like winds with many days of very dry air and sunny weather. This type of weather can make the winter snow disappear by sublimation in many places before the air temperature definitely remains above zero in summer.

It may be inferred that there were similar conditions in many other areas on the leeward side of Greenland, as well as in several places in the interior of western Greenland, where high coastal mountains shielded the land from the westerly winds.

The climate of the westcoast of Greenland may have had favourable influence of a relatively warm ocean current, as it has to-day.

Conclusion. Ice-free areas in Greenland may have harboured hardy plants and animals throughout the Last Glacial.

2.4. SUMMARY

There is geological evidence of ice-free areas in Peary Land, throughout the whole Pleistocene. The Alpine topography in several areas in Greenland indicates that there were many nunataks during the Last Glacial.

There is palynological evidence that some hardy higharctic plants survived in refuge areas somewhere in the Godthaab Fjord region during the Last Glacial.

Phytogeographical data do not supply conclusive evidence as to ice-free areas; they do not contradict the assumption of ice-free glacial refuge areas in Peary Land and in the Godthaab Fjord region; they may even indicate that more plant refuges existed during the Wisconsin time than the two mentioned above.

Along the west coast of Greenland south of 71° N lat. emerged large shelf areas may have remained ice-free.

The Last-Glacial climate in low lying ice-free areas in Greenland may have been favourable enough to permit hardy plants and animals to survive there.

2.5. LAST-GLACIAL BREEDING BIRDS

The following criteria for species that may have bred in Greenland under conditions of the Wisconsin Glacial, have been applied:

(a) Present breeding range somewhere in the North Atlantic.
(b) At present breeding north of the July-isotherm of 5° C.
(c) At present breeding on high mountains with steep slopes or cliffs.
(d) Feeding on marine organisms.
or else:
(e) At present breeding on marsh land.
(f) At present feeding on both plants or animals.
(g) At present either migratory or pelagic.

Especially sea or coastal birds breeding on high cliffs or steep slopes will almost certainly have found breeding opportunities, provided there was open sea in the vicinity. This may have been the case even during the worst of the Wisconsin climates, owing to off-shore winds and strong currents between coastal islands.

Taking these criteria as a basis I have selected the following 35 species of birds, presented in systematical order, which may have bred in Greenland during the Wisconsin, all of which are known to breed in Greenland at present:

Gavia stellata
Fulmarus glacialis
Anser caerulescens
Branta bernicla
Somateria mollissima
Somateria spectabilis
Histrionicus histrionicus
Bucephala islandica
Clangula hyemalis
Falco rusticolus
Lagopus mutus
Charadrius hiaticula
Arenaria interpres
Calidris canutus
Calidris maritima
Calidris alba
Phalaropus fulicarius
Stercorarius pomarinus
Stercorarius parasiticus
Stercorarius longicaudus
Larus hyperboreus
Larus glaucoides
Xema sabini
Pagophila eburnea
Rissa tridactyla
Sterna paradisaea
Plautus alle
Uria lomvia
Cepphus grylle
Fratercula arctica
Nyctea scandiaca
Anthus spinoletta
Calcarius lapponicus
Plectrophenax nivalis
Corvus corax

3. Labrador

As erratics from areas west of the coastal mountains have been found on the highest summit areas and on the eastern slopes of the mountains, the mountains must have been overrun by inland ice from the interior of Labrador (Tanner 1944; Ives 1957, 1963; Wheeler 1958).

Discussion. It is still an unsolvend matter during which glacial time the coastal mountains were overrun by inland ice. It may have happened before the Last Glacial. But even if the summit areas of the highest coastal mountains remained nunataks during the Last Glacial, the ice flowing from the interior through the west-east valleys

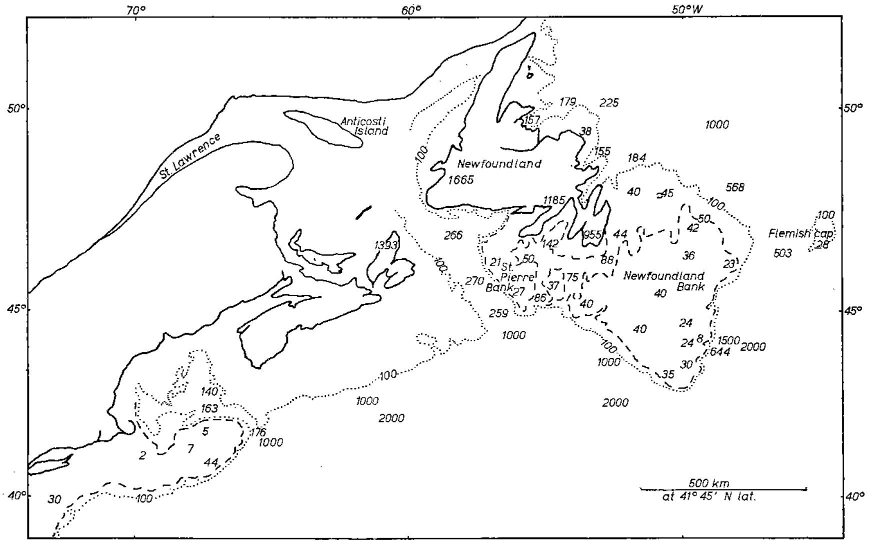


FIGURE 4. Present Newfoundland Bank of less than 50 fathoms depth, which was possibly ice-free land during the maximum of the Last Glacial. Depth in fathoms, height in feet.
— — — = 50 fathom isobath. .... = 100 fathom isobath.

(IVES 1957) presumably covered the coastal areas completely and extended far out on the shelf (TANNER 1944). As the shelf area with a depth less than 90 metres between Newfoundland and Ungava Bay is on the whole quite narrow or nearly absent I reject the idea of Last-Glacial refuge areas along the Labrador coast.

4. **Newfoundland Bank** (Fig. 4)

The thickness of the Laurentide ice sheet around the Gulf of St. Lawrence and on Newfoundland is not known (FLINT 1961). The Shickshock Mountains on Gaspé Peninsula and the Long Range on Newfoundland were covered completely by the Laurentide ice sheet (FLINT 1961). Therefore, the minimum altitude of the ice surface must have been 1269 m and 795 m, respectively.

It is likely that considerable quantities of Laurentide ice were drained through Cabot Strait (HOLTEDAHL 1958; SHEPARD 1963). If the thickness of the ice on the Shickshock Mountains was 700 m, the ice sheet in Gulf of St. Lawrence must have been 2200 m thick. If the Long Range on Newfoundland was covered by an ice-sheet of 500 m thick, the surface gradient of the ice between Gaspé Peninsula and the Long Range was 1/450. Calculations with this very small surface-gradient have shown that the ice passing through Cabot Strait would have terminated in a calving ice front southwest of the easternmost area of Newfoundland Bank.

Part of Newfoundland may have had an independent ice cap. Even assuming

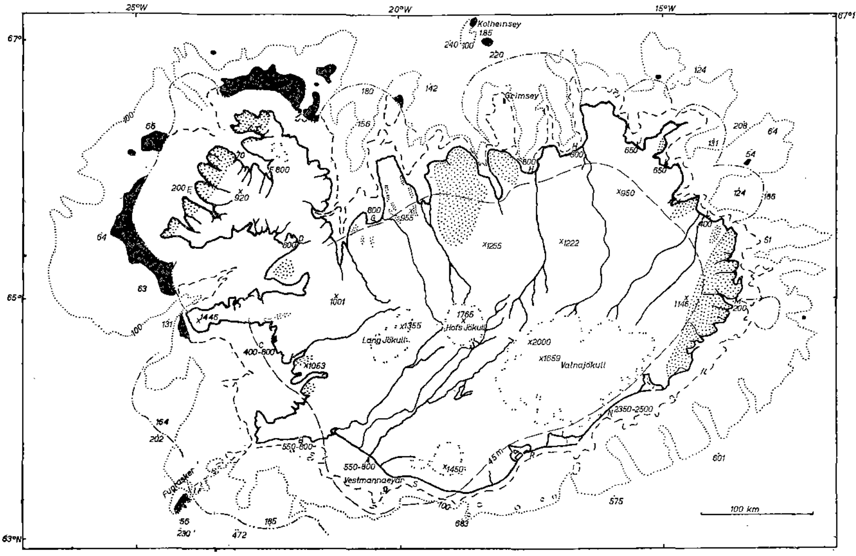


FIGURE 5. Iceland. *Stippled areas* = regions not covered by inland ice from the interior, but which had glaciers of local origin and were partly ice-free during the maximum of the Last Glacial.

— — — = 45 metre isobase.
- - - - - - - = 50 fathom isobath.
. . . . = 100 fathom isobath.
— · · — · · = reconstructed outer border of inland ice.

The figures at the sites A-N represent the heights (in metres above present sea-level) of the ice-surface during the maximum of the Last Glacial. These figures, inferred from literature sources (see 5.1.1) have been used for she reconstruction of outlet-glaciers (see 5.2.1). *Black areas* = present shelf areas of less than 50 fathoms depth, which were possibly ice-free land during the maximum of the Last Glacial.

for this ice cap a thickness of 500 m in easternmost Newfoundland and a surface-gradient of 1/150, the ice could scarcely have reached the westernmost border of Newfoundland Bank. Therefore, Newfoundland Bank was probably not covered by Laurentide or Newfoundland ice during the maximum of the last major glacial episode.

5. **Iceland**

5.1. EVIDENCE OF ICE-FREE AREAS

It is generally assumed that 90% of Iceland was covered by inland ice and glaciers during the Last Glacial. There is evidence that some areas remained ice-free throughout that time.

5.1.1. *Geomorphological evidence*

There is a marked difference between the landscapes which were certainly glaciated and those which according to their situation in the periferal regions, their altitude and the presence of deep incised fjords may have been ice-free throughout the Last Glacial. The glaciated areas have smoothly rounded valley slopes and regular forms whereas the unglaciated areas show a very irregular topography with many short valleys which were formerly filled with independent cirque-glaciers (AHLMANN & THORARINSSON 1937, RUTTEN 1949). (See Fig. 5, data for ice-free areas mainly compiled from THORARINSSON 1937, RUTTEN 1949, RUTTEN & VAN BEMMELEN 1955, STEINDORSSON 1937, 1954, 1963, SCHWARZBACH 1955, KJARTANSSON 1957, EINARSSON 1961.)

Discussion. In the paragraph on possibly ice-free shallow shelf areas I will discuss the possibility for some islands off the coast of Iceland to have escaped total glaciation.

5.1.2. *Palynological evidence*

In the oldest pollenzones of the peat profiles in north and east Iceland a species of *Betula* occurs, probably a tree-birch, *Betula pubescens*, but this is not certain. In the same zone of the peat profiles in southwest Iceland *Betula* is lacking. The upper zones of the profiles were dated by radiocarbon method and Hekla ash layers. By extrapolation the oldest zone was tentatively dated as Late-Glacial, with the *Betula* peak in the Allerød. The quick appearance of *Betula* after the retreat of local ice led EINARSSON (1961) to the assumption that it survived in ice-free refuge areas in the vicinity as indicated by geomorphologists (THORARINSSON 1937, a.o.). In the southwest *Betula* does not occur before the Boreal zone.

Discussion. If ice-free refuge areas occurred on the mainland of Iceland they were situated in relatively high mountains. It may be doubted if climatic circumstances were favourable enough for the growth of tree-birches.

5.1.3. *Phytogeographical evidence*

The flora of Iceland has greatest affinity to that of western Europe. As most species of the Icelandic indigenous flora apparently do not possess a mechanism for long-range dispersal across extensive stretches of water, many botanists (a.o. HADAC 1948, SÖRENSEN 1953, LÖVE & LÖVE 1951, 1956, A. LÖVE 1963, D. LÖVE 1963, STEINDORSSON 1963) assume that the greater part of the present flora of Iceland reached the island as plantassociations across landbridges in Late-Tertiary or even Early-Pleistocene times. Hence, most of the present flora survived at least the last two glaciations in Iceland. As for the Last Glacial, the survival theory is supported by present distribution patterns in Iceland of some 100 species of vascular plants. These species are almost exclusively confined to certain districts (centric species) which according to geologists probably remained unglaciated during the Last Glacial. The majority of these centric species in Iceland are the same as the presumed survivors of the Last Glacial in Scandinavia (STEINDORSSON 1963) or Greenland (LÖVE & LÖVE 1951).

The survival theory is reinforced by the work of LÖVE & LÖVE (1956) who studied the chromosome number of the whole Icelandic flora. Of the indigenous species 71% turned out to be polyploids. This high frequency of polyploids is attributed to their surviving the Pleistocene glaciations in ice-free areas in Iceland and, therefore, reflects the climatic extremes in the past. A small number of species differs in chromosome number from specimens of the same species in other northern countries. This is considered extra evidence of the fact that they survived at least the last glaciation in Iceland (LÖVE & LÖVE 1956).

Discussion. There are no geological indications for landbridges in Late-Tertiary or Early Pleistocene times (RUTTEN, oral comm., SCHWARZBACH 1963). Therefore, the landbridge theory is firmly opposed by geologists. Though much research of the bottom of the North Atlantic remains to be done there is strong evidence against recent landconnections between western Europe and Iceland. Had the Wyville-Thomson ridge ever been a landbridge it would have been exposed to subaerial weathering and erosion, the results of which would still have been visible in the sediments on both sides of the ridge. These sediments are lacking (HEEZEN & THARP, in LÖVE *et al.* 1963).

As the Icelandic flora has greatest affinity to the flora of Scandinavia (97% of the Icelandic plant species occur also in Scandinavia) the existence of a landconnection between Iceland and Scandinavia might be inferred in the first place. There are no traces of such a landconnection in the North Atlantic, nor in submarine ridges, nor in the structure of the earthcrust under the ocean floor, nor in sediments (HEEZEN & THARP 1963, in LÖVE *et al.* 1963).

There are more objections against landbridges apart from geological ones. First, during Late-Tertiary times, the climate was warmer than it is at present. If a landconnection existed plant species typical for mild circumstances could have spread to Iceland. It is impossible that a part of this temperate flora survived at least four glacial periods in ice-free areas in Iceland.

More than half of the Icelandic vascular plants are species with a boreal distribution, whereas arctic-alpine species comprise 33% of the flora; most of the arctic species are lowarctic, and higharctic species are practically absent. This composition does not reflect a temperate flora that immigrated across a landbridge during a period with a milder climate than at present, nor a flora that survived one or more ice ages in Iceland. But it does reflect the present climatological circumstances in Iceland. Therefore, most of it must have spread to the island in postglacial time. Nevertheless, part of the arctic-alpine species may have survived the Last Glacial in Iceland.

I agree with botanists that only a small number of the Icelandic species could have been dispersed by sea-currents and that the present flora may not be particularly rich in species with wind dispersed seeds. However, I am convinced that much about dispersal of plants (and animals) so far has escaped our attention and therefore, one is inclined to underestimate the possibilities of dispersal (see also HULTÉN 1937, POLUNIN 1960, DEEVEY 1949, MAYR 1942, TURRILL 1951). Among the postulated agents of dispersal the part played by migrating birds is probably underestimated by many phytogeographers. In this connection attention to the following facts are noteworthy:

(a) Many species of birds breeding in Iceland and Greenland migrate to and from the British Isles.

(b) Among these migratory birds are geese and ducks, which are fast fliers. According to MEINERTZHAGEN (VAN OORDT 1960) during migration geese develop a speed of 69-91 km, ducks one of 72-97 km an hour. These are air speeds, and the actual speed in relation to the ground will be greater (LANDSBOROUGH THOMSON 1964). During a gale, defined as a wind of Beaufort force 8 or more, the wind velocity may be from 63 to 118 km an hour. In favourable circumstances, therefore, migrating birds might theoretically cover 130-215 km an hour. Thus a speed of 150-190 km in relation to the ground will occasionally occur.

(c) The distances between some landmasses in the North Atlantic area are:

FROM	TO	KM	CALCULATED DURATION OF FLIGHT (ground speed 150-190 km)
Scotland (Hebrides)	— Iceland	785	5,2 — 4,1 hrs
NW Ireland	— Iceland	985	6,5 — 5,2 hrs
Scotland (Mainland)	— Faeroes	321	2,1 — 1,6 hrs
Faeroes	— Iceland	410	2,7 — 2,2 hrs
Iceland	— Greenland	293	2,0 — 1,5 hrs

(d) The passage of food in captive ducks and geese from the time of ingestion to evacuation took 3 or 4 hours, up to 7 to 10 hours in extreme cases, with maintenance of germinal force (RIDLEY 1930).

(e) Assuming a ground speed of 150-190 km/h in favourable circumstances the duration of flight between some of the North Atlantic areas and Iceland is such that seeds eaten shortly before the birds take off can be transported endozoically without losing their germinal force. Indeed, it is likely that the rate of metabolism is considerably increased during a strenuous flight (D. LÖVE 1963), but little is known on this subject, apart from the fact that during migration birds use a lot of the fat stored in their bodies before migration (Landsborough Thomson 1964). It is still a matter of doubt whether long distance migratory birds exert themselves very much during a flight with a favourable wind direction.

(f) Seeds can also be transported epizoically by birds. Again I will confine myself to geese and ducks, which according to Ridley (1930) probably carry more seeds on their bodies and legs than in their viscera. Admittedly, they clean and trim thoroughly before they take off, but they do not clean their feet. They most frequently occur in lowlands and mud flats in their winter quarters but some species also occasionally occur in hilly country or low mountains. Moreover, seeds from hills and mountains in the immediate vicinity of the wintering areas of geese and ducks will, of course, be transported to the feeding grounds and may thus stick to the feet of the birds just before they start their spring migration. In Iceland and in their other North Atlantic breeding grounds the geese are not confined to low areas. The Pink-footed Goose (*Anser fabalis brachyrhynchus*) and the Barnacle Goose (*Branta leucopsis*) also breed on hills and mountains. The Barnacle Goose does not at present breed in Iceland, but may have done so in glacial and early postglacial times.

Excluding other migratory birds, counts made in recent years resulted in a total number of 50,000 geese wintering in the British Isles (Scott, Boyd & Sladen 1953-54, Boyd 1961-62, Atkinson-Willes 1963, Brotherston 1964). Doubtless they used to be far more numerous. The greater part of all Icelandic breeding birds migrate to and from western Europe. The total number of migrating birds may be estimated at some hundreds of thousands or even millions. Among them are 18 species of drift-migrators from Scandinavia (Timmermann 1939).

Therefore, the great affinity of the Icelandic flora to the European may be attributed to the accidental transportation of seeds or parts of plants by migratory birds wintering in western Europe. As migration probably existed already during the Pleistocene, hundreds of thousands of birds migrating during hundred of thousands of years offered ample opportunities for accidental transport. Many plant species now indigenous may have come to Iceland before the Last Glacial. Part of them, especially arctic, or arctic-alpine circumpolar plant species may have survived the Last Glacial in Iceland. The present centric distribution pattern of many species supports this theory, but does not prove it, because other factors might have induced similar distribution patterns:

(a) Potential Last-Glacial nunatak areas are mountains. Many of their present-day plant species are alpine.

(b) The most important ice-free areas are the high Vestfirdir, Eyafjördur and Austfirdir districts. These are almost completely composed of Tertiary effusive and intrusive rocks. Here weathering agencies worked much longer than elsewhere in Iceland. This may have led to edaphic conditions specially suited for some species of plants.

(c) The hypsithermal interval must have driven many plants to higher grounds, *i.c.* to the same areas that probably remained ice-free during the Last-Glacial. Therefore, the distribution pattern they show now may reflect warm and not glacial conditions.

(d) Postglacial lava effusions covered 12,000 square kilometres.

(e) With the invasion of the Vikings and the introduction of cattle and sheep a period of fast and wide-spread destruction of the natural vegetation set in, leading to an extensive soil erosion. This may have eradicated many plant species in the afflicted areas, while they remained undisturbed in the bordering mountains.

Conclusions. Landbridges are not necessary for the spreading of plants to Iceland. Migratory birds may have played a greater role in the spreading of plants to Iceland than has hitherto been assumed and they may explain the great affinity between the floras of Iceland and the European mainland. Centric distribution does not prove glacial survival, but may support the theory, as do the high percentage of polyploids among Icelandic plants and the results of the palynological investigations, which are still in a preliminary stage.

5.1.4. *Zoogeographical evidence*

LINDROTH (1930) studied the insect fauna of Iceland and discovered a close relationship to the insect fauna of Europe. The present Icelandic insect fauna must be relatively young. LINDROTH has analysed the possibilities of spreading of insects from Europe to Iceland. They are: (1) by sea-currents; (2) on drift-wood; (3) by wind; (4) flying; (5) by birds; (6) via landconnections. The first five possibilities apply to only a very small number of insect species. According to LINDROTH landbridges remain the only explanation. The theory of postglacial landbridges between Iceland and Europe met with firm geological opposition. Landbridges in Tertiary time do not agree with the recent character of the Icelandic insect fauna. So LINDROTH assumed a landbridge during one of the interglacials. Consequently the insect fauna must have survived at least the Last Glacial in refuge areas. According to LINDROTH there is some fair agreement between the ice-free areas indicated by geologists and the centres of dispersal of many insect species.

Discussion. As the present-day insectfauna of Iceland is predominantly non-arctic LINDROTH (1930) assumed that the insects spread to Iceland via a landconnection during an interglacial period. If this is so it is not clear how this insect fauna could survive a glacial period in Iceland.

LINDROTH (1930) accepts the possibility that larvae and eggs are transported by birds, endozoically and epizoically. Many insects lay each egg in a different place, so that for dispersal it is necessary that at least one female egg and one male one are transported, and deposited in each other's close vicinity in a suitable habitat in Iceland. According to LINDROTH this coincidence is too improbable and, therefore, he rejected the possibility of the spreading of insects to Iceland by birds.

In my opinion this coincidence need not be as exceptional as it seems. In addition to what has already been said in the paragraph on the dispersal of plants by birds, the following facts should be well taken into account:

1. Among the birds migrating to and via Iceland are the geese species *Anser anser*, *Anser albifrons (flavirostris)*, *Anser fabalis* (*brachyrhynchus*), *Branta bernicla* (*hrota*), *Branta leucopsis*. Counts made in recent years resulted in a total number of 50,000 geese wintering in the British Isles and migrating to and via Iceland (SCOTT, BOYD & SLADEN 1953-54; BOYD 1961-62; ATKINSON-WILLES 1963; BROTHERSTON 1964).
2. These geese gather in large flocks in their feeding habitat before starting their spring migration to and via Iceland (RUSSELL WEBBE 1958).
3. They travel in large flocks of hundreds or even thousands of birds.
4. They start at the end of April or at the beginning of May.
5. They make a quick nonstop flight to Iceland.
6. They land in large flocks close together in a habitat similar to the one they came from in the British Isles.

From a faunistical point of view the insects must have survived south of the Vatnajøkull, probably in the Hornafjördur area, and in the area adjacent to the southern side of the Myrdalsjøkull (LINDROTH 1930). These areas are close to and on the windward side of present glaciers. They would soon have been covered by expanding ice during a glacial period and consequently they are not among the possible unglaciated areas indicated by THORARINSSON (1937) and other scientists. These areas are on the routes of migratory birds. (TIMMERMANN 1937-39; SCOTT, BOYD & SLADEN 1953-54). Therefore, birds may have spread these insects to southern Iceland.

Conclusion. The predominantly non-arctic character of the insectfauna of Iceland at present contradicts the hypothesis of its Last-Glacial survival in Iceland. Postglacial spreading of insects from western Europe to Iceland may have been furthered by large numbers of birds, regularly migrating to Iceland in spring.

5.2. POSSIBLY ICE-FREE AREAS ON THE SHELF

Some areas on the continental shelf at present less than 90 meteres deep may have remained ice-free during the maximum of the Last Glacial.

Discussion. Some authors dealing with the problem of refuge areas for plants and animals have pointed to the possibility of ice-free land on part of the now submerged shelf. To check this possibility some outlet-glaciers were reconstructed. The charts issued by the Hydrographic Department of the British Admirality were used to draw an accurate bottom-profile of the fjords and shelf across which the outlet-glaciers moved seawards.

5.2.1. *Reconstruction of outlet-glaciers*

The reconstruction of the outlet-glaciers was based on the following principles derived from literature on present-day glaciers and ice sheets:

(a) When the bottom of the fjord or shelf was horizontal or nearly so, a surface gradient of the ice of 1/150 was used.

(b) When the glacier had to move up-slope and the gradient of the bottom was less than 1/150 the surface-gradient of the ice was maintained at 1/150.

(c) When the glacier had to move up-slope and the gradient of the bottom was larger than 1/150, the value of the bottomgradient was used for the surface-gradient of the ice. In any case the surface-gradient must be equal to or larger than the bottom-gradient, otherwise the glacier cannot move any further forward.

(d) When the bottom-gradient was larger than 1/150 the same gradient was used for the ice surface. If, however, this stretch was followed by a stretch where the ice had to move up-slope again, the surface-gradient was maintained at 1/150.

(e) For the thickness of the ice the highest values that could be found in literature were used (see 5.1.1).

(f) In some cases the thickness of the ice and the surface-gradient could be inferred from the cirque bottoms in the fjord walls. This was the case along the coast of the northwestern peninsula.

(g) The reconstructed outlet-glaciers ended where 9/10 of their mass was submerged.

(h) The present-day depths of fjords and shelf were used, without taking into account postglacial uplift and sedimentation (in Figure 5 the 45 m isobase is shown).

(i) A surface-gradient of 1/75 was used for the interior of Iceland.

GLACIOLOGICAL LITERATURE

AHLMANN 1922, 1944, 1948, CHARLESWORTH 1957, DEMOREST 1943, DRYGALSKI & MACHATSCHEK 1942, ENQUIST 1916, 1918, FLINT 1962, FLINT & DEMOREST 1942, FRISTRUP 1960, GOULD 1935, HAEFELI 1961, HESS 1904, HOBBS 1911, KETTNER 1960, VON KLEBELSBERG 1949, KOERNER 1961, LJUNGNER 1949, MELLOR 1958, PATERSON 1951, PERUTZ 1953, ROBERTS 1950, ROBIN 1964, RUSSELL 1893, SHARP 1948, 1951, 1953, 1954, SVENSSON 1959b, TARR 1909, THIEL & OSTENSO 1961, WASHBURN & GOLDTHWAIT 1937, WHITE 1956, WRIGHT 1939.

Reconstructions of glaciers were only made in those parts of Iceland where a broad shelf less than 90 m deep occurred. The results are shown in Fig. 5.

Discussion. According to THORARINSSON (written communication) the area off Cape Reykjanes and the Vestmannaeyjar Islands were probably ice-free during the Last Glacial.

Conclusion. It is highly probable for part of the shallow Icelandic continental shelf to have remained ice-free during the maximum of the Last Glacial.

The ice-free shelf areas lie considerably outside the 45 m isobase. Therefore, I assume that these areas were not pressed down during the Last Glacial. They may even have been raised.

5.3. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

At present in most of Iceland easterly winds prevail; of these east winds are the most frequent (WEATHER BUREAU U.S.A. 1943: 13). During the Last Glacial the polar anticyclone may have extended farther southwards, causing an even higher frequency of easterly winds than there is at present. The assumed ice-free shelf areas were chiefly off western Iceland on the lee side for the prevailing winds. Here *föhn*-like winds frequently caused clear or broken skies, prevented fogs and promoted incoming radiation. Hence, it may be concluded that temperatures were fairly favourable. From Table 2 it may tentatively be gathered that even if we assume that summer mean air temperatures were 6° C lower during the maximum of the Last Glacial, summer temperatures may have been favourable enough to sustain a moderate plant and animal life in the assumed ice-free areas off western Iceland.

TABLE 2

PRESENT SUMMER TEMPERATURES IN ICELAND

Weather Bureau U.S.A., Dept. of Commerce 1943, *World Meteorol. Organization* 1962, *Meteorol. Office, London* 1964, 1965.

	Monthly average			Monthly average of daily max. temperatures		
	June	July	Aug.	June	July	Aug.
Vestmannaeyjar	9,0	10,5	10,4	12.8	14,4	13,8
Keflavik	9,2	10,7	10,4	—	—	—
Reykjavik	9,5	11,1	10,8	—	—	—
Stykkisholmur	8,7	10,5	11,5	12,0	13,6	12,9
Graenholl	6,7	7,7	7,2	—	—	—
Grimsey	5,5	7,2	6,7	8,9	10,5	10,0
Akureyri	9,2	10,7	10,1	11,8	14,3	13,5
Holari Hornafirdir	9,1	10,5	9,9	—	—	—

5.4. SUMMARY

Phytogeographical data do not supply conclusive evidence as to ice-free areas; but they do support the assumption of ice-free glacial refuge areas for plants in the regions indicated as unglaciated areas by geologists. The still very scanty data from palynological research also support the survival theory.

The predominantly non-arctic character of the insect fauna of Iceland at present clashes with the hypothesis of its Last-Glacial survival in Iceland.

There is no geological evidence for past landbridges between Iceland and other North Atlantic areas.

The possibilities of the spreading of plants and insects to Iceland from Europe may be underestimated. Migratory birds may have played an important part as dispersal-agents before, during and after the Last Glacial.

Though the greater part of the Icelandic continental shelf was probably covered by ice, there remained a fairly large ice-free area, especially off the extreme northwest of Iceland. Here the Last-Glacial climate may have been favourable enough for hardy plants and animals to survive.

5.5. Last-Glacial breeding birds

Taking as a basis the criteria mentioned in the paragraph on Greenland I have selected the following 34 species of birds, presented in systematical order, which may have bred in Iceland during the Last Glacial; 27 of these species are known to breed in Iceland to-day:

Gavia stellata
Fulmarus glacialis
Anser fabalis
Branta leucopsis
Branta bernicla
Somateria mollissima
Somateria spectabilis
Histrionicus histrionicus
Bucephala islandica
Clangula hyemalis
Falco rusticolus
Lagopus mutrus
Charadrius hiaticula
Arenaria interpres
Calidris canutus
Calidris maritima
Calidris alpina
Calidris alba
Phalaropus fulicarius
Stercorarius parasiticus
Stercorarius longicaudus
Larus hyperboreus
Xema sabini
Pagophila eburnea
Rissa tridactyla
Sterna paradisaea
Plautus alle
Uria lomvia
Cepphus grylle
Fratercula arctica
Nyctea scandiaca
Calcarius lapponicus
Plectrophenax nivalis
Corvus corax

6. **Spitsbergen and Spitsbergen Bank** (Fig. 6)

6.1. Evidence of complete glaciation of Spitsbergen

Geological evidence suggests that during former glacial maxima coalescent glaciers completely covered the islands of the Spitsbergen archipelago and flowed outwards over the shallow shelf to terminate in deep water (Flint 1961).

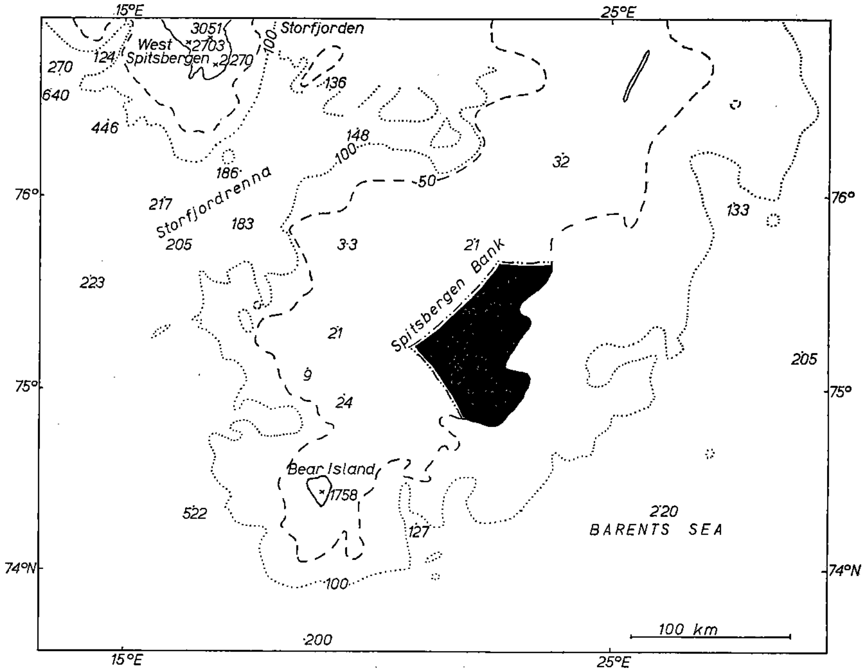


FIGURE 6. Spitsbergen Bank. *Black area* = present shelf area of less than 50 fathoms depth, which was possibly ice-free land during the maximum of the Last Glacial.
—·—·· = supposed border of glaciers from Spitsbergen and Bear Island.
— — — = 50 fathom isobath.
.... = 100 fathom isobath.
Depth in fathoms, height in feet.

6.2. Possibly ice-free areas on Spitsbergen Bank

Spitsbergen Bank may have been emergent during the maximum of the Last Glacial and then have formed a peninsula attached to Edgeöya, c. 180 km wide and over 400 km long. The greater part of the bank is flat with a present depth between 36 and 54 m. The bank is separated from West Spitsbergen by the Storfjord and Storfjordrenna, the latter with a maximum depth of 371 m and about 80 km wide between the 90 m isobaths at its narrowest area. Outlet-glaciers of western West Spitsbergen must have flowed to the west where thy reached deep water at distances varying from 40 to 72 km from the present coast line. Outlet-glaciers of eastern West Spitsbergen and western Edgeöya must have drained to the south and southwest through Storfjord and Storfjordrenna and, therefore, part of Spitsbergen Bank may have remained ice-free.

The areas of the bank not covered by ice from Spitsbergen may have been covered by perennial snow. At present the yearly precipitation of Spitsbergen is small, but so is the evaporation. The same conditions may have prevailed during the Last Glacial. Strong winds may have swept the flat country clean of snow, causing local snowdrifts, which in the arctic summer are quite welcome for plant and animal life.

6.3. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

Spitsbergen Bank must have had a favourable effect on the climate of the west coast of the bank itself and of Spitsbergen, because the presumed North Atlantic current probably found a much smaller strait between Spitsbergen Bank and NW Norway. Therefore, a larger quantity of fairly warm water must have been diverted along the west coasts of Spitsbergen Bank and Spitsbergen. This must have added to the possibility of open coastal water, in spite of lower air temperatures and a large amount of cold water melting from glaciers and icebergs.

The blocking of the sea between Spitsbergen and NW Norway must also have increased the speed of the sea-currents both along the west coasts of Spitsbergen Bank and Spitsbergen and along the NW Coast of Norway and the south coast of Spitsbergen Bank. The greater the speed of the sea-current, the greater the transport of pack-ice and ice-bergs to the north. This too must have made open coastal waters all the more possible.

In summer large quantities of melting water from icebergs calving from outlet-glaciers in north-west Norway and Bear Island probably have decreased temperatures.

A smaller amount of the warm ocean current could penetrate into Barents Sea, because the strait north of Norway was approximately half as large as at present. Hence, Barents Sea probably was colder than at present.

TABLE 3

PRESENT SUMMER TEMPERATURES IN SPITSBERGEN AND BEAR ISLAND
World Meteorol. Organization 1962, *Meteorol. Office, London* 1964, 1965.

	Monthly average			Monthly average of daily max. temperatures		
	June	July	Aug.	June	July	Aug.
Isfjord Radio	2,1	5,0	4,5	5,0	7,0	6,1
Grönfjorden	1,7	4,9	4,2	4,0	7,0	6,2
Björnöya	2,4	4,5	5,2	3,9	6,7	6,8

As explained in Chapter 13 there are reasons to believe that the general decrease in temperatures was less in high than in lower latitudes. The weighing of unfavourable against favourable factors influencing summer temperatures cannot as yet yield a quantitative result. Considering Table 3 it seems clear that if summer mean air temperatures were 6° C lower during the Last-Glacial maximum than at present, circumstances on Spitsbergen Bank were too bad to sustain plant and animal life.

7. Norway

7.1. EVIDENCE OF ICE-FREE AREAS

The evidence of ice-free areas in Norway throughout the Last Glacial has long been a controversial issue, first and foremost between geologists and botanists, but also among geologists and geographers.

7.1.1. *Geological and geomorphological evidence of ice-free areas*

The following points have been put forward as evidential for the existence of ice-free areas during the Last Glacial:

(a) An alpine morphology with Matterhorn-like peaks. These peaks must have projected above the ice as true nunataks (ENQUIST 1918, AHLMANN 1919, 1922, HELTZEN 1948).

(b) The occurrence of many cirques, eroded by local cirque glaciers above the surface of the inland ice (ENQUIST 1918, AHLMANN 1919, STRÖM 1938).

(c) The lack of visible traces of glacial erosion (UNDÅS 1934, 1938, GRÖNLIE 1925, 1940).

(d) The total absence of foreign erratics (AHLMANN 1919, UNDÅS 1938).

(e) The presence of strongly weathered erratics ascribed to deposition during a glaciation prior to the last, and since exposed to weathering.

(f) Boulders indicated as erratics considered as a residue of weathering in situ.

(g) The presence of a thick layer of finely weathered material attributed to weathering processes that started before and continued during the Last Glacial. If during the Last Glacial inland ice or local glaciers had moved across this layer, it would have been removed (DAHL 1954).

(h) The postglacial time has been too short to develop such a layer of finely weathered material.

(i) Traces of glaciers like sloping dry drainage channels cut in fjordwalls along the edges of valley glaciers, and shore-lines washed out in ice-dammed lakes indicating the maximum height of the ice surface. Plateaus between those fjords in the coastal regions of NW Norway must have been free from inland ice (AHLMANN 1919, GRÖNLIE 1925, 1940).

(j) Calculations of the thickness of the ice based on the density of the underlying rock, depression of the area under the weight of the ice—judged by the oldest shorelines—density of the ice and eustatic lowering of the sea-level led GRÖNLIE (1940) to conclude that some coastal plateaus cannot have been covered by inland ice.

7.1.2. *Geological and geomorphological evidence against ice-free areas*

Opponents of the theory of ice-free areas do not consider the evidence mentioned in 7.1.1. as furnishing a clear proof of ice-free areas, because:

(a) An alpine morphology may survive a total glaciation under a thick ice sheet, as must have happened in the Antarctic (AHLMANN 1944, HOPPE 1963). The peaks may have been formed by strong postglacial cirque erosion. On some of the peaks far-transported boulders were found (BERGSTRÖM 1959, SVENSSON 1959).

(b) Many cirques may have been formed by Late-Glacial and Postglacial cirque glaciers.

(c) Glacial striae may have disappeared by postglacial weathering.

(d) Absence of foreign erratics is negative evidence.

(e) Intensely weathered boulders may be the result of postglacial weathering.

(f) These boulders are real ice-transported erratics.

(g) A thick layer of finely weathered material may be the result of strong postglacial weathering only.

There are many mountains or high plateaus which were certainly overridden by ice, and at present they are covered by extensive *Felsenmeere* or by a thick, finely desintegrated layer. In some instances the weathered layer is covered by a thick layer of boulder clay or many unweathered erratics are found on the weathered layer. (HOLTEDAHL 1950, 1953; STRAND 1950; HOLTEDAHL & ROSENQUIST 1958). Therefore, the weathered layer may either have been preserved unter the ice cover, or have resulted from postglacial weathering.

(h) Strong mechanical weathering may produce a thick desintegrated layer in some types of rock during the relatively short time of the postglacial.

7.1.3. *Conclusion*

There is no agreement among geologists as to the existence of ice-free areas in Norway during the maximum of the Last Glacial The difficulties are mainly offered by the great diversity of effects of weathering on the various rock types and the rate of the weathering processes (HOLTEDAHL 1960).

7.1.4. *Field observations in Andöy and Söröy*

I wanted to clarify my view of the problem of Last-Glacial refuges in northwestern Norway by own field observations. For this purpose I visited *Andöy*, in July 1963, where AHLMANN (1929), GRÖNLIE (1925, 1940) and UNDÅS (1938) had found areas thought to have remained ice-free throughout the Last Glacial, and *Söröy*, where according to UNDÅS (1938) some plateaus had never been covered by inland ice and where NORDHAGEN (1935) had assumed ice-free refuges on phytogeographical grounds.

ANDÖY (Vesterålen)

On the narrow plateau remnant between Trolltind (436 m) and Ramnheia (428 m), c. 69°16′ N lat., 16°6′ E long. the following observations were made:

1. Traces of glacial erosion were absent.
2. In some places a weathering layer of one metre was found (Fig. 7).
3. Part of Ramnheia was covered by a dense vegetation without any stone or block (Fig. 7).
4. The lower parts of the cirque walls to the east of the mountains were well rounded, presumably caused by inland ice moving northwest (Fig. 8).

5. The higher parts of the cirquewalls were sharp ridges (which may have projected over local and inland ice) (Fig. 8).

6. Inland ice from the mainland of Norway could easily discharge through the large and deep Andsfjord east of Andöy. South of Ramnheia a side branch of the inland ice moving north through Andsfjord could flow to the west through a 5 km wide gap in the mountains.

Figure 7 was taken on the eastside of Ramnheia from the top of a very steep head wall of a cirque (440 m). The section through the weathering layer was brushed clean by sheep seeking shelter against westerly winds on the lee of the plateau. This section clearly shows a gradual transition from bedrock via blocks with fissures to small stones and fine earth. From these facts I inferred that the layer was a weathering product *in situ*.

The sharp ridges between the cirques may have been the result of glacial erosion by local cirque glaciers during Late-Glacial and Postglacial times. Postglacial weathering and denudation probably also contributed to the sharpness of these ridges. It is quite likely that the ridges between the cirques were small already at the beginning of the Last Glacial. If inland ice, mainly moving to the north-west, had crossed the highest parts of the cirque walls, the ice would have eroded downwards the ridges. That this did not happen is proved by the old plateau surface gradually tapering down on the cirque walls to the east (Fig. 9).

All observations made are consistent with the assumption that the plateaus have remained free of inland ice.

A *soil sample* taken from the finely desintegrated surface layer of Ramnheia was analysed at the Physical-geographical Laboratory of the University of Amsterdam. The size frequency distribution is shown in Figure 10, no. 2.

The fraction less than 1 micron was separated and examined for clay minerals with a Guinier-de Wolff II camera by KUMMER, LEVELT and VEEN in cooperation (Table 4). The following data from their report indicate that mechanical weathering has been predominant and that chemical weathering has been very slight or absent:

(a) Montmorillonite, vermiculite and the vermiculite-illite mixed layer occur in a high degree of crystallinity.

(b) The regular interstratification of the vermiculite-illite mixed layer.

(c) The presence of feldspar.

Fieldobservations have convinced me that the area of investigation was not overrun by inland ice during the Last Glacial. The clay mineralogical examination of the fraction less than 1 micron shows that the weathering is not the result of processes which started as early as Late-Tertiary or Early-Pleistocene times. What is most likely is that the area was overrun by inland ice during the Penultimale Glacial and that weathering started at the end of this time.

SÖRÖY (Vesterålen)

On the plateaus of SOPPEN (270 m) and FUGLEN (370 m), c. 70°39′ N lat., 22° E long., on the peninsula north of Sørvaer, the following observations were made:

1. Traces of glacial erosion were absent.

2. The flat east side of Soppen-Plateau (240-270 m) was covered by a thick layer of fine earth.

TABLE 4

ESTIMATED RÖNTGEN-INTENSITIES OF DIFFERENT CLAY-MINERAL COMPONENTS IN THE GRAIN-SIZE FRACTION $<1\mu$

Area	Height	Sample	Depth	montmorillonite	chlorite	vermiculite	vermiculite-illite mixed layer	illite	kaolinite	quartz	feldspar
Ramnheia	378 m	2	20—30 cm	+(+)	tr	(+)	(+)	tr	tr	tr	tr
Fuglen	320 m	3	15—20 cm	tr	?	tr	(+)	?	?	(+)	tr
	320 m	4	40—45 cm	tr	tr	+(+)	+(+)	?	tr	+	tr
	320 m	5	70—75 cm	tr	tr	+(+)	+(+)	?	?	+	tr
	370 m	6	0—10 cm	tr	(+)	+(+)	+	+	tr	(+)	tr
	360 m	7	20—30 cm	tr	tr	+(+)	(+)	+	tr	+	tr

The Röntgen data have been obtained in the Physical-Geographical Laboratory of the University of Amsterdam by means of a Guinier de Wolff Camera. For this table a scale has been used in which the highest intensity of reflection is indicated with +++++, and the lowest intensity with $(+) = \frac{1}{2}+$. Reflections indicated with tr (=trace) are so low in intensity that they cannot be estimated more accurately.

The intensity of a reflection of an observed mineral-component in a mixture of different components is determined by both the degree of crystallinity and the quantity of the mineral component present. Also the chemical composition of the lattice of a certain clay-mineral component (for instance low or high iron content, and the K^+content of illite) determines the reflected energy. In this way the estimated intensities must only be regarded as a very rough indication of the relative importance of the different clay-minerals present in a sample taken from the fraction smaller than 1 μ.

3. This area was covered by a dense vegetation without any stone or block (Fig. 11).

4. On the SE slope of Fuglen at a height of 320 m, two profile pits could be dug to a depth of 70-100 cm. (Samples 3, 4 and 5 are from one pit and 7 from the other; see Fig. 10; no. 3, 4, 5, 7; and Table 4).

5. The summit of Fuglen (370 m) was also rather flat, without any signs of differential glacial erosion. The surface consisted of small and large stones with fine earth in between. Here the vegetation was scanty. It cannot be decided whether there were erratics or not. (Sample 6 was taken near the summit; see Fig. 10: no. 6; and Table 4).

6. There is a very striking morphological difference between these plateaus and the interior of Söröy between Breivikbotn and Dönnesfjord. In the interior, at about the same height as Soppen and Fuglen, amidst mountains up to an altitude of 550 m, the landscape shows abundant signs of glacial erosion (polished rocks, glacial sills and lakes, many perched boulders) (Fig. 12).

It is my impression that the interior of W Söröy had a heavy local glaciation during the Last Glacial. But, inland ice could easily pass round the northwest peninsula of Söröy and quickly discharge into the Arctic Ocean, and it probably

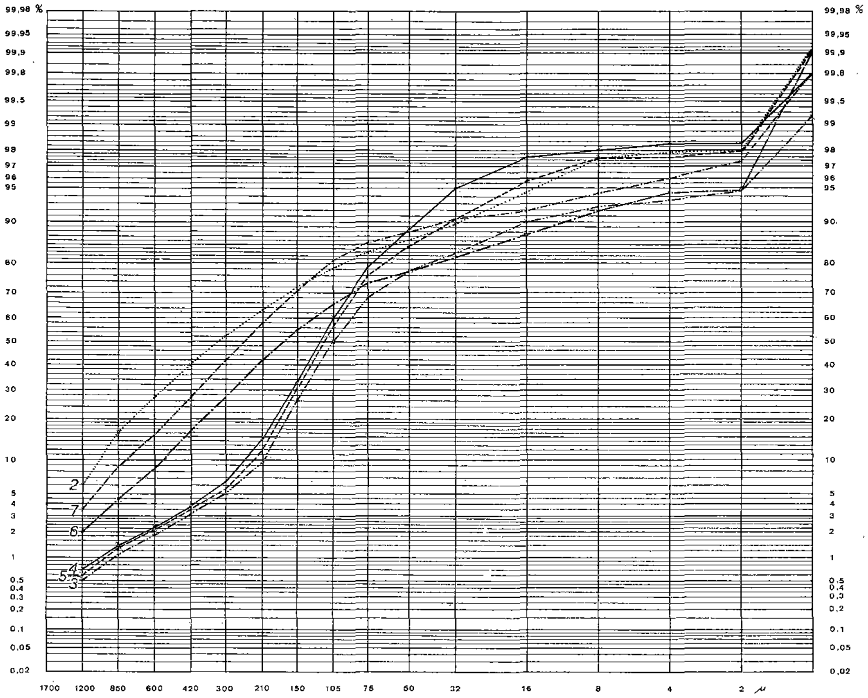


FIGURE 10. Size frequency distribution of the samples 2, from Ramnheia (Andöy, Vesterålen), and 3, 4, 5 and 7, from Fuglen (Söröy, W Finnmark).

did not reach high enough to flow across the plateaus of Fuglen and Soppen, which may have been surrounded by inland ice.

From the sites from which samples 3, 4, 5, and 7 were taken, the surface sloped upward in three directions. Both profiles showed a stratified yellow-brown soil, containing a few small angular stones. Some parts of the eastside of Fuglen were completely covered by small solifluction terraces. Hence, I concluded that the rather thick layer of fine grained material was not the result of weathering *in situ* only, but also of the influx of solifluction, eolian and meltwater material.

Samples 3 — 7 were submitted to the Physical-geographical Laboratory for the same examination as the sample from Andöy.

The fraction less than 1 micron from the samples 3 and 6 was also examined with the Philips Röntgendiffractometer, by means of which the camera examination was confirmed. Table 4 shows that there are only slight differences in the results of the examination. The following data from the report by KUMMER, LEVELT and VEEN indicate that the crystalline structures have not been exposed to chemical weathering of any significance, but that they must be the result of mechanical weathering of the parent rock:

(a) Vermiculite and the vermiculite-illite mixed layer occur in a high degree of crystallinity.

(b) The regular interstratification of the vermiculite-illite mixed layer.

(c) The presence of feldspar.

(d) The virtual absence of kaolinite.

According to KUMMER, LEVELT and VEEN these data indicate also that the mechanical weathering processes were of short duration, certainly post-Tertiary. Whether they have been at work since the end of the Penultimate glaciation, or only since the end of the Last Glacial cannot be decided.

The geological map of Söröy is still under preparation (Norske Geol. Undersökelse, written comm. 1963). The provisional geological map shows that samples 3 — 5, and 7 are from sites with highly metamorph cambro-siluric sediments; 6 and 7 from a site with gneissic rocks (BJÖRLYKKE 1940).

Staalet Plateau (SÖRÖY), c. 11 km NNE of the new settlement of Dönnesfjord.

The Staalet Plateau (570 — 610 m), c.70°45′N lat. 22°50′ E long., is surrounded by cliffs on three sides. The plateau is a desert of large angular blocks (Fig. 13). Part of the blocks form active blockstreams, mainly from NE to SW. The blockstreams may form rock glaciers in spring. That they are active blockstreams is inferred from the facts that the blocks were angular, only scarcely covered by lichens, not in equilibrium, and that where a blockstream reached a small depression there was a striking difference between the fresh appearance of the front of the blockstream and the older surface of the depression.

Strong periglacial weathering of a higher area on the NE side of the Staalet Plateau must have supplied the enormous quantity of angular blocks. The blockstreams were erasing former relief by gradually filling up a small depression, the bottom of which was horizontal. Here there was a suggestion of stone rings with a diameter of about 5 metres. This area had a thin layer of fine earth through which meltwater trickled; this gave rise to a scanty vegetation.

Whether the tremendous mass of blocks is a result of postglacial weathering only, or also of weathering during the Last Glacial and earlier, cannot be decided. The blocks on the surface are probably a recent weathering product. However, it was impossible to judge the thickness of the block cover. The underlying blocks may be much older.

Another small area with some fine earth on the southwest side of the plateau had a rather luxuriant vegetation. For the rest the block desert was devoid of any plant growth, with the exception of small pockets of some square dm where between some blocks fine earth had gathered.

In my opinion the Staalet Plateau was not covered by inland ice or by glaciers from the inland of Söröy during the Last Glacial, because:

(a) The gorge between Staalet and Reppe Fjeldene does not show any signs of glacial erosion. (The saddle in this gorge has a height of 300 m).

(b) To the east of Staalet there was a sharp ridge between cirques. The ridge may have acquired its present shape through postglacial weathering and denudation, but the narrow ridge would have been eroded downwards by a large glacier flowing perpendicularly to the trend of the ridge. The ridge is much lower than Staalet.

(c) The edges of the plateau were not rounded.

(d) On the plateau of Staalet no erratics or any marks of glacial erosion could be found. However, both traces of former glaciation may have been covered by the blockstreams.

e) The plateau could not be overrun by ice because of its altitude.

(f) The peninsula of Staalet is bordered by broad fjords which could easily divert glaciers flowing from the interior of Söröy round Staalet.

(g) The high islands east of Söröy and the broad and deep Söröy Sund (maximum depth 500 m) probably diverted the inland ice round Söröy, except for the low transverse valley between Öifjord and Dönnesfjord, through which inland ice flowed to the north (UNDÅS 1938).

(h) The shallow fjords of Söröy do not indicate large ice masses.

(i) The periferal situation of Söröy.

Staalet Plateau was somewhat sheltered against the wind by higher parts on its W and NE sides. Hence, it may have had a *nevé* cover during the Last Glacial.

According to the provisional geological map both Fuglen and Staalet consist of gneissic rocks. However, the morphology of the two plateaus differs widely. This large difference may be attributed among other things to differences in local climat-

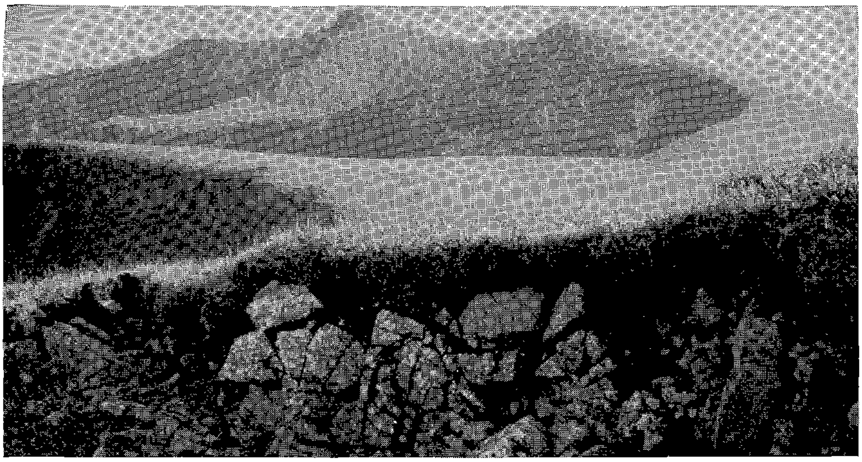


FIGURE 7. Ramnheia (Andöy, Vesterålen). Part of Ramnheia is covered by a dense vegetation without any stone or block. In foreground, section through weathering layer (at 440 m), showing a gradual transition from bedrock to fine earth. To the left, cirques on the east side of Ramnheia. July 12, 1963.

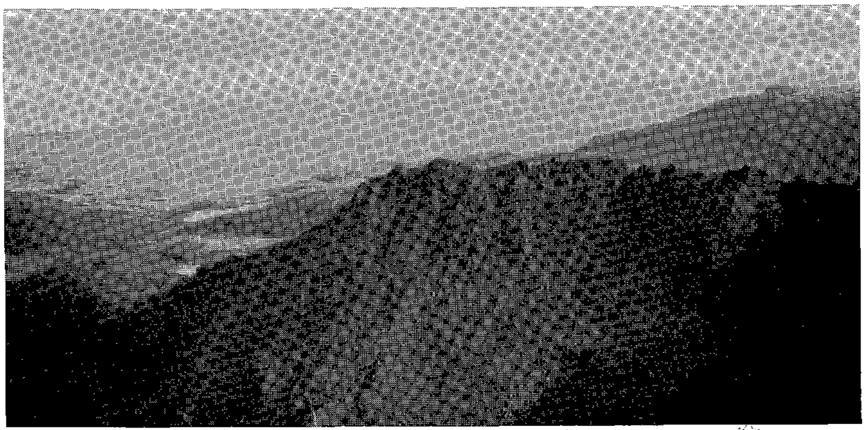


FIGURE 8. Ramnheia (Andöy, Vesterålen). Sharp ridge between cirques to the east of Ramnheia. Andsfjord in background. July 12, 1963.

FIGURE 9. Ramnheia (Andöy, Vesterålen). Old plateau surface of Ramnheia gradually tapering down on the sharp ridge between cirques on the east side. July 12, 1963.

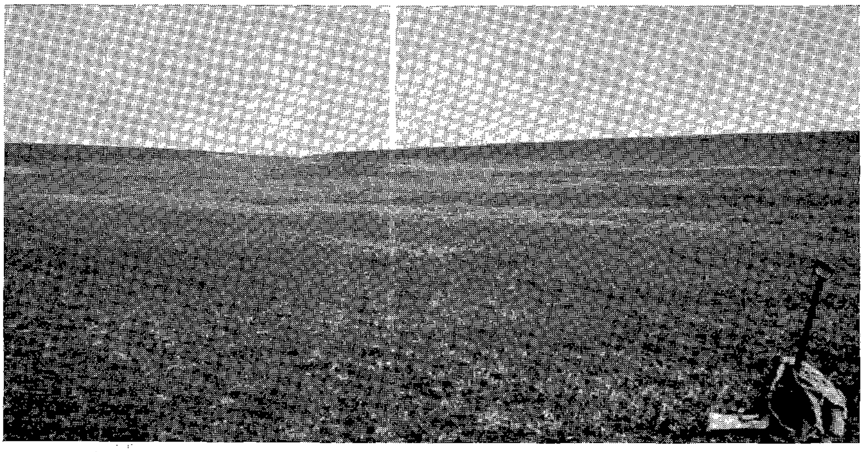


FIGURE 11. Soppen Plateau (Söröy, W Finnmark). Part of Soppen (at 270 m) is covered by a dense vegetation without any stone or block. July 21, 1963.

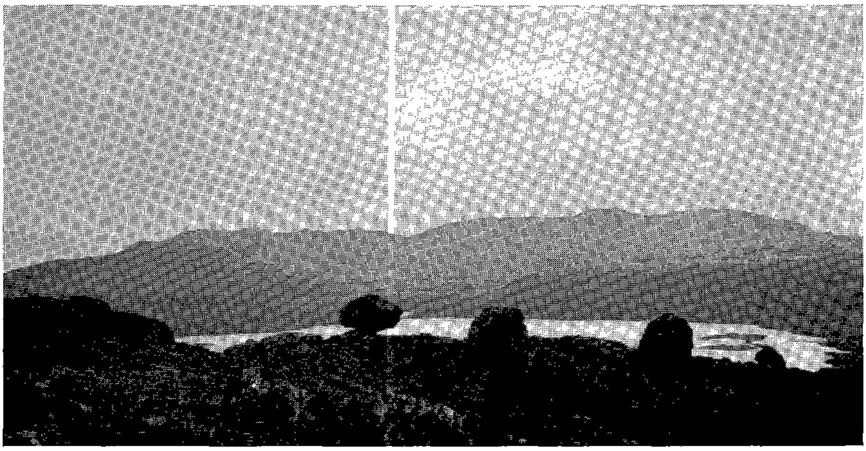


FIGURE 12. Perched boulders and glacial lake at 300 m in the interior of W Söröy (W Finnmark). Juy 26, 1963.

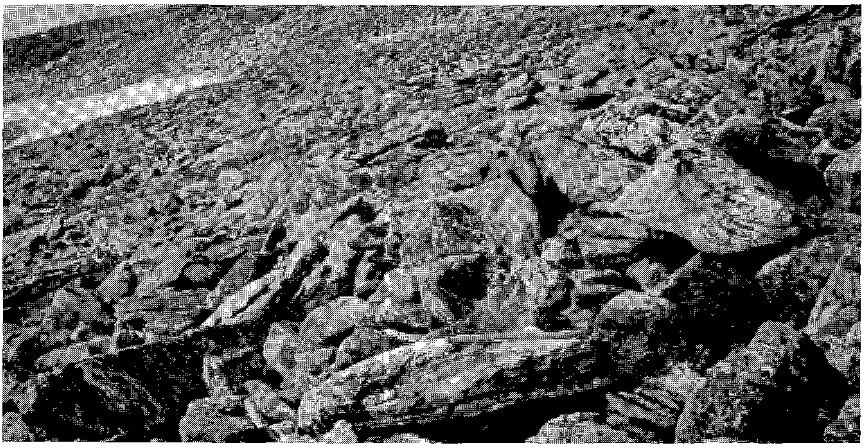


FIGURE 13. Desert of angular blocks on Staalet Plateau (Söröy, W Finnmark). The ruler in foreground is 25 cm. July 25, 1963.

ological circumstances, in wind exposure and in pre-Peistocene relief. Future geological investigation may also find lithological differences between the two plateaus.

Summary. Ramnheia (Andöy), Soppen, Fuglen and Staalet (Söröy) and other comparable plateau remnants on these islands may have remained ice-free during the Last Glacial. They may have offered refuges for hardy plants. The plateaus were probably surrounded by inland ice and glaciers of local origin. Through this and through their altitude they were unsuitable as refuge breeding grounds for the arctic Anatidae discussed in this paper, though possibly this is not true for *Branta leucopsis*, which breeds on steep cliffs, provided low land with vegetation is close at hand.

7.1.5. *Phytogeographical evidence*

According to most botanists at least part of present-day Scandinavian plant species may have survived the Last Glacial in west and northwest Norway (Nordhagen 1935, 1937, 1963, Hultén 1937, 1950, 1955, Dahl 1946, 1947, 1955, Sörensen 1949, Faegri 1960). Their conclusions are mainly based on the present distribution of subarctic and arctic-alpine species. These distribution patterns can be arranged according to the following characteristics:

(a) Restriction of distribution of species to one isolated area in Scandinavia (unicentric species), either in the south or in the north.

(b) Restriction of distribution of species to two isolated areas in Scandinavia (bicentric species), one in the north and one in the south.

(c) Occurrence of a number of rare arctic-alpine plants which have their main distribution in Greenland or on the North American mainland (the west-arctic element from the Scandinavian point of view) in one of the centres referred to under (b). These species are more numerous in the northern than in the southern centre. In Eurasia these species often only occur in small isolated areas at a large distance from Scandinavia, e.g. in the Carpathians, Altai Mountains, easternmost Siberia. Some of these species are lacking in east Greenland or Iceland. They never occur in Scotland.

(d) Some of the uni- or bicentric species or subspecies are endemic.

(e) Some arctic-alpine plants, among which west-arctic species, only occur in or near areas which, as is gathered from geomorphological evidence, may have remained unglaciated during the Last Glacial, especially in north and northwest Norway.

(f) Some of the southern unicentric species are totally absent from the adjacent area to the south with habitats perfectly suited to the ecological needs of these species. They sporadically occur west of their distribution centre. Therefore, Nordhagen (1963) assumed that they immigrated postglacially from coastal areas in west Norway and not from the south.

(g) The distributional group "G" of Hultén (1950), including 9 species, has an isolated western mountain distribution in Scandinavia. These species go high up into the mountains where they are very common. Farther to the east they are common in the lowlands of Russia where their main distribution area begins. Between the areas of Norway and Russia the species are rare or totally absent. According to Hultén (1950) group "G" in all probability survived the Last Glacial time in western Norway. Hultén (1950) recognizes four more distributional groups (C, D, E and S) which probably survived in northern Norway.

Discussion. If the seeds of west-arctic plants were transported accidentally by wind or by birds to such wide-spread areas as Greenland, Scandinavia, Ural, Eastern Alps, the Baikal region, it is highly surprising that they should be concentrated in separate areas in Norway, whereas they do not occur in other parts of the Scandinavian mountains nor in Scotland. Moreover, Norway has a number of west-arctic plants lacking in Iceland and Spitsbergen, which are much closer to Greenland (NORDHAGEN 1937: 214). Therefore, the theory of postglacial dispersal of the west-arctic element to Scandinavia is rejected. It is assumed that the present west-arctic species are relics of species with a much larger distribution before the Last Glacial.

The isolated occurrence in Scandinavia of arctic-alpine species having phytogeographical connections to the east may be attributed either to unsuitable ecological conditions or to historical factors (HULTÉN 1955). According to HULTÉN ecological conditions can hardly provide a reasonable explanation for the disjunctions east of Scandinavia. Hence, the isolation must have resulted from historical factors. The first possibility is that arctic-alpine plants spread to Scandinavia from the east before the Last Glacial. During this time some of them survived in refuge areas in west, northwest and northern Norway. From there they spread to their present areas after deglaciation.

A second possibility is that Scandinavia was completely glaciated and the plants reached this peninsula from the east along a northern route after the retreat of the last inland ice. During the hypsithermal interval the forests extended northwards and into the mountains. Consequently many arctic-alpine plants became extinct in most regions in northern Russia and in Scandinavia, except in the areas with higher mountains (HULTÉN 1955).

NORDHAGEN (1963) rejects the possibility of the hypsithermal interval being cause of the bicentric distribution, because some of the Scandinavian bicentric species have recently been found in *Pinus-silvestris*-forests in low mountains. Though this may be true as regards some species, still the greater part of the arctic-alpine species only occur above the tree-line in high mountains in the south and north.

According to NORDHAGEN (1935, 1937, 1963) the refuge areas should not be localized on the nunataks in the present distribution centres of the species, but in coastal regions in west, northwest and northern

Norway. From the coastal refuge areas the survivors migrated to the interior districts in postglacial times, meeting their ecological needs there. But as NORDHAGEN agrees that the arctic-alpine plant species evaded the improved climatic conditions in the coastal regions during deglaciation, he cannot avoid accepting the continuation of this process during the hypsithermal interval.

Finally, I regard the phenomena under (e), (f),and (g) as the strongest evidence of ice-free refuges for plants in Norway.

Conclusion. The present distribution of Scandinavian plant species may be attributed to:

(a) Survival of the Last Glacial of arctic-alpine plants in coastal refuge areas in west, northwest and northern Norway.
(b) The influence of the hypsithermal interval.
(c) The combined effect of (a) and (b).

Therefore, the phytogeographical evidence cannot be considered to offer conclusive proof of ice-free refuges, but it strongly suggests the possibility that such areas existed.

7.1.6. *Zoogeographical evidence*

According to LINDROTH (1949) 97 species of *Carabidae* in all probability survived the Last Glacial time in refuge areas, along the west and northwest coast of Norway. Another 33 species of *Carabidae* probably did so too, but in their case there is less certainty.

Evidence. Among the Scandinavian *Carabidae* there is a number of dimorphic species. These species have brachypterous and macropterous forms. The forms differ genetically. The macropterous beetles are homozygotes, the brachypterous ones are heterozygotes. The brachypterous beetles cannot fly.

Within the distribution area the ratio between the shortwinged forms and the long-winged ones was computed in different localities. These ratios were given in diagrams on maps. Generally, the number of macropterous individuals increases towards the periferal parts of the total distribution area. In some parts of the area the ratio brachypterous *versus* macropterous is particularly large. The latter areas are considered to have acted as distribution centres for the species in fairly recent times. This assumption is based on the fact that macropterous forms have a much greater spreading capacity than brachypterous forms. ("The air-borne troops go first, the infantry comes later".)

A number of dimorphic Carabid species has a fairly high percentage of brachypterous forms on Hitra, Lofoten, Vesterålen and the islands of the coasts of Troms and Finnmark. This percentage is much higher than that among the populations in the adjacent areas on the mainland of Scandinavia. It is assumed that the species with such high percentages of brachypterous forms survived the Last-Glacial period in refuge areas on these islands or in the neighbourhood of them, perhaps on areas now submerged.

Circumstances during the Last Glacial in these confined areas favoured the survival of the brachypterous forms, whereas the macropterous forms were easily transported by active flight and wind into areas which were quite unfavourable, i.e. the Atlantic and the glaciated areas. Selection increased the percentage of the brachypterous forms.

Part of the presumed survivors show the following peculiarities in their distribution pattern:

Nine species have isolated areas in west or north Norway, whereas their main distribution area is in Siberia. These species are lacking towards the northeast, or else the western distribution area has only a weak connection with the distribution area farther east. In the north of Scandinavia there is a disjunction between Swedish and Norwegian areas of these species.

Fourteen species only occur in W Norway or in W Norway with offshoots to parts of Sweden where they would not occur if the spreading of the species had taken place from the south in post-glacial times. Some species have no gap in their distribution areas; they are ubiquitous.

Many other non-dimorphic *Carabidae* have the same distribution patterns. They are assumed to be Last-Glacial survivors (LINDROTH 1949).

A great number of dimorphic species have a continuous population with a comparatively high percentage of brachypterous forms along the Norwegian west coast. Their distribution pattern does not show any signs of Last-Glacial survival. LINDROTH assumes that at least a large number of these species did survive the Last-Glacial period in refuge areas along the west coast of Norway.

According to LINDROTH (1949) the distribution pattern itself of some of the *Carabidae* may be sufficient to indicate that the species survived the Last Glacial in Scandinavia. If they did, the distribution pattern must show the following characteristics:

(a) an isolated mountain area in Scandinavia,
(b) a multicentric distribution in the Scandinavian mountains,
(c) in addition, a separated area in the south of Finland.

It is not necessary for every glacial survivor to show all of these three qualities in their distribution pattern.

A bicentric distribution may be caused either by ecological or by historical factors. In Scandinavia the gap between the two centres nearly always coincides with low mountains. High-alpine species cannot find a suitable habitat here. There is only one high-alpine species among the Scandinavian *Carabidae* with a bicentric distribution. So the bicentric distribution of the non-high-alpine species can only be explained by historical factors (LINDROTH 1949).

LINDROTH concludes that the survival of 52 species is indisputable. For another 45 species survival is almost certain. For yet another 33 survival is also possible. At present fifty per cent of all these species cannot bear an arctic climate. LINDROTH therefore points to the possibility that, during the Last Glacial the refuge areas along the Norwegian westcoast had a climate which allowed birches to grow.

Discussion. LINDROTH's explanation of distribution patterns and of concentrations of brachypterous forms is admittedly strong. However, some species of *Caribidae* in Scandinavia show centres with high percentages of brachypterous forms in areas which were beyond any doubt completely covered by inland-ice during the Last Glacial. Consequently there must have been several causes for the distribution of brachypterous and macropterous beetles.

The 9 dimorphic *Carabidae* which presumably survived the Last Glacial in Norway all but one are boreal-subarctic species. Therefore, LINDROTH (1949) concluded that climatic conditions in the refuge areas must have been more favourable than has hitherto been assumed. But if subarctic conditions had existed in the refuge areas decrease of mean temperatures would have been by 3° C only, which is far less than the often accepted drop in summer temperatures of 6° C.

Conclusions. The present distribution of many Scandinavian *Carabidae* species suggests that these beetles have survived the Last Glacial in coastal refuge areas in Norway. This theory is reinforced by the concentration of a large percentage of brachypterous forms of dimorphic *Carabidae* in some of the presumed refuge areas. The theory of the survival of *Carabidae* is weakened by two facts. Firstly, some of presumed refuge areas were certainly glaciated. Secondly 50% of the presumed survivors is non-arctic.

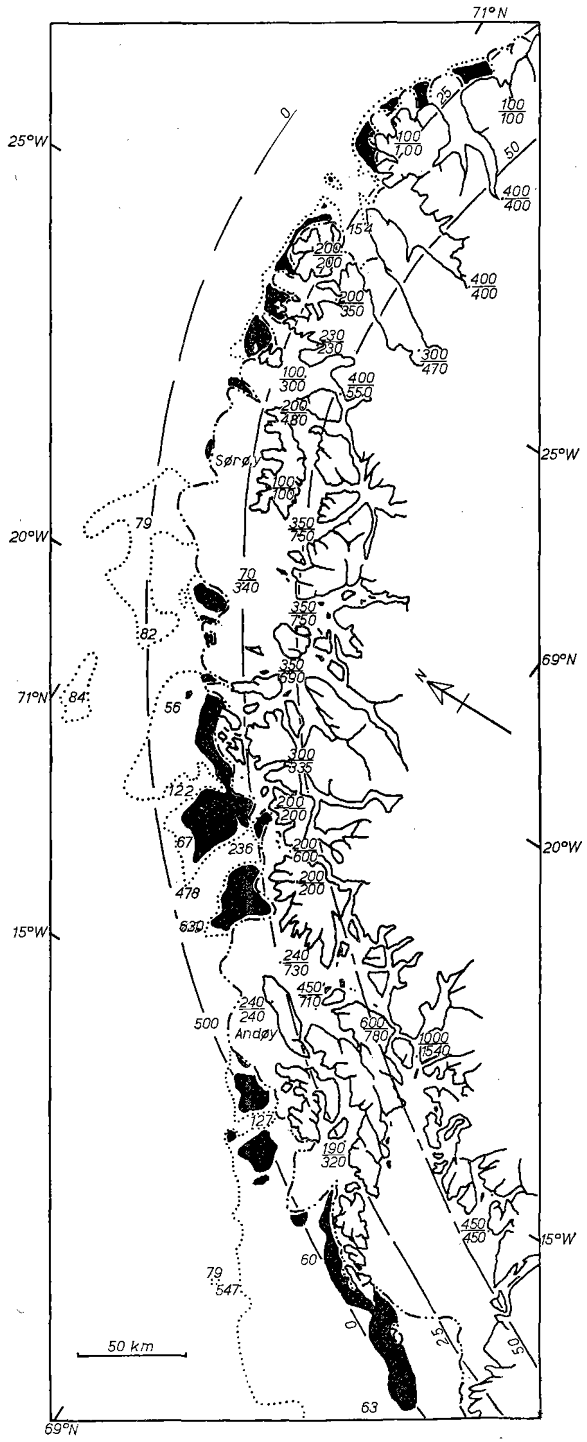
7.2. POSSIBLY ICE-FREE AREAS ON THE SHELF (Fig. 14, 15)

7.2.1. *Reconstruction of outlet-glaciers*

From a reconstruction of over 50 outlet-glaciers I learned that along a stretch of coast of 1075 km, from 69°50′ N lat. to the Russian border, 4,800 square kilometres of continental shelf, at present less than 90 metres deep, may have remained ice-free during the maximum of the Last Glacial. South of 69°50′ N lat. only Langgrunds Banken (c. 62°50′ N lat. and 5°15′ E long.) possibly remained free from inland ice.

Discussion. Many authors dealing with the problem of refuge areas for plants and animals have pointed to the possibility of ice-free land on part of the now submerged shelf (DAHL 1947, GRÖNLIE 1942, O. HOLTEDAHL 1929, 1953, 1960, H. HOLTEDAHL 1955, HULTÉN 1955, LINDROTH 1949, NORDHAGEN 1935, 1947, UNDÅS 1942).

To examine this, over 50 outlet-glaciers were reconstructed. The charts issued by the Hydrographic Department of the British Admiralty



In $\frac{1000}{1540}$ etc. the top figure gives the height (in metres above present sea-level) of the ice-surface during the maximum of the Last Glacial, the bottom figure gives the thickness of the ice during that time. These figures, inferred from literature sources and taken from bathymetrical maps, have been used for the reconstruction of outlet-glaciers (see 7.2.1). *Black areas* = present shelf areas of less than 50 fathoms depth, which were possibly ice-free land during the maximum of the Last Glacial. Depth in fathoms, height in feet.

FIGURE 14. North-west Norway. —— —— = 50 m, 25 m and 0 m isobases. …… = 100 fathom isobath. —· ·—· · = reconstructed outer border of inland ice.

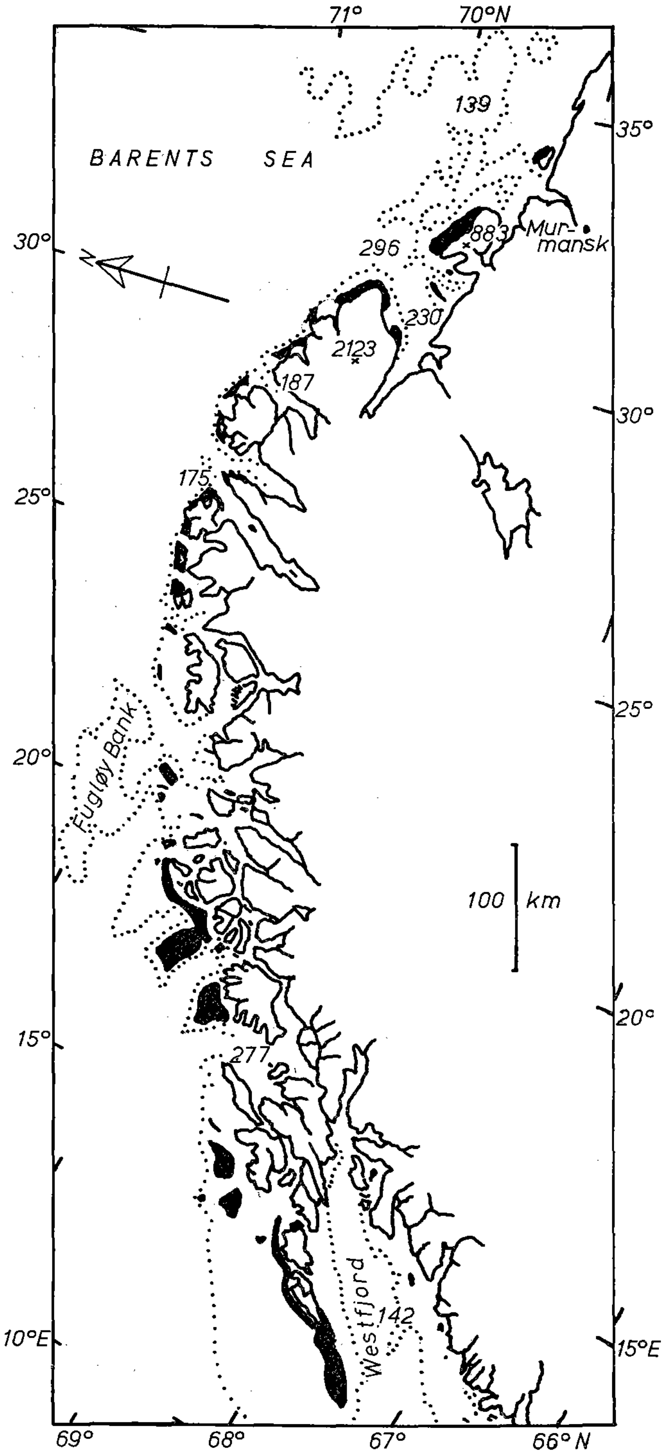


Figure 15. North-west Norway and Kola Peninsula. For legend see Figure 14.

were used to draw an accurate bottom-profile of the fjords and the shelf across which the outlet-glaciers moved seawards. Altitudes of the ice surface were taken from literature sources (AHLMANN 1919, 1922, ENQUIST 1918, GRÖNLIE 1925, 1940, GUSTAVSON & GRÖNHAUG 1960, HAFSTEN 1956, HELTZEN 1948, H. HOLTEDAHL 1950, 1951, 1955, O. HOLTEDAHL 1929, 1953, 1960, HOLTEDAHL & ROSENQUIST 1958, KEINDL 1936, 1938, LIND 1955, NORDHAGEN 1935, 1937, STRÖM 1945, SVENSSON 1959a, UNDÅS 1934, 1938, 1942). The reconstruction was based on the principles stated in the chapter on Iceland, with the exception of the last one (5.2.1.i).

It must be stressed that the following factors all tend to exaggerate the extent of the reconstructed outlet-glaciers:

(a) In many cases the outlet-glaciers must have formed *piedmont*-glaciers where they flowed from the fjords on to the foreland. *Piedmont*-glaciers have as a rule a a very gentle slope (RUSSELL 1893, MARTIN 1908, TARR 1909, SHARP 1953). A surface-gradient of the ice of 1 : 150 was used, which is the lowest value to be found (SHARP 1953). For the fjord and valley glaciers this value will generally be far too small.

(b) The altitude of the ice surface has been determined by the present altitude of lateral moraines, striae and other traces of glacial erosion. The altitude of the ice surface must have been less during the Last Glacial as the land was pressed down under the weight of the inland ice.

(c) The isostatic lowering of the land probably decreased the down-slope bottom-gradient and increased the up-slope bottom-gradient, both causing a steeper surface-gradient of the ice in many cases.

(d) No doubt deep fjords, resulting from glacial erosion during preceding glacial periods, existed at the beginning of the Last Glacial. It may be presumed that during the Last Glacial there was further glacial erosion of the fjord bottom. Therefore, during a large part of this time the thickness of the outlet-glaciers was less than can be determined by the present depths of the fjords and the highest traces the ice left behind on the steep fjord sides. This must inevitably have led to a smaller extension of the ice on the shelf.

(e) A eustatic lowering of sealevel of 90 metres has been assumed, whereas DONN, EWING & FARRAND (1962) computed a lowering of 114.5 — 133.7 m for the Early Wisconsin and one of 105.5 — 123.4 for the Classical Wisconsin stage. With these values a far greater extent of the continental shelf would have been emergent, for instance around Langgrunds Banken (see also HOLTEDAHL 1955:126). On the other hand, if this be true, calving ice-fronts must be localized further seaward.

Conclusion. The total shelf area that remained ice-free during the Last Glacial probably was much larger than shown in Figures 14 and 15.

It is noteworthy that according to HOLTEDAHL (1955:125) the topographical features of the area around the outer part of the Breisunddup depresssion (62°30′N lat.) suggest that there was land during the time the depression was filled by a glacier tongue. Here the outer areas of the shelf were largely covered by gravel, up to 19% of which was of a well rounded type, comparable to beachgravel or glacio-fluvial gravel. Therefore, HOLTEDAHL (1955: 126) suggested that larger areas of the shelf than those bounded by the 100 m isobath were dry land during the last glaciation. The area referred to by Holtedahl is in the immediate vicinity of Langgrunds Banken, the only area sourth of 69°50′ N lat. that, according to my reconstructions of outlet-glaciers, remained free from inland ice.

TABLE 5

PRESENT SUMMER TEMPERATURES IN NORWAY
World Meteorol. Organization 1962, *Meteorol. Office, London* 1964, 1965.

	Monthly average			Monthly average of daily max. temperatures		
	June	July	Aug.	June	July	Aug.
Bodö	9,9	13,6	12,7	—	—	—
Tromsö	8,7	12.0	11,1	12,2	15,6	13,8
Vardö	6,2	9,1	9,7	8,4	10,8	11,6

7.3. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

Table 5 shows that even if summer mean air temperatures were 6° C lower during the maximum of the Last Glacial than at present, summer temperatures of northwestern and northern Norway may have been favourable enough to sustain a moderate plant and animal life (see also Chapter 13).

7.4. SUMMARY

There is no agreement among geologists about the existence of areas in Norway that remained unglaciated during the Last Glacial.

Areas which according to some geologists were probably ice-free are either on true nunataks in the interior, on steep fjords sides in coastal regions, or on coastal mountains bordered by deep fjords, especially in west, northwest and northern Norway.

Phytogeographical and zoogeographical data do not afford conclusive evidence for ice-free areas, but suggest the survival of many arctic-alpine plant species and of part of the *Carabidae* fauna in ice-free refuge areas, especially in coastal regions of west, northwest and northern Norway.

Reconstructions of oulet-glaciers have shown that a considerable area of the Norwegian continental shelf, at present less than 90 metres deep, north of 69° 50′ N lat., probably remained ice-free during the maximum of the Last Glacial. South of 69° N lat. only Langgrunds Banken (c. 62°50′ N lat. and 5°15′ E long.) possibly remained ice-free. Generally speaking there is a fair agreement between the geological, phytogeographical and zoogeographical evidence for the localization of the ice-free refuge areas and between this evidence and that of the reconstructed ice-free shelf areas.

The presumed survivors among the present flora and insect fauna may have found refuge areas on the emergent shelf during the Last Glacial.

7.5. Last-Glacial breeding birds

Taking as a basis the criteria mentioned in the paragraph on Greenland the following selection has been made of 35 species of birds, presented in systematical order, which may have bred in Norway during the Last Glacial; 21 of these species are known to breed in Norway to-day:

Gavia stellata
Fulmarus glacialis
Anser albifrons
Anser fabalis
Branta leucopsis
Branta bernicla
Somateria mollissima
Somateria spectabilis
Clangula hyemalis
Falco rusticolus
Lagopus mutus
Charadrius hiaticula
Arenaria interpres
Calidris canutus
Calidris maritima
Calidris minuta
Calidris alpina
Calidris alba
Phalaropus fulicarius
Stercorarius parasiticus
Stercorarius longicaudus
Larus hyperboreus
Xema sabini
Pagophila eburnea
Rissa tridactyla
Sterna paradisaea
Plautus alle
Uria lomvia
Cepphus grylle
Fratercula arctica
Nyctea scandiaca
Anthus spinoletta
Calcarius lapponicus
Plectrophenax nivalis
Corvus corax

8. North Sea area

This area comprises the unglaciated part of Denmark, NW Germany, the Netherlands, the unglaciated area south of the Newer Drift border in the British Isles, and the unglaciated continental shelf—less than 90 metres deep—of the North Sea and the English Channel.

The botanical, palynological and zoological data from the North Sea area fairly consistently point to predominantly subarctic, or even arctic, conditions during the cold phases of the Last Glacial. During the optimum of the Rodeback (=Amersfoort), Brörup and Alleröd interstadials probably boreal circumstances prevailed (Andersen 1961, Andersen, de Vries & Zagwijn, 1960; Arnold & Libby 1951, Charlesworth 1957, Coope, Shotton & Strachnan 1961, Coope 1962, Degerböl & Krog 1959, Farrington & Mitchell 1951, Flint 1961, Godwin 1956, Gross 1958, Guenther 1955, Hallik & Kubitski 1962, van der Hammen 1951, Jessen 1949, Mitchell & Parkes 1949, Movius 1960, Pannekoek *et. al.* 1956, Penny 1964, Reid 1949, Sutcliffe & Zeuner 1957-58, Tomlinson 1963, van der Vlerk & Florschütz 1950, West 1963, Wright 1937, Wright 1961, Zagwijn 1961, Zeuner 1959).

9. Northern Eurasia

9.1. Tundra zone

For the distribution of tundras, ice sheets and local mountain glaciations see Figure 1a, which is compiled from maps of Frenzel (1960), Sachs & Strelkov (1961), and Flint (1961).

9.2. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

Table 6 shows a steep temperature gradient between northern inland stations and islands off the northcoast of Eurasia. No doubt this is due to the cold sea containing large amounts of melting sea ice.

TABLE 6

PRESENT SUMMER TEMPERATURES IN NORTHERN EURASIA
World Meteorol. Organization 1962.

	N. Lat.	E. Long.	Monthly average		
			June	July	Aug.
1 Murmansk			10,0	13,4	11,1
2 Archangelsk			15,0	18,0	17,0
3 Narjan Mar	67 39	53 01	7,9	12,2	11,3
4 Russkaya Gavani			1,0	5,0	5,0
5 Malye Karmakuly	72 23	52 44	3,0	8,0	8,0
6 Salehard	66 32	66 32	8,8	14,1	12,0
7 Ostrov Dikson	73 30	80 14	0,7	4,9	5,4
8 Tura	64 10	100 04	13,0	16,4	12,3
9 Olenek	68 30	112 26	10,9	14,9	10,1
10 Hatanga	71 59	102 28	5,7	12,5	8,8
11 Mys Čeljuskin	77 43	104 17	—1,0	1,5	0,8
12 Verhojansk	67 33	133 23	12,9	15,7	11,4
13 Čokurdah	70 37	147 53	6,5	10,5	7,5
14 Zyrjanka	65 44	150 54	13,0	15,6	12,0
15 Mys Uzlen	66 10	169 50	2,0	5,8	5,4
16 Hirnej	67 20	168 14	6,7	10,9	7,9
17 Anadyr	64 47	177 34	5,4	10,8	9,6
18 Mys Smidta	68 55	179 29	1,5	4,0	2,9
19 Ostrov Četyrehstolbovoj	70 38	162 24	0,7	2,3	2,0
20 Ostrov Kotelnyj	76	137 54	—0,2	2,5	2,0

The weather stations close to the Last-Glacial emerged shelf areas in southern Barents Sea (Fig. 16) show relatively high summer temperatures (1, 3 and 5). As discussed in Chapter 13 the air circulation during the maximum of the Last Glacial may have been such as to cause the decrease of mean air temperatures in high latitudes to be less than in lower latitudes. Moreover, circumstances in the southern Barents Sea may have been similar to those in NE Greenland with a high frequency of dry *föhn-like* winds (see 2.3). The mainland station 6 in the Kara Sea area shows fairly high summer temperatures, whereas the marine station (7) clearly shows the cooling effect of the Arctic Ocean. During the maximum extent of the ice sheets, a quite considerable shelf area of the Kara Sea may have been dry land. This area must have been surrounded on three sides by thick ice-sheets. It must have had a very dry arctic climate with a high frequency of bright weather. Hence, summer temperatures may have been well above zero.

Station 8 is just outside the area which was covered by two coalescent ice sheets during the Last Glacial. As it lies outside the Last-Glacial tundra zone (see Fig. 1a) Last-Glacial summer temperatures cannot have been more than

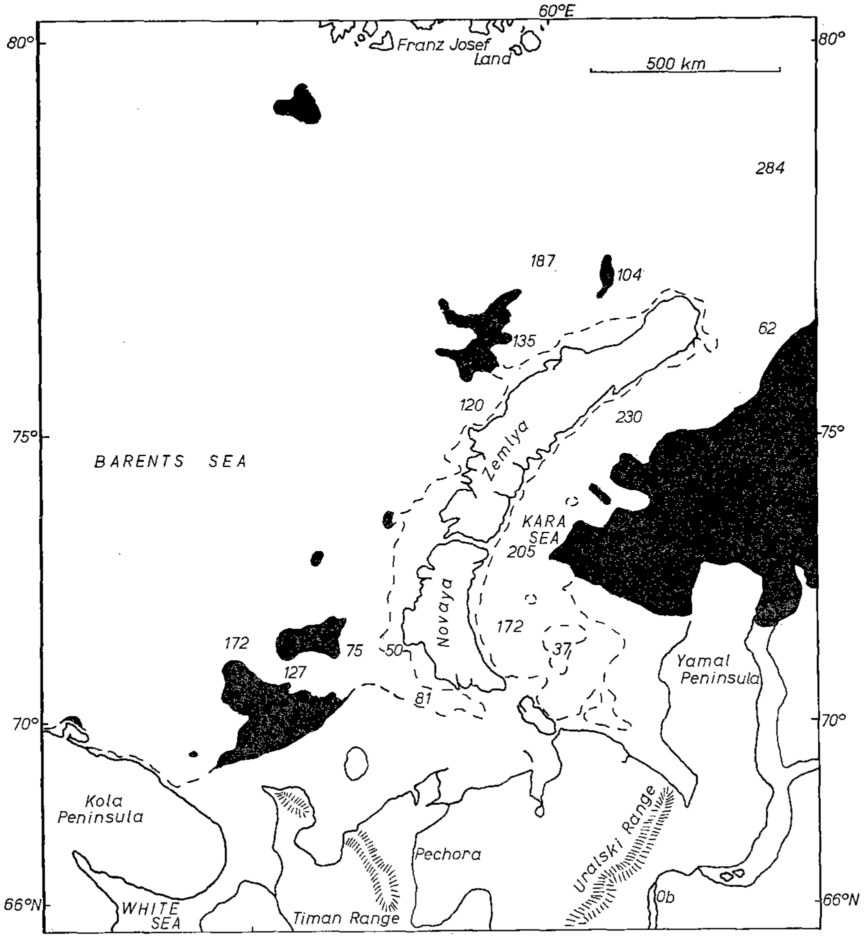


FIGURE 16. Barents Sea and Kara Sea.

Black areas = present shelf areas of less than 50 fathoms depth, which were possibly ice-free land during the maximum of the Last Glacial. Depth in fathoms.

— — — = 50 fathom isobath.

a few degrees below the present ones. The decrease was certainly less than 6° C.

In eastern Siberia the weather stations show large local differences in summer temperatures. Here too, the contrast between mainland stations and those on coasts or on islands is striking. During the maximum of the Last Glacial a very large shelf area must have been dry land, shifting the coast line a thousand kilometres northwards. This circumstance must have intensified the continental character of the Last-Glacial climate in eastern Siberia, with very dry and fairly warm summers.

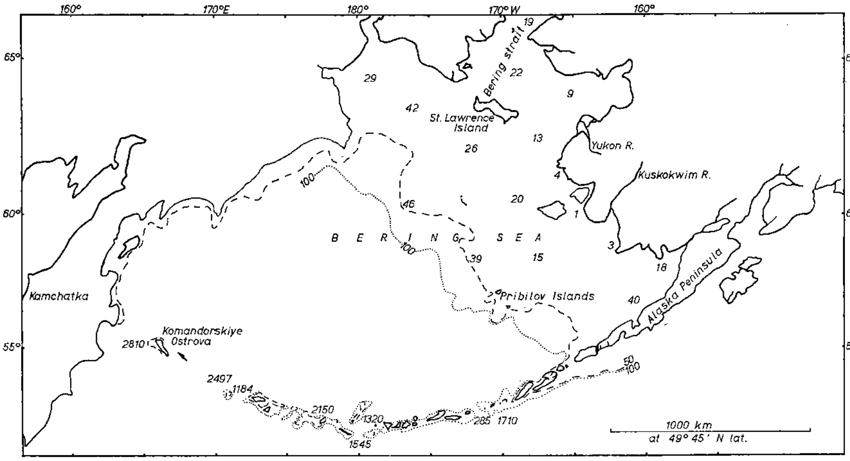


FIGURE 17. Bering Sea.
Depth in fathoms.
— — — = 50 fathom isobath. ······ = 100 fathom isobath.

10. Bering Sea area

This area comprises easternmost Siberia, unglaciated Alaska and Yukon, and the continental shelf less than 90 metres deep off the northern coasts of these regions and of Bering Strait and Bering Sea (Fig. 17).

10.1. CONTINENTAL SHELF

The continental shelf was certainly emergent during the maximum of the Last Glacial as may be deduced from the present depths and concluded from submarine rivervalleys, and the present distribution of species of fresh water fish on both sides of Bering Strait (WALTERS 1955). As a result of the important study of the flora of this area by HULTÉN (1937) it may be concluded that the Bering Sea region was an important refuge area for a considerable number of plant species during the Last Glacial.

Discussion. The following circumstances may have had a considerable influence on the surface temperatures of the Last-Glacial Bering Sea:

(a) The emergent Bering Strait blocked cold water and pack ice from the Arctic Ocean.

(b) The eustatic lowering of sea-level considerably reduced the size of the straits between the Aleutian Islands (Fig. 17). This must have prevented large scale drifting of icebergs originating from outlet-glaciers of southern Alaska and of the south coasts of the Aleutians into Bering Sea.

Both circumstances must have had a favourable effect on the surface temperatures of the sea water, and, hence, on the climate. On the other hand, the narrow straits in the Aleutian range must have limited the flow of relatively warm Pacific water into Bering Sea. It is impossible to evaluate the combined effect to these circumstances.

10.2. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

Stations 1,2 and 9, lying on the arctic coast, have low summer temperatures at present (Table 7). During the maximum of the Last Glacial the north coast was shifted far to the north. South of the Last-Glacial arctic coast there was a large area of dry land, with a maximum south-north extension of 1600 to 1700 km. Southwesterly winds must have prevailed in the adjoining Alaska area during the Last Glacial (see 11.3). If these winds prevailed to the same extent across the flat emerged Bering Sea shelf area, they must have been warmed by the soil surface and may have had a favourable effect on the temperatures along the arctic coast. Therefore, even in the northern Bering Sea area summer temperatures may have been high enough for plants and animals to live during the Last Glacial.

Table 7 shows that the inland stations (3, 6) have fairly high summer temperatures. Undoubtedly the large area of Bering Sea shelf, emerged land during the maximum of the Last Glacial, made summer temperatures increase by blocking arctic sea water and heating the air. Therefore, I assume that Last-Glacial summer temperatures were only slightly lower than they are now, so that plants and animals could survive in the Bering Sea area. This is confirmed by recent studies by PAUL A. COLINVAUX (written comm. 1967).

TABLE 7

PRESENT SUMMER TEMPERATURES IN THE BERING SEA AREA
Weather Bureau U.S.A., Dep. of Commerce 1944, *World Meteorol. Organization* 1962.

	Monthly average		
	June	July	Aug.
1 Barter Island	1,2	5,2	4,4
2 Barrow	0,6	3,9	3,3
3 Fairbanks	14,7	15,4	12,4
4 Kotzebue	6,6	11,5	10,3
5 Nome	7,7	9,7	9,4
6 Bethel	10,9	12,6	11,3
7 St. Paul Island	4,9	7,5	8,7
8 Anadyr	5,4	10,8	9,6
9 Mys Smidta	1,5	4,0	2,9

11. Canadian Arctic Archipelago

11.1. INTRODUCTION

The Glacial Map of Canada (1958), compiled from many sources of geological information and air photograph interpretation, shows that the northwestern islands of the Canadian Arctic archipelago were not overrun from the south by the Laurentide inland ice during the Last

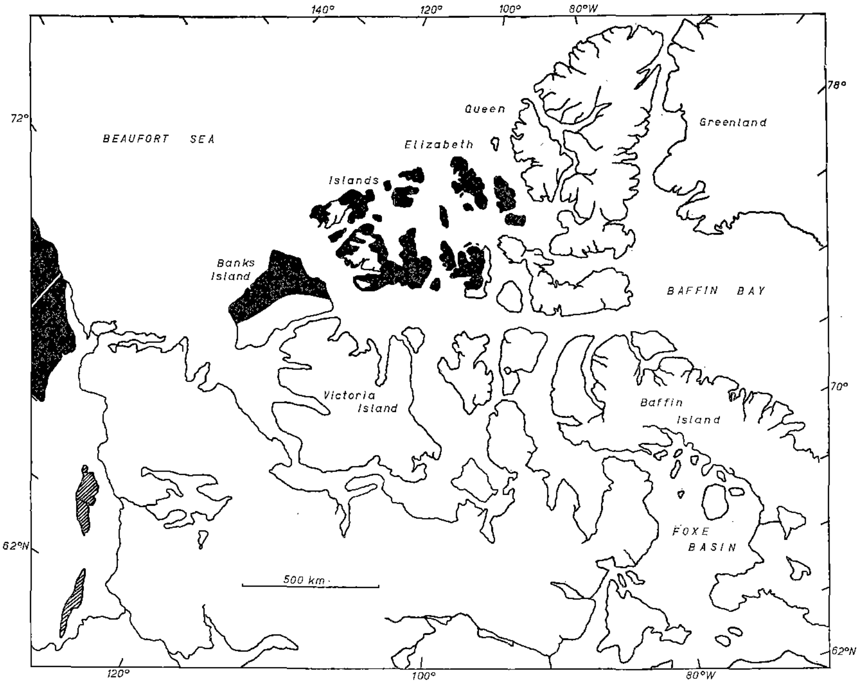


FIGURE 18. NW Canadian Arctic Archipelago and part of N Alaska. *Black areas* = unglaciated during the Last Glacial. *Hatched area* = probably unglaciated during the Last Glacial (GLACIAL MAP OF CANADA 1958).

Glacial. Some of the islands were partly covered by an independent ice sheet or by a perennial snow cover (Fig. 18).

There is evidence from radiocarbon dated organic remains found in recessional moraines that the retreat of the Laurentide inland ice from the Canadian Arctic occurred approximately at the same time and at the same rate as it did in the Great Lakes region to the south.

11.2. EVIDENCE OF ICE-FREE REFUGE AREAS

There is evidence that the ice-free areas in the north-western Canadian Arctic Archipelago were refuge areas for hardy plants and animals throughout the Last Glacial.

11.2.1. *Palynological evidence*

Peat from western Banks Islands contained pollen of birch in addition to that of tundra plants. Willow twigs from the peat were radiocarbon dated over 38,000 B.P. (No 1 (GSC)—26; CRAIG & FYLES 1960: 10). The peat layer (here given the number 4) overlay the following succession, numbered 3 to 2 from top to bottom:

3. Stony material, which may constitute a glacial deposit, possibly Pre-Wisconsin, or else be merely colluvium.
2. Pockets of pond silt with peat containing the remains of trees suggesting a warmer climate than at present. (The tree species are not mentioned.) Possibly the peat was formed in an interglacial time. Its radiocarbon age was over 35,000 B.P.

Discussion. The peat from the uppermost layer (4) is not compressed and, hence, was not overridden or covered by ice. The radiacarbon age supports the inference from geomorphological investigations that the western part of Banks Island was not glaciated during the Wisconsin. The peat of layer 4 may date from the Last Glacial or from the Last Interglacial. Still, since it remained undisturbed, it is hardly likely to be older than Wisconsin (over 70.000 years).

11.2.2. *Evidence from subfossils*

Plant debris from depth 4.5 ft in a 5 ft layer of alluvium overlying sand terrace on SW coast of Banks Island (71°40′ N lat., 123°50′ W long). were dated by radiocarbon method 10,660 ± 170 B.P. (GSC—240). The dated layer yielded bones of muskox (*Ovibos moschatus*) (DYCK, FYLES & BLAKE 1965).

Discussion. The phases of retreat of the Laurentide inland ice in the Canadian Arctic are clearly marked by recessional moraines and have been dated with radiocarbon method. From these data it is clear that the Laurentide inland ice retreated in the north approximately at the same time and at the same rate as in the southern periferal areas in the Great Lakes region (CRAIG 1965, CRAIG & FYLES 1960, DYCK & FYLES 1963) The plant remains dated 10,660 ± 170 B.P. must be from plants growing on the site immediately after the local retreat of the Laurentide ice. At that time the Mackenzie River Delta area and the eastern islands of the Canadian Arctic Archipelago were still covered by inland ice. Therefore, plants and animals could not have immigrated into the Canadian Arctic Archipelago after the local retreat of the ice, but must already have been present in the immediate vicinity of the inland ice. But then the muskox must have been present there at least since the beginning of the Last Glacial. If the muskox could live in the NW Canadian Arctic throughout the Last Glacial, there must have been plant life, and other animal life as well.

Plant growth immediately after the retreat of the local ice has also been established on Bathurst Island. Here basal organic matter with a radiocarbon age of 9,200 B.P. contained seeds and leaves of plants which do not occur on Bathurst Island at present, but are restricted either to more southerly or to more easterly islands in the archipelago. This suggests that conditions on Bathurst Island may have been more favourable to plant growth and peat formation in early postglacial time than they are to-day (Blake 1964: 5). In this connection I refer to paragraph 13 in which I suggest that refuge areas in high latitudes might have had relatively high temperatures when the inland ice sheets had their maximum extension. This assumption is in agreement with the time and rate of melting of the Laurentide inland ice in the Archipelago during Late-Glacial times.

11.2.3. *Phytogeographical evidence*

From the description of the flora of the Western Canadian Arctic Archipelago by Porsild (1955) the following facts are to be considered evidence for the survival of a number of plant species in the Western Canadian Arctic Archipelago during the Last Glacial:

(a) The occurrence of 33 higharctic circumpolar plants predominantly in scattered isolated areas. If these plants had migrated to the archipelago in postglacial time the distribution patterns would have been different from what they are now. Most of these species at present occur as far north as land goes.

(b) The occurrence of 42 arctic-alpine circumpolar species with nearly the same distribution pattern as the group referred to under 1.

(c) The occurrence of 26 Arctic Archipelago endemics, adapted to a dry continental climate. All but one have their main area of distribution in the Archipelago.

(d) The occurrence of a number of higharctic Amphi-Atlantic species, still largely occupying territory that was probably never glaciated at all.

According to Porsild (1955) four more groups of species may have survived the Last Glacial in the archipelago, but I consider this as less certain.

Phytogeographical evidence has also been given by Hultén (1937) on the basis of distribution maps of c. 2000 plant species from the flora of the Bering Sea region. Hultén arranged the species in equiformal areas of distribution from which he derived maps of progressive equiformal distribution areas. With the aid of isochores, lines bordering areas with the same number of species, he found centres of distribution. Some of the centres are geographically isolated; the species concerned are arctic and arctic-alpine elements. These centres are considered to have been refuge areas during the Last Glacial. The plant species may have survived within the areas or in the close vicinity. Some of the centres are situated in the north-western Canadian Archipelago.

Discussion. The flora of the *Canadian Arctic Archipelago* as a whole has a great affinity to the *Alaska-Yukon* flora. If the pre-Wisconsin flora of the Archipelago was wiped out during the Last Glacial, the present flora must have immigrated in postglacial time. However, at present there is a sharp floristic boundary at the Mackenzie River. To the west of it there is a flora regarded as old by Porsild (1955) because it is quite varied, with high percentages of isolated species and endemics. Moreover, the plant communities in the unglaciated areas of Alaska-Yukon seem to be at their climax. The great age of the flora west of the Mackenzie River is attributed by PORSILD (1955) to the fact that large areas in Alaska and Yukon were not glaciated during the Last Glacial.

Eastward of the Mackenzie River the mainland was certainly glaciated during the Last Glacial. This glaciated area has at present a young flora, which is inferred from the low percentage of endemic forms and the relatively few species of Asiatic or Cordilleran affinity (PORSILD 1955). On the contrary, the flora of the Western Canadian Arctic Archipelago has many affinities with the Asiatic flora. This may be a result of a primary geographical relationship or else it may be attributed to post-glacial spreading of plant species from Alaska and Yukon to the western Arctic Archipelago. However, in that case it is not clear why these plants did not spread across the Mackenzie River towards the east (PORSILD 1955).

It should also be remarked that the drawing of distributional maps highly depends on the degree of taxonomic splitting or lumping. If a taxonomist uses a narrower species concept his distribution maps will inevitably show more small isolated areas. If, on the other hand, a taxonomist lumps previously recognized species, maps based on his taxonomy will rather show large continuous distribution areas. Though HULTÉN (1937) and POLUNIN (1959) both prefer a wide species concept, the latter lumps more forms together than does HULTÉN; e.g. POLUNIN's *Arctostaphylos alpina s.l.* (POLUNIN 1959:XIII) includes *A. rubra* and *A. erythrocarpa* of other authors. Consequently, *A. alpina s.l.* has a larger distribution than *A. rubra* (HULTÉN 1937:62). The same applies to *Astragalus australis s.l.* (including *A. aboriginorum* and *A. richardsonii*).

The degree of endemism recognized in a critical area depends amongst other things upon the species concept of the scientist working in the area. Thus, one taxanomist may distinguish a fair number of endemics, whereas another finds none at all.

As regards endemism in the Arctic, POLUNIN (1950) remarks that endemism does not necessarily indicate isolation or survival, but may even indicate the opposite, as in some cases endemics may be of hybrid origin.

Moreover, a high proportion of arctic plants "run into" each other so intricately in some part or other of their ranges that it is difficult to discern where in the maze of available phases one species stops, and the next begins (POLUNIN 1959:XIII). Therefore, endemism in arctic plants is difficult to evaluate.

Isolated species may be characteristic of limy soils, but restriction to particular areas may also be due to dispersal by wind or birds, possibilities, which, according to POLUNIN (1960), are often underestimated (see also paragraph 5.1.3). PORSILD (1955) in his study of the vascular plants of the Western Canadian Arctic also points to the part played by lithological and edaphic factors and by dispersal agents in the distribution of plants. Finally, in judging the merits of distribution patterns of plant species in the Canadian Arctic Archipelago it should be stressed that the area is not as yet very well known. This is well illustrated by the fact that during a biological investigation of Prince of Wales Island (MANNING & MACPHERSON 1961) 55 species of plants were collected. When identified by PORSILD, he found that 46 of these species had not been recorded from the island before.

A recent study of the flora of parts of the northwest of *Queen Elizabeth Islands* led SAVILE (1961) to the conclusion that the present flora of this area has resulted from recent immigration. He based his opinion on the following characteristics of the flora:

(a) The number of species is small (49).
(b) There are no endemic species, in contrast to more southern parts of the Canadian Arctic Archipelago.
(c) The local distribution of several species and their occurrence in small colonies suggest that they have reached this region only recently.
(d) Numerous species known to occur all over the Canadian Arctic Archipelago are absent.

Hence, SAVILE rejects the idea that the northwestern Queen Elizabeth Islands were ice-free refuge areas for plants during the Last Glacial. If there was a refuge area for plants in the Canadian Arctic Archipelago it must have been in western Banks Island (SAVILE 1961).

In spite of POLUNIN's critical remarks (1959, 1960) on the meaning of endemism and disjunct distribution of plants in the Arctic, he believes there is no reason to doubt that many plants persisted in unglaciated areas (the northernmost parts of Greenland and the Canadian Arctic Archipelago), in some cases probably throughout the Pleistocene, in others at least through its Last-Glacial maximum (POLUNIN 1960:162).

11.3. PRESENT AND LAST-GLACIAL SUMMER TEMPERATURES

In the area that was unglaciated during the Last Glacial the average temperature for July is now about 4° C (see especially the weather stations 5, 7, 8 and 9 in Table 8). Summer fog is generally confined to the immediate vicinity of the coast. These fogs seldom go more than 15 miles inland and probably never more than 20. In the interior of islands as large as Banks Island a considerable area is practically free from this kind of fog, which is the commonest type of arctic fogs (STEFANSSON 1942, cited by RAE 1951: 29). The coastal fogs prevent heating by direct solar radiation. Therefore, the interior of the islands may have higher summer temperatures than is recorded by the coastal weather-stations. The fairly rich vegetation inland of Prince Patric and Borden Islands as compared to the rather barren west coast may be due to geological circumstances but possibly also to the absence of fog in the interior (STEFANSSON 1942, cited by RAE 1951: 29).

If all over the world summer mean air temperatures were 6° C lower during the maximum of the Last Glacial than they are at present, all plants and animal life of the Canadian Arctic Archipelago probably became extinct. But, in the unglaciated northwestern islands the total area of sea-straits must have been reduced considerably by the eustatic lowering of sea-level. Therefore, the climate was probably more continental in character than it is at present, with relatively favourable summer temperatures. As mentioned in paragraph 11.2.2. seeds and leaves of plants growing in Bathurst Island towards the end of the Late-Glacial indicate milder conditions than to-day, contrasting with what has been observed along the southern border of the Laurentide ice sheet and in Denmark and the Netherlands. (In Denmark the average July temperature at the end of the Late-Glacial must have been 6° C lower than it is at present.) The factors which caused such relatively mild summer temperature in Bathurst Island during Late-Glacial times may also have been at work during the maximum of the Last Glacial, enabling hardy plants and animals to persist in the unglaciated northwestern Canadian Arctic Archipelago throughout the Last Glacial.

The suggestion that there were relatively high temperatures in high latitudes during glacial circumstances has been corroborated by the results of palynological investigations in Alaska. Here the difference between the present-day flora of the unglaciated areas of Alaska and that of the Late-Glacial is very small (Livingstone 1955), contrasting with the large differences that occurred in western Europe. From this it may be concluded that the Late-Glacial climate in Alaska was only some degrees colder than it is to-day.

Rather favourable climatic conditions in Alaska may have resulted from a high frequence of southwesterly winds during Wisconsin time. Evidence for the prevalence of these winds is presented by the extensive glaciation on the southern sides of Alaska Range, Brooks Range, and Mackenzie Mountains, whereas the north and northeast sides had a far more restricted glaciation-Flint 1961, Karlstrom 1961).

Table 8

Present summer temperatures in the Canadian Arctic Archipelago
Meteorol. Division, Dep. of Transport 1948, 1959, Rae 1951, *World Meteorol. Organization* 1962.

	Monthly average			Monthly average of daily max. temperatures		
	June	July	Aug.	June	July	Aug.
Holman Island	2,2	6,1	5,0	6,7	11,1	8,9
Cambridge Bay	1,1	7,7	6,7	4,4	12,2	10,0
Fort Ross	0,0	4,4	2,2	2,8	7,7	5,0
Arctic Bay	2,2	6,1	5,0	5,5	10,5	8,3
Resolute	0,6	4,6	2,9	2,8	7,7	5,5
Alert	—0,1	3,9	0,8	—	—	—
Eureka	2,7	5,7	3,8	5,5	8,9	5,5
Isachsen	—0,2	3,7	1,4	2,2	5,5	3,3
Mould Bay	0,2	4,0	1,8	1,1	6,1	3,9

11.4. Summary

There is geological evidence of ice-free areas in the northwestern Canadian Arctic Archipelago. It is highly probable that a tundra vegetation persisted here during the Last Glacial.

During the final phase of the Late-Glacial the climate in the northwestern Canadian Arctic Archipelago was possibly milder than it is at

present, in contrast to what has been observed south of the Laurentide inland ice and in western Europe.

It is tentatively concluded that during the Full-Glacial the Cordilleran and Laurentide ice sheets indirectly caused relatively high temperatures though lower than at present, in Alaska and the northwestern Canadian Arctic Archipelago, in the same way as during the Late-Glacial.

11.5. LAST-GLACIAL BREEDING BIRDS

The following criteria for species that may have bred in the northwestern Canadian Arctic Archipelago under conditions of the Wisconsin glacial, have been applied:

(a) Present breeding range of species or subspecies restricted to a region somewhere in the Canadian Arctic Archipelago.
(b) Present breeding range extending north of the July-isotherm of 5° C.
(c) Present breeding habitat on marsh land.
(d) Present food consisting of both plant and animal matter.
(e) At present either migratory or pelagic outside the breeding season.

Applying these criteria I selected the following 36 species of birds, presented in systematical order. All these species are known to breed in the Canadian Arctic to-day:

Cygnus columbianus
Anser albifrons
Anser caerulescens
Anser rossii
Branta canadensis
Branta bernicla
Somateria spectabilis
Clangula hyemalis
Falco rusticolus
Lagopus lagopus
Lagopus mutus
Pluvialis squatarola
Pluvialis dominica
Charadrius semipalmatus
Arenaria interpres
Calidris canutus
Calidris pusilla
Calidris bairdii
Calidris fuscicollis
Calidris alba
Tryngites subruficollis
Phalaropus fulicarius
Stercorarius pomarinus
Stercorarius parasiticus
Stercorarius longicaudus
Larus hyperboreus
Larus argentatus
Rhodostethia rosea
Xema sabini
Pagophila eburnea
Sterna paradisaea
Nyctea scandiaca
Eremophila alpestris
Calcarius lapponicus
Plectrophenax nivalis
Corvus corax

12. Tundra, boreal woodland or boreal forest south of the Wisconsin Laurentide ice sheet

12.1. INTRODUCTION

In order to form a clear picture of the Wisconsin events in North America it is desirable to make a subdivision of that period. Unfortunately, there is no general agreement on any of the subdivisions so far proposed. Therefore, I tentatively compiled one, mainly based on a combination of subdivisions proposed by SUEZ (1954), FLINT (1956), RUHE, RUBIN & SCHOLTES (1957), DE VRIES & DREIMANIS (1960) (Table 9).

Though a newer subdivision has been given for some areas (WRIGHT & FREY 1965: 53) the older names have been preferred for clearness'sake.

TABLE 9

TENTATIVE SUBDIVISION OF WISCONSIN PERIOD

Valders substage
Two Creeks interstadial
Cary (Mankato) substage
Tazewell-Cary interstadial
Tazewell substage
Farmdale-Tazewell interstadial
Farmdale substage
Port Talbot interstadial
Iowan substage

Inactive periglacial phenomena occur in many parts in the northern U.S.A. (excluding Alaska), mostly outside the latest Wisconsinice-border. Permafrost may have occurred locally in many places. However, the origin and climatic significance of many inactive periglacial phenomena are still open to discussion (BLACK 1964). There is abundant evidence of boreal woodland and boreal forest immediately south of the ice border during some of the substages and interstadials of the Wisconsin. It is very unlikely, that a tundra, as defined in the introduction of this study, occurred in the periglacial zone south of the Laurentide inland ice throughout the Last Glacial.

12.2. EVIDENCE OF EVERGREEN BOREAL FOREST AND BOREAL WOODLAND ALONG THE ICE-BORDER SOUTH OF THE LAURENTIDE INLAND ICE

12.2.1. *Evidence from subfossils*

At Port Talbot, on the northern shore of Lake Erie, S Ontario, wood of white spruce (*Picea glauca*) was found in interstadial beds. The second half of this interstadial has been dated 47,500 ± 250 (Gro 2597) and 47,000 ± 2,500 (Gro 2570). Fragments of wood found in till of Southwold drift overlying these interstadial beds, were dated 44,200 ± 1,500 (Gro 2580). This wood marks the end of the Port Talbot interstadial (DE VRIES &DREIMANIS 1960).

Conclusion. On the northern shore of Lake Erie inland ice advanced into a landscape with at least some trees about 44,200 B.P.

At Plum Point near Port Talbot, on the northern shore of Lake Erie, S Ontario, interstadial beds were found, covered by a drift sheet with reworked wood. The age of this wood (28,200 ± 1,500—24,600 ±1.600) marks the end of an interstadial which preliminarily has been called Plum Point interstadial (DE VRIES & DREIMANIS 1960).

Conclusion. On the northern shore of Lake Erie ice advanced into a landscape with at least some trees about 24,600 B.P.

In S and SW Ohio numerous logs have been found in groups in bedded sand and gravel of multiple till sheets. The age of the wood ranged between 27,500 and 16,600 B.P. Nearly every millenium within this range is represented at least by some logs. The wood is mainly of spruce (*Picea*) (GOLDTHWAIT 1958).

Of many logs the bark firmly sticks to the wood, which indicates that the trees were alive when they were buried by the advancing ice. This is also indicated by broken trunks that are splintered at the point of breaking; they would have had smooth surfaces if they had been dead. In addition, many trees, from different localities, show a marked decrease in the size of their year-rings during the last 60 to 100 years before they were overridden by the ice (GOLDTHWAIT 1958, BURNS 1958). The greater ringwidth agrees with the present-day annual growth of *Picea mariana* and *Picea glauca* in the boreal woodland near Knob Lake (54° N lat.), Quebec. Scattered growth of these trees is indicated by the fact that many logs were found in groups (GOLDTHWAIT 1958). Logs from other localities have year-ring sizes which fairly agree with the present annual growth of trees in the boreal forest of north central Ontario.

From these data GOLDTHWAIT (1958, 1959) and BURNS (1958) concluded that the inland ice advanced into extensive belts of living evergreen forests in which spruce (*Picea*) largely prevailed. MARTIN (1959) suggested that in some localities these woods had the character of boreal forests, in other ones that of boreal woodland, being relatively dense along drainage ways with glacial outwash, but perhaps enclosing patches of tundras on hill-tops. The climate must have been cool, almost subarctic (BURNS 1958); close to the ice border GOLDTHWAIT (1959) estimated that in central Ohio during that period of the Wisconsin the mean July temperature was c. 20°F (c. 11° C) lower than it is at present.

From a comparison with other C-14 dates it appears that this period of advancing ice may be mainly correlated with the Farmdalian. So far there are no data suggesting that any Wisconsin inland ice advanced farther south into Ohio. See map in GOLDTHWAIT (1958).

Conclusion. In S and SW Ohio an oscillating ice front repeatedly advanced into living evergreen boreal forests or boreal woodland in which spruce (*Picea*) largely prevailed during a long period between 27,500 and 16,000 B.P.

At Scranton, Iowa, tree stumps with root systems in place were found at numerous levels in a layer of silt loam, resting on Tazewell loess. One C-14 analysis from the root system of a tree in situ from the upper foot of the loam just below Cary till, yielded a date of 14,470 ± 400 (W-512). A horizontal bench in the forest bed showed as many as three to four trees per square metre. The wood was fir (*Abies*), hemlock (*Tsuga*), larch (*Larix*) and spruce (*Picea*). All over the section of the forest bed fragments of wood and gastroped shells were found concentrated along bedding planes. This suggests that the silt, containing the forest bed, is a water-laid sediment, derived from a source of early Wisconsin loess (RUHE, RUBIN & SCHOLTES 1957). Trunks of these trees, rooted in place, were bent over (though not broken) towards the south which indicates that they had been buried alive by ice advancing from the north.

At Cook Quarry, Iowa, wood was also found just below the base of the Cary till. This wood of hemlock yielded a date of 14,040 ± 1,000 (C-664) which fairly agrees with that of W-512 mentioned above. Both radiocarbon values date the earliest advance of the Des Moines lobe in the area, which is tentatively placed in the Cary substage (RUHE *et. al.* 1957). The Des Moines lobe marks the maximum southward extension of the Wisconsin inland ice in this area.

At Scranton no. 2 section, Iowa, tree stumps with root systems in situ were found in an interstadial soil developed in Tazewell loess. The wood has been dated at 13,901 ± 400 (W-517).

Conclusion. In Iowa inland ice advanced into a dense living evergreen boreal forest about 14.500 B.P., when the Cary ice reached its maximum extension.

In this paragraph it was made clear that in the initial fase of the Cary substage the ice advanced into living evergreen boreal forest. When the Cary ice retreated in N Ohio it was soon followed by a spruce and a spruce-fir association. Wood of these trees was dated at c. 13,000 B.P. According to BURNS (1958) there was no evidence of a tundra in N Ohio during that time. When the climate ameliorated the evergreen forest was presumably succeeded by a deciduous forest (BURNS 1958).

At Two Creeks, Manitowoc County, Wisconsin, the type locality of the Two Creeks interstadial forest beds, a spruce forest developed immediately after the retreat of the Cary ice. When the Valders ice advanced at the end of the Two Creeks interstadial, the forests were first flooded by a glacial lake and then covered by the inland ice. All logs of trees found in situ show signs of having been buried alive (FLINT 1956, LEOPOLD 1956, WILSON 1932). Spruce wood from the type locality of the Two Creeks Forest bed was dated at 11,130 ± 350 (Y-227) (PRESTON, PERSON & DEEVEY 1955).

Central Michigan was also covered by dense spruce and fir forests during Two Creeks (LEOPOLD 1956). In S Connecticut and N Maine there was possibly a parklandscape (LEOPOLD 1956).

In the St. Lawrence lowland, lacustrine layers were deposited immediately after the retreat of the Wisconsin ice. Marine sediments were superimposed on them. These marine sediments show evidence of at least one readvance of the ice. Based on a comparison with Late-Glacial layers in N Maine the lacustrine layers are dated at c. 12,000-11,000 B.P. Palynological analysis of the deepest lacustrine layer showed a predominance of trees (*Picea*, *Pinus* and *Betula*). The climate was subarctic (Terasmae 1960).

Conclusion. Evergreen boreal forests or boreal woodland early followed the retreating ice in Wisconsin and in the St. Lawrence lowland area at the beginning of the Two Creeks interstadial. During this interstadial evergreen boreal forests existed in Wisconsin and central Michigan, whereas there was an open park-landscape in S Connecticut and N Maine. In Wisconsin the forests could persist until they were overrun by the Valders ice c. 11,130 B.P.

From the Valders substage no macroscopic remains of plants are known except many logs from W Ohio which were radiocarbon dated at 14,500 to 8,500 B.P., thus including Valders time. Every millenium is represented by a few logs at least. One of these logs is from a tree stump rooted *in situ* in the Castalia marshes, N Ohio. It was dated by radiocarbon method at 8,513 ± 500 B.P., and thus assigned to the final fase of Valders time. During the time this tree was growing the St. Lawrence river must still have been blocked by inland ice (Goldthwait 1958).

Conclusion. In W Ohio inland ice advanced into a landscape with at least some trees about 8,500 B.P.

Summary. Trees, in many cases undoubtedly still alive, were buried by advancing ice about

44,200 B.P.	on the north shore of Lake Erie, Ontario
24,600 B.P.	on the north shore of Lake Erie, Ontario
27,500—16,000 B.P.	in S and SW Ohio, where the Last-Glacial inland ice reached its greatest extension during this period
14,500 B.P.	in Iowa, where at this time the Des Moines ice-lobes represents the greatest extension of the Last-Glacial inland ice
11,130 B.P.	at Two Greeks, Wisconsin
8,510 B.P.	in W Ohio

Trees soon followed retreating ice or grew immediately south of the inland ice border about

13,000 B.P.	in N Ohio

12,000 B.P. at Two Creeks, Wisconsin, in central Michigan, S Connecticut and N Maine.

The trees, predominantly spruce (*Picea*) must have formed evergreen boreal forest or boreal woodland along the southern border of the Laurentide inland ice during at least long periods of the Last Glacial.

12.2.2. *Palynological evidence*

Pollen diagrams almost invariably show the preponderance of AP in the layers that were deposited immediately after the retreat of the inland ice. The prevailing tree species were spruce (*Picea*) and fir (*Abies*) (GOLDTHWAIT 1959).

The NAP never indicate a plant community typical of the present-day Canadian arctic tundra.

In the base of 185 pollen profiles of Wisconsin sediments from sites situated between the Atlantic coast and 94° W long., no evidence has ever been found of a tundra south of the Laurentide inland ice during the Wisconsin glacial period (SEARS 1948).

Analyses of 28 bogs at other sites yielded evidence of forests along the southern Wisconsin Laurentide ice border. In 23 of these bogs spruce is the prevalent species (40-90% of AP), in 5 there is a spruce-fir predominance (80-90% of AP). In the Great Lakes area and in the Atlantic coastal regions pine was an early invader with spruce and fir (POTZGER 1951).

In N Maine DEEVEY (1951) investigated large sections of sediments of small lakes. The deepest sediments are invariably inorganic sediments, gradually changing into gyttja and peat at higher levels. In the oldest sediments he found a preponderance of herbaceous pollen with enormous quantities of grass and sedge pollen, with a very small portion of pollen of the shrubs of alder and willow. According to DEEVEY this preponderance of NAP, representing from 100 to nearly 600% of the forest tree pollen, can only mean that the vegetation of the period was tundra, and that the tree pollen (consisting of pine, spruce, and birch in about equal proportions, with an occasional grain of oak, beech, or hemlock) was blown from a great distance. (DEEVEY 1951: 195, 196). DEEVEY called these pollen zones the L-zones and tentatively correlated them with the Late-Glacial pollen zones of northwestern Europe. He puts the boundary between this "Late-Glacial" and the "Post-Glacial" at the final and permanent fall of the NAP to values below 100% (DEEVEY 1951: 198).

In my opinion the validity of the investigations of DEEVEY (1951) should be seriously doubted, as the number of pollen counted was far too small. In the oldest parts of the sediments with a strong preponderance of NAP, DEEVEY (1951) found very few pollen and so occasionally counted between 60 and 100 pollen grains only, or even less in five cases, the minimum being 47 (DEEVEY, 1951:182). In these counts he considers only the proportion of NAP to AP to be reliable at all (DEEVEY 1951: 182). Firstly, however, proportion of NAP to AP cannot be relied on until sufficient numbers of tree pollen have been counted. In some of DEEVEY's diagrams the indication that the NAP comprised 600% of the AP total, really means that at least 7 to 14 forest tree pollen and at most 24 — 50 forest tree pollen have been counted. Even the maximum is far below the minimum required for modern pollen analysis (FAEGRI & IVERSEN 1964).

Secondly, if the great preponderance of NAP does reflect the reality, this preponderance may be due to the strong local overrepresentation of the aquatic and swamp vegetation that may have been present along the borders of the lakes, as may be inferred from the regional physiographic situation and also by the presence in the pollen diagrams of the genera *Drosera*, *Epilobium*, *Typha*, *Lycopodium*, *Equisetum* and *Isoetes*.

In Livingstone County, Michigan, ANDERSEN (1954) made pollen analyses of clay sediments from lake deposits. ANDERSEN eliminated part of the pollen, assumed to be rebedded. The lowest portion of the pollen diagram, assigned to the final part of the Two Creeks interstadial, shows a prevalence of *Picea* (40-60% of AP), followed by *Juniperus* (10-15%) and *Populus* (5%). Among the herbs, 30-35% of the pollen total, are such species as *Artemisia sp.*, *Shepherdia canadensis*, *Elaeagnus commutata* and *Saxifraga triscupidata*, all indicating an open tree stand. *S. canadensis* is a low shrub now growing especially in glades in northern spruce forests, as does *S. triscupidata* which at present also grows in many parts of the Arctic. *E. commutata*, moreover, is a typical pioneer plant on dry unstable soil. The next, younger layer of the section shows a lower percentage of *Picea* (40-50%) indicating a more sparse tree vegetation which was possibly due to climatic deterioration during the Valders readvance. ANDERSEN (1954) concluded that there was a boreal woodland, a kind of parklandscape, rather than a forest during the last substage of the Late-Glacial in Livingstone County, Michigan.

ANDERSEN (1954) deals with the substage following the Two Creek interstadial. This substage used to be called Mankato, the term also used by ANDERSEN, but the name "Valders" has also been in use for this substage (see Table 9).

LEOPOLD (1956) made palynological investigations in Middletown, S Connecticut. She found that this area must have been ice-free long before the Two Creeks interval; in my opinion from the Tazewell substage onward. During a time much older than c. 13,500-12,500 B.P., up to the end of the Late-Glacial, the coldest phases are marked by a vegetation dominated by herbs (to 80% of the total pollen are NAP). The shrubs in this zone, *Salix*, *Ilex* and *Alnus*, represent up to 25% of the total pollen sum. At least in the younger herb zone, possibly of Cary age, spores of two subarctic or alpine forms of *Lycopodium* have been found. This zone is preceded by an important peak in the *Betula* curve. The *Betula* pollen are of a small type (modal size 20 μ) which LEOPOLD tentatively ascribed to the dwarf birch *B.glandulosa* with a subarctic and alpine distribution. LEOPOLD concluded that the herb zone represents a cold interval during which S Connecticut was not densely forested but had a relatively open vegetation. The spruce intervals represent warmer, but still cool intervals and were most certainly characterized by dense forest (LEOPOLD 1956: 866).

MARTIN (1958 b) analysed anorganic sediments in Chester County, Pennsylvania, an area that was never glaciated during Wisconsin but which is situated 54 miles outside the Wisconsin ice-border. The sediments of the coldest time were dated at 13,540 ± 270 and 13,630 ± 230 and, therefore, I suggest to assign them to the Tazewell-Cary interstadial or to the initial fase of the Cary substage, although MARTIN (1958 b) speaks of a full glacial time without defining it. In the pollen diagrams representing the coldest zone, the F-zone, MARTIN found a strong preponderance of NAP, sometimes up to 77% NAP against c. 16% *Pinus*, and 1-2% *Picea*. According to MARTIN this zone reflected a taiga-tundra with widely scattered spruce and pine in a grass sedge steppe. The herb dominance must represent the open vegetation in the surroundings and cannot be ascribed to the local overrepresentation of the local swamp vegetation, because there was no high percentage of ferns and *Compositae*.

MARTIN suggested that large areas with a treeless vegetation existed on the higher grounds, while a taiga-woodland occurred along the river. This type of vegetation may have had the same structure as the vegetation we find now in the area of Fort Chimo, Labrador-Ungava. In a floristic sence both vegetations were quite different, because the rich variety in heath and heathlike plants, the less frequent *Gramineae* and *Cyperaceae*, the predominance of Larch (*Larix*) and the presence of Jack pine (*Pinus Banksiana*) in the Fort Chimo area did not occur at all in the F-zone of the sediments in Chester County. From this it may be concluded that the present Canadian subarctic flora did not occur south of the inland ice-sheet in Pennsylvania during Late-Glacial time.

LIVINGSTONE & LIVINGSTONE (1958) made palynological analyses of sediments of Gillis Lake on Cape Breton Island, Nova Scotia. The inland ice retreated from Nova Scotia shortly before the Two Creeks interstadial. In the oldest pollen zones which must represent the Cary (= Mankato) substage, the following trees were found: *Betula* (18-30%), *Pinus* (up to 30%) and *Picea* (5%). *Salix* decreased from 20 to 5%, *Cyperaceae* constituted 18-30% and *Artemisia* up to 5% of the pollen sum. In these zones the initial values of *Salix* are high, which is characteristic of a tundra. On the other hand the relatively high proportions of the tree species indicate that the vegetation was not completely open and may have been a subarctic woodland. According to LIVINGSTONE & LIVINGSTONE (1958) the term "Hemiarctic vegetation" of ROUSSEAU (1952) may be applied.

During the Two Creeks, zone L2 of DEEVEY (1951), *Betula* increased to 60 a 70%, *Pinus* decreased to 5% and *Picea* to 2% of the pollen sum. *Salix* decreased further to less than 3%; *Cyperaceae* increased from 2 to 30% indicating that these pollen may have originated in a local swamp vegetation; *Artemisia* is present with less than 3%. This pollen association may represent a *Betula* forest or woodland.

During the Valders readvance, zone L3 of DEEVEY (1951), *Betula* decreased to c. 30%, *Pinus* increased to 20% and *Picea* remained 2%. *Alnus* is then present with 2-7% of AP. The percentages of *Salix* and *Artemisia* are below 3%. These tree pollen frequencies reflect almost the same type of vegetation as that occurring here during the Cary (= Mankato) substage. A sample of the youngest layer (zone L3) was dated at 10,340 ± 220 B.P.

In central Massachusetts the vegetation contributing the pollen assemblage of the Herb Zone at Rogers Lake persisted for over 2,000 years. The absence or infrequency of trees, shown by the presence of shade-intolerant herbs, the absence of macrofossils of tree species, and the relatively low accumulation rate of tree pollen, is ascribed to unfavourable climatic conditions (DAVIS, in: WRIGHT & FREY 1965).

Macrofossils of *Salix herbacea*, *Vaccinium uliginosum* and *Dryas integrifolia* from the Herb Zone of a Late-Glacial deposit at Cambridge, Massachusetts, may indicate that the vegetation bore a floristic resemblance to tundra (DAVIS, *l.c.*: 393). *Salix herbacea* and *Vaccinium uliginosum* now occur in the alpine zone of the high mountains of New England; *Dryas integrifolia* is found south of arctic America in the Gulf of St. Lawrence region on calcareous rocks and gravel (Davis, *l.c.*: 393). In the same deposit of Cambridge were the remains of a beetle *Deronectes griseostriatus*, at present a boreal species.

From the macrofossils of arctic-alpine plant species and of a boreal beetle, and the infrequency of tree pollen in the Herb Zone it may tentatively be concluded that subarctic conditions prevailed in NE USA during Late-Glacial time.

Discussion. An open vegetation occurring after the local retreat of the inland ice in areas within the outer border of the Laurentide ice sheet may be ascribed to other causes than merely a severe climate. Unstable soil, due to widespread occurrence of buried dead-ice masses, and the time needed for the immigration of trees, may have delayed the development of forests for a considerable time.

Deevey (1951) objected against the methods used by most palynologists. To his opinion the oldest deposits palynologists analysed were the deepest peat layers, not the inorganic sediments just below them, which might have reflected a vegetation without any trees preceding the spruce-fir phase. Secondly he points out that many of the investigated bogs developed in kettles of a morainic landscape that were certainly filled with dead ice for a long time. Thus the oldest peat layers do not represent the oldest vegetation, but rather the vegetation long after the retreat of the ice, when the climate had considerably ameliorated. The first objection can no longer be made, for the investigations reported by Sears (1948), Potzger (1951), Andersen (1954), Leopold (1956), Martin (1958), Livingstone & Livingstone (1958), and Davis (1958) all included inorganic deposits. As regards Deevey's second objection all depressions, sediments of which were analysed, cannot be expected to have once been filled without any exception with dead ice.

Summary. In the base of 185 pollenprofiles of Wisconsin sediments from sites situated between the Atlantic coast and 94°W long, no evidence has ever been found of a tundra south of the Laurentide inland ice during the Last Glacial.

Analyses of 28 bogs at other sites than those referred to above gave positive evidence of forests in which spruce generally dominated along the southern border of the Laurentide inland ice during the Last Glacial.

Pollen diagrams from zones of the colder phases of the Late-Glacial time reflect a relatively open vegetation. This vegetation is similar to present subarctic woodland in a structural sense, and possibly also from a floristic point of view.

In Pennsylvania there may locally have been comparatively large treeless areas on higher ground, while there may have been a taiga-woodland along the rivers during the coldest phase of the Late-Glacial time. This vegetation closely resembles the present subarctic vegetation in Labrador-Ungave in a structural sense, but not from a floristic point of view.

With one or two exceptions plant species typical of the present Canadian Arctic tundra have not been positively identified.

12.3. PERIGLACIAL PHENOMENA

Sporadic permafrost may have occurred along the southside of the Wisconsin Laurentide ice, for example in northern Illinois (FRYE & WILLMAN 1958), east-central Iowa (SMITH 1962) and in many areas of western Wisconsin during at least some time of the Wisconsin time. The frost phenomena in western Wisconsin are the same as those found in the zones of discontinuous to continuous permafrost in northern Alaska and Canada to-day. If the fossil frost phenomena were caused by the same climatic conditions the temperatures in western Wisconsin must have been 10° to 15° C lower than they are now (BLACK 1964), which is a considerable decrease. In the northeast of the United States many inactive periglacial phenomena have been recorded, which might indicate permafrost during Late-Glacial time, but there is no conclusive evidence of permafrost during earlier Wisconsin.

More or less in contrast to the presence of possible permafrost phenomena elsewhere, c. 3,000 exposures of sediments of Wisconsin age in western Ohio, indicate that here permafrost was extremely rare, if it occurred at all (GOLDTHWAIT 1959: 202).

In the northern United States ice pushed ridges are lacking, which RUTTEN (1960) ascribed to a drainage direction away from the advancing ice-front, preventing the development of a thick permafrost layer. This view is consistent with SMITH's supposition (1962) that aridity may have prevented the development of periglacial frost phenomena in west-central U.S.A.

Eight wind-abraded bedrock outcrops (HARTSHORN, cited in WRIGHT & FREY 1965) in eastern Massachusetts, Rhode Island, and eastern Connecticut showed dominant Late-Glacial wind directions from north or northeast. Only two outcrops were cut by winds from the northwest or west, the directions that would be expected at present.

Discussion. It seems clear that the problems, the origin and climatological significance of many inactive periglacial phenomena are still unsolved. The dating of many inactive forms in the United States is also uncertain. More knowledge is required before periglacial processes can be distinguished from more temperate ones (WRIGHT 1961; SMITH 1962; BLACK 1964; MAARLEVELD 1966).

At present discontinuous and continuous permafrost occurs in extensive areas in tundra zones and the zones of evergreen boreal woodland and boreal forest in North America and Eurasia. Hence, permafrost features due to more severe climates in the past need not indicate former tundra conditions.

Late-Glacial wind directions predominantly from the north or northeast in northeastern U.S.A. may be an explanation for the rather severe climatological conditions that have been inferred from palynological data of that period. These wind directions support the ideas, brought forward in paragraph 11.3 and Chapter 13, about the type of air circulation during the period of coalescent Cordilleran and Laurentide ice sheets.

Conclusion. As far as we can tell to-day, it seems unlikely that there was a continuous zone of permafrost along the ice-border south of the Wisconsin Laurentide ice at any time of the Wisconsin period and certainly not continuous in time throughout the Wisconsin.

12.4. SUMMARY

There is a fair agreement between the results of the palynological investigations and those of the study of macroscopic remains of trees. There was certainly evergreen boreal forest or boreal woodland during periods of ice advance, even during those substages when the inland ice locally reached its greatest extension. During the cold phases of the Late-Glacial time there was a boreal woodland along the ice border. In northeastern U.S.A. a nearly treeless subarctic landscape may have existed during these phases.

As the presence of the same type of boreal forest or woodland has been inferred for several substages, it is assumed that climatic circumstances during these substages did not diverge very much.

There was not a zone of arctic tundra with a continuous permafrost along the southern border of the inland ice-sheet.

The marginal zone along the southern border of the inland ice did not afford a suitable habitat for arctic tundra birds throughout the Last Glacial because:

(a) The vegetation was not sufficiently open for arctic birds.
(b) Perennially frozen ground was almost absent and hence the drainage system was quite different from what it is in the present tundra. Therefore, suitable tundra pools, lakes and swampy areas, used as breeding and feeding habitats by arctic birds, were lacking.
(c) The climate was too mild for arctic birds.

(d) No coastal habitat was available for the numerous littoral and marine arctic birds.
(e) The absence of the long arctic days in summer.

This leads us to the conclusion that the present arctic birds of North America must have survived the Wisconsin time in tundra regions of either:

(1) *the Bering Sea area, including the ice-free areas of Alaska* (*Chapter* 10)
(2) *the northwestern Canadian Arctic Archipelago* (*Chapter* 11)
(3) *in Greenland* (*Chapter* 2)
(4) *on possible ice-free areas off the coast of New Foundland and Labrador* (*Chapter* 4 *and* 3)

The occurrence of a comparatively large number of species or subspecies of birds having at present a limited distribution in the Bering Sea area, the Canadian Arctic and Greenland indicates that these birds must have survived the Wisconsin Glacial somewhere in these parts of the world (see Zoogeographical Part).

13. General circulation of the atmosphere and temperatures in high latitudes during the maximum of the Last Glacial

It may be assumed that under the influence of the large extent of inland ice the general atmospheric circulation pattern changed. The large inland ice sheets caused large cold anticyclones. These shifted the storm tracks in the direction of the equator from the centre of the ice sheets to the southern periferal zones, feeding the ice sheet there and causing further outflow to the south and east (BROOKS 1949, LJUNGNER 1949, REX 1950, SVENSSON 1959a). The inland ice sheets increased the meridional temperature gradient, causing stronger trade winds, which lowered temperatures in equatorial regions (BROOKS 1949, VIETE 1950), causing also stronger and more frequent southerly to southwesterly winds on the Pacific and Atlantic, which, on their turn, increased the speed of the warm northerly ocean currents in both oceans. Hence, the ocean currents had less time to cool and reached northern latitudes with relatively high temperatures (PETTERSSEN 1949). Therefore, the combined effect of the higher frequency of strong south to southwesterly winds and the relatively warm northward flowing ocean currents may have been that refuge areas in high latitudes had relatively mild climates. The lowering of temperatures was very probably less in arctic regions than at middle and lower latitudes (ANGSTRÖM 1949, BROOKS 1949, WILLETT 1949, REX 1950) (see also 11.3). Consequently the general drop of temperature of 6° C (FLINT 1961), which has been inferred from various data (Last Glacial tree limit, periglacial phenomena, palynological data) may be too large for the arctic regions during the maximum extent of the ice. As distinct from the temperature relations during the maximum extent of the inland ice, the arctic and subarctic regions may have been very cold during initial stages of the Last Glacial when a different type of general circulation may have prevailed, for instance type C of WILLETT &

SANDERS (1959: 192-193). But then, northern biota, especially higharctic species could, if necessary, easily have found extensive ice-free areas more to the south.

In summary: The period with the maximum extent of inland ice was not necessarily that with the lowest temperatures in the northernmost refuge areas. There may have been a considerable time lag between the period with optimum circumstances for the initial development of ice sheets and the time of the maximum extension of the ice (WILLETT 1950). During the latter the ice sheets may have grown on the southern periferal parts as a result of excessive precipitation, whereas in the northern parts the ice may have been shrinking, not only as a result of the shifting of the feeding area southwards, but also of an increased ablation in the north.

For microclimates occurring in arctic regions I refer to SÖRENSEN's investigations in NE Greenland (Paragraph 2.3).

14. Displacement of centres of heavy glaciation

During the development of inland ice sheets the centres of ice outflow must have gradually shifted their positions. Therefore, the large regions with inland ice sheets may all have been covered by ice during the Last Glacial, though not simultaneously. It has long been assumed that the westside of the Scandinavian mountains was heavily glaciated during initial phases. During a later phase the ice divide shifted to the east. Formerly this fact was attributed to the deposition of snow by westerly winds across the completely snow and ice filled western valleys (ENQUIST 1916). In recent years LJUNGER (1949) studied the glacial development in the South Chilian Andes and in Scandinavia. He concluded that during the Last Glacial the glaciation in both areas started with a heavy mountain glaciation, followed by an ice sheet to the west of the mountains, due to prevailing westwinds. In a later phase the ice divide shifted to the east of the present watershed in Scandinavia. LJUNGER (1949) ascribed this to a change in atmospheric circulation. He assumed that at that time the polar anticyclone extended as far south as southern Scandinavia. Hence, cyclonic storms were forced to follow a more southern tract. These moved round southern Scandinavia and caused eastwinds to drop their moist content in the Baltic areas. At the same time the ice in western Norway shrank to such an extent that, according to LJUNGER (1949), the northwestern parts of Norway were certainly ice-free. By that time the continental glaciation had its greatest extension to the east and south. During the alpine stage of the Scandinavian glaciation the ice had its greatest extension in the north.

The above picture of a change in the circulation pattern of the atmosphere during the Last Glacial under the influence of the developing ice sheets is similar to that of BROOKS (1949); REX (1950), and VIETE 1950) (see 13).

14.1. SHIFTING OF REFUGE AREAS

The aim of this work is to find those areas where plants and birds may have found refuge areas during the Last Glacial. From what was said above it may be clear that the possible refuge areas may have shifted, not only from north to south during the initial phase, but also in other, even opposite directions, a.o. by secondary effects on the climate by the developing ice sheets. This shifting of the refuge areas complicates matters even more. On the other hand, through this shifting plants and animals had a much greater chance of survival.

15. Ocean currents

The distribution of glacial marine sediments in the northwestern Pacific and in the Atlantic between Newfoundland and Ireland indicates that a North Pacific and a North Atlantic current probably flowed very much as they do at present (BRAMLETTE & BRADLEY 1940, MENARD 1953). Along the Norwegian coast there was a current to the north during the time the Oslofjord region, Denmark and Skåne (S. Sweden) were covered by inland ice. This is proved by frequent findings of rhomb-porphyry, larvikites and tönsbergites in samples from the shelf of W Norway down to a depth of 620 m (occurring in the Oslofjord area only), and of flint originating from Denmark and Skåne. These rock types must have been dropped through the melting of drifting icebergs (HOLTEDAHL 1955). The northernmost area where rhomb-porphyry has been found is Andøy, Vesterålen.

It is assumed that both ocean currents had lower temperatures than at present. Between Newfoundland and Ireland the North Atlantic Drift was never completely covered by drifting ice (BRAMLETTE & BRADLEY 1940). Along the west coast of Canada and Norway many icebergs must have originated. Nevertheless the sea was not completely choked by ice as is proved by the frequent occurrence of rock types transported by icebergs from southern Scandinavia far to the north. A large amount of meltwater may have covered the surface of the currents completely. Nevertheless the relatively warm currents were not without influence because the greater part of the icebergs stuck into the warm salt water below the supposed thin surface layer of cold meltwater. Therefore, the icebergs were not only transported northwards but they melted rapidly, both events preventing the coastal seas from becoming completely blocked by ice. Hence, indirectly, the possibly submerged warm ocean currents still had a large influence on the climate. The same assumption is made for the situation along the west coast of southern Greenland and along the coasts of Iceland.

16. Some physiographical features of the possibly ice-free shelf areas

For the theory of the possibility of relatively mild temperatures in high latitudes during the maximum extent of the inland ice I refer to Chapter 13, and for the influence of relatively warm sea currents to Chapter 15. Taking into account the considerations discussed in these chapters and also the present summer temperatures I assume that hardy plants and animals may have survived on the emergent shelf areas (Fig. 3, 4, 5, 6, 14, 15, 16 and 17).

From these maps it may be inferred that many glaciers ended on the emergent shelf. Hence, large braiding meltwater streams may be assumed. In the coastal waters many outlet-glaciers ended. Cold fresh melting-water rose to the surface of the sea at the calving front of these glaciers, causing an abundance of pelagic organisms; this formed rich feeding grounds for surface feeding birds, as was proved at present for Fulmars and Kittiwakes at the calving front of glaciers in West Spitsbergen by STOTT, HARTLEY & FISHER (1936).

On the flat shelf areas tundras with many ponds and lakes may be presumed to have existed, offering breeding and feeding habitats for many kinds of Anatidae. Off-shore there were islands of different size, some of which fairly large. At least in Iceland and along the Norwegian coast stacks on the shelf and steep mountain slopes on the present islands or on the mainland, locally ice-free, offered breeding sites for some species of birds, even above glaciers, as at present can be observed in Greenland and Spitsbergen.

B. ZOOGEOGRAPHICAL PART

17. Introduction

For a detailed analysis the arctic species of swans, geese and ducks (*Anatidae*) were selected. This group seemed very suitable for the aim of this study on the following grounds:

(a) arctic *Anatidae* have representatives in each of the distributional groups a-h mentioned in Chapter 1,

(b) 38 percent of the arctic *Anatidae* show some form of geographical variation,

(c) the group comprises both higharctic and lowarctic forms.

In the following chapters the Last-Glacial breeding grounds of the geographical forms of the arctic *Anatidae* are placed in the potential refuge breeding grounds detected in the Physical Geographical Part of this study. These Last-Glacial breeding grounds are arranged in the vicinity of the present breeding ranges of the species and subspecies studied. Whenever this proved appropriate Last-Glacial breeding grounds have been searched for along the present migration route (for instance in *Anser albifrons flavirostris*).

LIST OF SPECIES OF ARCTIC ANATIDAE

Cygnus columbianus — panarctic
Anser albifrons — panarctic
Anser erythropus — subarctic
Anser fabalis — boreal-panarctic
Anser caerulescens — panarctic
Anser rossii — panarctic
Anser canagicus — lowarctic
Branta canadensis — temperate-boreal-panarctic
Branta leucopsis — panarctic
Branta ruficollis — subarctic-lowarctic
Branta bernicla — panarctic
Polystica stelleri — lowarctic
Somateria mollissima — boreal-panarctic
Somateria fischeri — lowarctic
Somateria spectabilis — panarctic
Histrionicus histrionicus — boreal-lowarctic
Clangula hyemalis — panarctic
Bucephala islandica — boreal-lowarctic

For taxonomy and nomenclature I mainly used DELACOUR (1954-64).

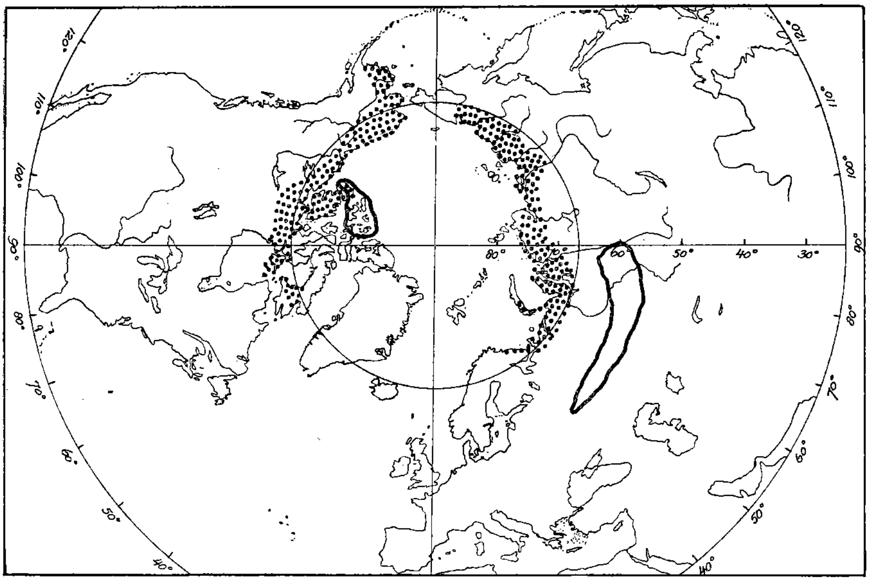


Figure 19. *Cygnus columbianus* (Ord). *Stippled area* = present breeding range. *Solid lines* = borders of Last-Glacial breeding grounds.

18. **Cygnus columbianus** (Ord)-Bewick's and Whistling Swan (Fig. 19)

A panarctic species, breeding at present between the July-isotherms of 12° and 2° C.

Two isolated and clearly morphologically differentiated subspecies are recognized:

bewickii - northern Russia and Siberia, from Kola Peninsula to the Kolyma River.
columbianus - from Alaska to Baffin Land.

The subspecies *jankowskii* is recognized by some authors (a.o. Alpheraki 1904, Delacour 1954) but according to others this race, though probably being part of a clinal variation, is not valid (a.o. Tugarinov 1941, Johansen 1956, Vaurie 1965, Portenko, *in litt.* 1966).

During the Last Glacial there were opportunities for regular breeding grounds in the following refuge areas:

bewickii — E, WS, ES
columbianus — NB, CA

Discussion

C. c. bewickii and *columbianus* may either be regarded as belonging to one species, as was done by Delacour (1954) and suggested by Voous (1960) and followed here, or else be considered a superspecies.

Palearctic *bewickii* is a lowarctic bird, breeding at present between the July-isotherms of 12° and 5° C. Nearctic *columbianus* is panarctic, breeding at present between the July-isotherms of 9° and 2° C.

During the Last Glacial important disjunctions in the circumpolar breeding range were caused by:

(a) The Greenland ice sheet.
(b) The North Atlantic.
(c) The Scandinavian ice sheet.
(d) The combined effect of the coalescing ice caps on Taimyr Peninsula and the Putorana Mountains, and the boreal forest extending far northward into eastern middle Siberia (possibly separating western and eastern populations of *bewickii*).
(e) The Laurentide inland ice reaching the Arctic Ocean in the Mackenzie Delta area (separating the present races *bewickii* and *columbianus*).

RECONSTRUCTION OF GLACIAL HISTORY

Judging by the holarctic extent of the present breeding range, the species probably already had a circumpolar distribution before the Last Glacial.

As *bewickii* is a lowarctic bird its Eurasiatic populations must have retreated southwards to find refuge breeding grounds in the extensive low tundras of Europe and western Siberia. Since these populations are lowarctic, it is not likely that they survived on the emerged shelf areas farther north than at present.

Some populations of *bewickii* may have found refuge breeding grounds in eastern Siberia too. The isolation between western and eastern Siberia was complete, which may have caused some geographical differentiation. As a rule E Siberian birds are at present a little larger than W Siberian ones. In postglacial times the Eurasian population moved northwards, at the same time spreading eastwards and westwards. At present there is a disjunction between the breeding ranges of *bewickii* and *columbianus* in easternmost Siberia from Kolyma River to W Alaska, where according to PORTENKO (*in litt.* 1966) the only swan known nesting at present is *C. cygnus*.

C.c. columbianus may have found refuge breeding grounds either in the north-west Canadian Arctic Archipelago, or in the northern Bering Sea area. The following evidence favours the first possibility:

(a) *C.c.columbianus* is panarctic.
(b) The present distribution covers extensive areas of the Canadian Arctic (see a.o. map in LINDUSKA 1964: 159).
(c) The main migratory route is one of the interior Pacific Flyways, following in autumn the route east of the Rocky Mountains to Lake Athabasca. From there about half of the total number of *columbianus* moves west to the coastal states of the Pacific Flyway, mainly to the Central Valley of California (cf. *A.albifrons gambelli*, *A.rossii* with nearly the same migratory route and

similarly restricted wintering grounds in California), the other half moves to Chesapeake Bay and Currituck Sound on the Atlantic Coast (BANKO & MACKAY, in: LINDUSKA 1964: 157). Though occasionally large flocks of Whistling Swans follow the British Columbia coast, the majority of the western Arctic breeding swans apparently migrate first eastwards to the Mackenzie Delta, and then southwards along the migratory route mentioned above (GUIGUET 1958). During spring migration probably the same routes are taken (SNIJDER 1957). At present the main migratory route may be reminiscent of the Last Glacial when for a considerable time this route remained an ice-free corridor between the glaciers from the eastern slopes of the Rocky Mountains and the expanding Laurentide ice sheet. This corridor connected the Canadian Arctic with the areas south of the inland ice. When these ice masses had merged migrating birds may have maintained the same course, as it was the shortest route to the south across the ice sheet.

(d) The morphological differences between *columbianus* on the one hand and *bewickii* on the other are so large that a complete isolation of these forms during the Last Glacial must be assumed. If *columbianus* had survived that period in the Bering Sea area some contact with *bewickii* in north-east Siberia was possibly maintained, which would have led to less geographical differentiation than exists to-day. The Canadian Arctic Archipelago was the only available breeding area where *columbianus* was completely isolated.

In postglacial time *columbianus* spread eastwards and westwards. As has been said above a relatively large disjunction between the present breeding ranges of *bewickii* and *columbianus* exists in easternmost Siberia. This disjunction can be ascribed to these forms having so far been unable to bridge the very large gap existing between their breeding ranges at the end of the Last Glacial.

I assume no population of *C. columbianus* to have survived the Last Glacial in the Bering Sea area. This is contrary to what might be expected, since there must have been suitable breeding habitat in this area. It also seems improbable that here *C. columbianus* should have given way to other bird species in competition for breeding sites, *C. columbianus* being the largest species among arctic waterfowl unless, of course, interspecific competition with *C. cygnus* occurred. Still possibilities for an unknown geographic form of *C. columbianus* surviving the Last Glacial in the Bering Sea area should not be precluded. If it had occurred, it could have spread eastwards and westwards in postglacial times, but since disappeared from both sides of the Bering Sea. As until recently swans have been widely hunted, both on their breeding grounds and on their wintering grounds in Japan and U.S.A. (KURODA & AUSTIN 1953, SNIJDER 1957, KORTRIGHT 1958, MACKAY, in: LINDUSKA 1964), I assume this human interference to have been the cause of the extinction of *C. columbianus* in the Bering Sea area. The habit of populations breeding in the same district to follow distinct migratory routes and to concentrate in vast numbers on comparatively limited wintering grounds, makes these swans very vulnerable to wildfowl hunters and wholesale slaughter.

HYPSITHERMAL INTERVAL

During the *hypsithermal interval* low tundras did not occur in Siberia from NE Taimyr to Bering Strait. Through this, the populations of *bewickii* and *columbianus* remained separated or once more became separated, a fact which may have intensified geographical differentiation started or continued during the Last Glacial (cf. *A. a. albifrons* versus *A. a. frontalis*; *A. fabalis rossicus* versus *A.f.serrirostris*; *B.b.bernicla* versus *B.b.orientalis*).

In North America *columbianus* could still have found breeding opportunities during the hypsithermal interval, during which the boreal forest may have locally extended to the coast of the Arctic Ocean. Through this, panarctic *columbianus* may have been forced back into the Canadian Arctic Archipelago. After the hypsithermal interval, lack of time to bridge the considerable gap between the Canadian Arctic Archipelago and eastern Siberia may have been one of the causes of the disjunction between the present ranges of *columbianus* and *bewickii*.

WINTERING GROUNDS

C. columbianus is a migratory bird. The following wintering grounds are known (DELACOUR 1954, GUIGNET 1958, BANKO & MACKAY, in: LINDUSKA 1964):

bewickii	— From the British Isles to central-western Asia, mainly in Ireland and the Netherlands, and China and Japan.
columbianus	— Mainly restricted to some areas in the interior of the western U.S.A., also along the Pacific coast from southern Alaska to California, and the Atlantic coast from Chesapeake Bay to Currituck Sound.

The wintering populations of *bewickii* and *columbianus* are completely allohiemic (SALOMONSEN 1955). The Pacific and Atlantic wintering populations of *columbianus* are equally allohiemic, but they partly share the same migratory route along the Mackenzie River north of Lake Althabasca. Some of the birds using this migratory route are from Alaska, others are from the central Canadian Arctic.

19. **Anser albifrons** (SCOPOLI)—White-fronted Goose (Fig. 20)

A panarctic species, breeding at present between the July-isotherms of 10° and 4°C. Four recent subspecies are recognized (DELACOUR 1954), one of which is an isolated form:

flavirostris — W Greenland.

The three other forms are of continual clinal variation:

albifrons — north Russia, northern west and middle Siberia.

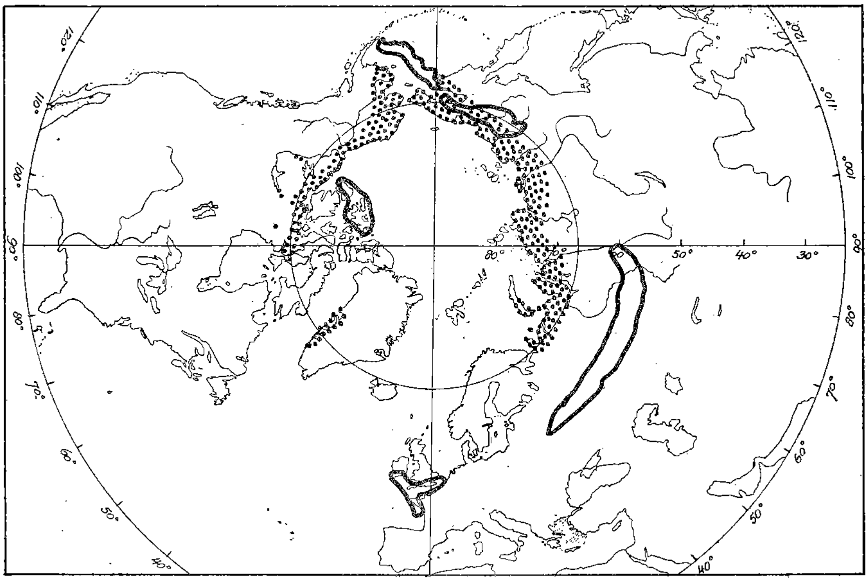


FIGURE 20. *Anser albifrons* (Scopoli). *Stippled area* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

frontalis — northern east Siberia and northwest North America.
gambelli — somewhere in the Canadian Arctic

During the Last Glacial possibilities for regular breeding grounds have existed in the following refuge areas:

flavirostris — WE
albifrons — R, WS
frontalis — ES, B
gambelli — CA

DISCUSSION

The western limit of the pre-Weichselian Eurasian breeding range was presumably situated east of Kola Peninsula, as the species probably avoided mountainous Scandinavia, preferring low tundras, as it still does to-day. From this Eurasian breeding area it retreated to the south while part of its most westerly population found new refuge breeding grounds in W Europe. It is not likely that populations of the White-fronted Goose settled in the low tundras along the N and W coasts of Norway, which remained ice-free during the maximum of the Last Glacial (see 7.2., Fig. 14). It is more natural that they were gradually driven to the S and SW than that they should have made a sudden leap across the ice sheet towards the coasts of Norway.

During the maximum of the Last Glacial important disjunctions in the still circumpolar breeding range were caused by:

(a) The Greenland ice sheet.

(b) The North Atlantic.

(c) The hilly and mountainous area between the Scandinavian and Alpine ice sheets (separating what at present are the races *flavirostris* and *albifrons*).

(d) The combined effect of (a) the coalescing ice caps on Taimyr Peninsula and the Putorana Mountains, (b) the Middle Siberian highlands, (c) the boreal forest extending far northward into eastern middle Siberia (FRENZEL 1960) (separating the present races *albifrons* and *frontalis*; cf. *B.b.bernicla* and *B.b. orientalis*).

(e) The partly glaciated Kolyma and Anadyr Mountains (separating the present races *albifrons* and *frontalis*).

(f) The Laurentide inland ice reaching the Arctic Ocean in the Mackenzie Delta area (separating the present races *frontalis* and *gambelli*; cf. white and blue phases of *A. caerulescens*, and *B.b.orientalis* and *B.b.nigricans*).

It is assumed that the North Atlantic area did not offer refuge areas suitable for the lowarctic race *flavirostris* except in the North Sea area.

RECONSTRUCTION OF GLACIAL HISTORY

The slight morphological differences between *flavirostris* and *albifrons* suggest that *flavirostris* is of western Eurasian origin and that the differentiation of *flavirostris* was caused by geographical isolation during the Last Galcial in a separate refuge area in the tundras of the North Sea region. By the end of the Last Glacial *flavirostris* followed the waning British ice sheets with its periglacial tundras and in this way gradually shifted its breeding grounds northwards, probably across Ireland and later via Faroer and Iceland to W Greenland, where it is still found to-day. Additional evidence for localizing the Weichselian breeding ground of *flavirostris* in W Europe is found in the location of its present wintering grounds in the British Isles, mainly in Ireland (ATKINSON-WILLES 1963).

However, other possibilities for the origin of *flavirostris* should be taken into account:

(a) *A.a.flavirostris* might equally well have detached itself from the easternmost American White-fronted Geese after these had spread across the North American tundras in postglacial times. Against this assumption the following objections can be made: (a) the existence of a disjunction between the breeding ranges of the easternmost North American Whitefronted Geese and *flavirostris* in W Greenland; (b) the considerable morphological differences between *frontalis* and *flavirostris*; (c) the absence of regular wintering grounds of *flavirostris* in North America.

(b) The existence of a North American race of White-fronted Goose (*gambelli*) sufficiently proves that the species occurred in the North American Arctic before the Last Glacial. If so, *A.a.flavirostris* might represent the easternmost population of this pre-Wisconsin *A.albifrons*, which managed to survive in an eastern North American refuge area. The considerable morphological differences between *flavirostris* on the one hand and *frontalis* and *gambelli* on the other contradicts this assumption. Besides, *flavirostris* is at present a lowarctic bird (SALOMONSEN 1950), whereas we have found that lowarctic refuge areas in eastern North America possibly only existed on Newfoundland Bank. Finally, if *flavirostris* derived from an American stock, present wintering grounds might be expected in North America and not exclusively in W Europe.

(c) *A.a.flavirostris* might represent an older differentiated Greenlandic population, which spread westward from Eurasia before the Last Glacial. But in that case the long isolation of the Greenlandic population from the Eurasiatic stock would probably have caused greater morphological differences than, in fact, are found.

The Weichselian breeding grounds of *albifrons* should be placed in R and WS, those of *frontalis* in ES and B. The separation between WS and ES was complete, whereas the populations in ES and B have possibly maintained some amount of contact. In postglacial time the Eurasian and Beringian populations moved northward, at the same time spreading eastward and westward. Somewhere in E Siberia the breeding areas of *albifrons* and *frontalis* merged and interbreeding occurred, giving rise to a zone of secondary intergradation in the Kolyma River area. Therefore, the present geographical variation of *albifrons* and *frontalis* is that of a stepped cline.

From the Bering Sea area *frontalis* could also spread eastward through N Alaska and into the Canadian Arctic where it could meet *gambelli*. The breeding area of *gambelli* has not yet been discovered. It is unknown whether the two forms interbreed and therefore it remains uncertain whether *gambelli* and *frontalis* are conspecific or not. The assumption that the two forms were for a long time isolated from each other is strengthened by the fact, that both forms have different wintering grounds and, where they sometimes do occur together, as, for example, in the Sacramento Valley, California, the flocks do not mix. *A.a.gambelli* seems to be the only subspecies of the American White-fronted Goose that migrates through the interior of North America. Moreover, voice and behaviour of *gambelli* are noticeably different from those of the other subspecies.

HYPSITHERMAL INTERVAL

During the hypsithermal interval low tundras did not occur in Siberia from NE Taimyr Peninsula to Bering Strait. Through this the populations of *albifrons* and *frontalis* have remained isolated from each other or they were again separated, a fact which may have intensified geographical differentiation started or continued during the Last Glacial (cf. *B.b. bernicla* versus *B.b.orientalis*). *A.a.albifrons* could still have found a breeding habitat in northern W Siberia and NW Taimyr Peninsula and on Novaya Zemlya (cf. *B.b.bernicla*).

The extension of the tundra in North America during this warmer period is not known. But there, too, the boreal forest may have locally extended to the coast of the Arctic Ocean. Through this, *frontalis* was forced to shift its breeding grounds to the Canadian Arctic Archipelago (as in *B.b.orientalis*), where there was a chance of an early contact with *gambelli*.

In Greenland *flavirostris* could easily have maintained breeding grounds during the hypsithermal interval.

Wintering grounds

A.albifrons is a migratory bird. The following wintering grounds are known:

flavirostris — British Isles, mainly Ireland.
albifrons — From the British Isles in the west to N India and Burma in the east.
frontalis — China and Japan, western U.S.A. esat to Louisiana, and south to Mexico.
gambelli — Restricted to Sacramento Valley, California, occasionally Texas and Louisiana.

The wintering grounds of *flavirostris* and *albifrons* regularly overlap in Central Wales and Lancashire, but here the flocks of both subspecies usually do not mix (Atkinson-Willes 1963).

The wintering grounds of *frontalis* and *gambelli* overlap in the Sacramento Valley, California, but as a rule the flocks keep apart and seem to prefer different feeding habitats (Delacour 1954: 108).

Hence the subspecies of *A. albifrons* are mainly allohiemic. When they are synhiemic they usually do not mix. The different winter quarters of the subspecies at least partly resulted from the Last-Glacial isolation of the subspecies, and contribute to the effect of geographical differentiation.

20. **Anser erythropus** (Linnaeus)—Lesser White-fronted Goose (Fig. 21)

A subarctic species, breeding at present between the July-isotherms of 14° and 7°C. Habitat: hilly and rocky forest tundra.

No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: R, WS, MS.

Discussion

In large areas of its present breeding range *A. erythropus* is sympatric with *A.albifrons*, but, as distinct from *albifrons*, *erythropus* prefers the higher parts of the forest tundra. Though resembling each other closely, they have apparently passed the species limit. In this connection three questions arise:

(a) Where did the isolation of *erythropus* occur?
(b) How did the different ecological preference arise?
(c) When was the species limit crossed?

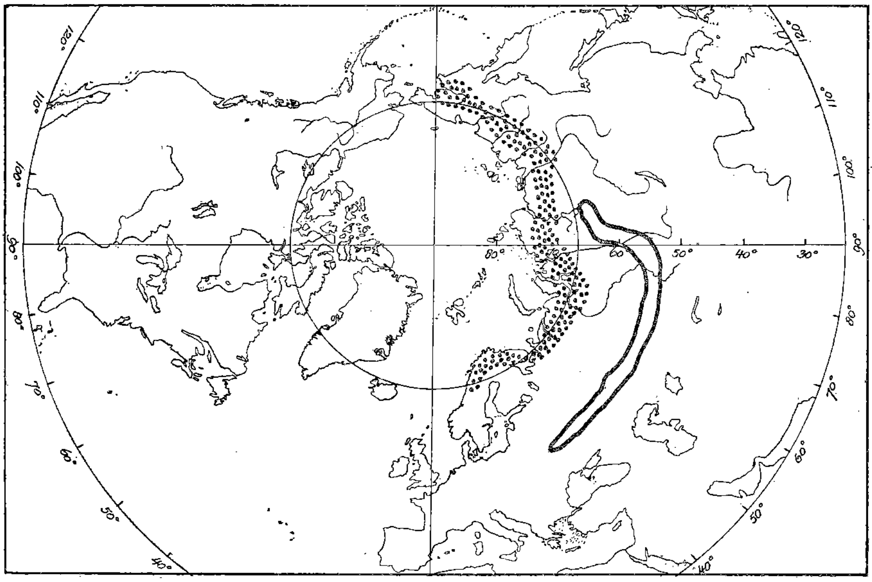


FIGURE 21. *Anser erythropus* (Linnaeus). *Stippled area* = present breeding range. *Solid line* = borders of potential Last-Glacial breeding grounds.

During long warm interglacial periods the tundra habitats of northern geese were restricted considerably, in the same way—and even more seriously—than during the hypsithermal interval. This must have resulted in the disintegration by large disjunctions of circumpolar breeding ranges, particularly during the exceptionally warm and long Mindel-Riss interglacial (BROOKS 1950).

RECONSTRUCTION OF GLACIAL HISTORY

Possibly during the Mindel-Riss interglacial referred to above members of the White-fronted Goose stock were forced into the Byrranga Mountains on Taimyr Peninsula, presumably the only region on the Siberian mainland where they could survive in a tundra forest refuge area surrounded by boreal forests. Here the presumed ancestors of *A. erythropus* adapted themselves to a mountainous and forest tundra habitat. Here they were completely isolated from the other white-fronted geese which were driven into separate eastern and western palearctic low tundras, and during optimal interglacial conditions possibly survived in the arctic islands only. This situation is comparable to what was to happen later during the hypsithermal interval (FRENZEL 1960) (Fig. 22).

During the severe Saale Glacial *A.erythropus* could certainly have found

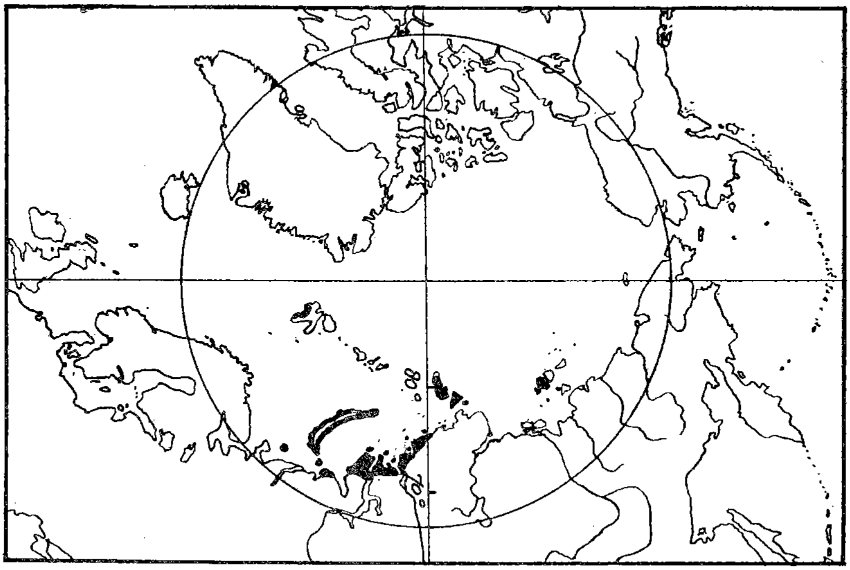


FIGURE 22. Tundras in northern Eurasia during the hypsithermal interval (*black areas*). After FRENZEL 1960.

extensive subarctic refuge breeding grounds in Eurasia, at least in the southern middle Siberian mountains.

The next interglacial (Saale-Weichsel) was not as warm as the previous one, but still *A.erythropus* may again have found refuge breeding grounds in those northern Middle Siberian mountains which were covered by a forest tundra. Here it was isolated from *A.albifrons*, if not geographically, at least ecologically. This hypothesis presupposes that the specific differentiation of *A.albifrons* and *A.erythropus* was completed during or before this period.

During the Last Glacial (Weichsel) *A.erythropus* could have found refuge breeding grounds in forest and scrub tundras in Russia, and in western and middle Siberia see map in (FRENZEL 1960).

The present absence of *A. erythropus* from North America asks for comment. If this species spread to subarctic North America during the Last Interglacial it would certainly have become extinct there, together with any other North American subarctic element (see 38.3, 38.4, and 39.3).

HYPSITHERMAL INTERVAL

The hypsithermal interval presumably forced the species back into its region of origin, viz. the Taimyr Peninsula, where it was isolated from the equally restricted range of *A.a.frontalis.*

WINTERING GROUNDS

A.erythropus winters in an area stretching from central Europe in the west to southern Japan in the east. In winter it is in large numbers found along the Caspian Sea (Delacour 1954), in the Kysyl - Agatsch Waterfowl sanctuary in Azerbaidzjan, where also the main wintering grounds of *B.ruficollis* are found (Uspenski 1965).

21. **Anser fabalis** (Latham)—Bean Goose (Fig. 23)

A boreal-lowarctic species, breeding at present between the July-isotherms of 26° and 4°C.

Two groups of subspecies are recognized: Forest Bean Geese and Tundra Bean Geese (Delacour 1954; Johansen 1941).

Within the *Forest Bean Geese* three recent subspecies of continuous clinal variation are recognized:

fabalis — Norway to Ural Mountains, between about lat. 62° and 70°N
iohanseni — western and middle Siberia, between about lat. 62° and 70°N.
middendorfi — eastern Siberia, south to Altai and northern Mongolia.

Within the *Tundra Bean Geese* three subspecies are recognized: one of them is an isolated and conspicuously differentiated island form, the other two forms are of continuous clinal variation:

brachyrhynchus — E Greenland, Iceland, Spitsbergen.
rossicus — northernmost Europe from Novaya Zemlya to Taimyr Peninsula.
serrirostris — northern E Siberia from the Khatanga River to Bering Strait.

Intermediates or mixed populations, sometimes covering extensive areas, have been recorded in all zones where Forest and Tundra Bean Geese have come into contact (Johansen 1945, 1956, Delacour 1954, Voous 1960).

During the Last Glacial there were possibilities for regular breeding grounds in the following refuge areas:

fabalis — SWE
johanseni — MS
middendorfi — M
brachyrhynchus — NW, I, WE
rossicus — R, WS
serrirostris — ES, B

DISCUSSION

During the maximum of the Last Glacial the refuge areas formed one more or less continuous breeding range, with disjunctions caused by:

(a) The boreal forest extending far northward into eastern middle Siberia (Frenzel 1960); (separating the present tundra races *rossicus* and *serrirostris*, comparable to the separation of *A.a.albifrons* and *A.a.frontalis*).

(b) The coalescing ice caps of the Werchojansk, Tsjerski and Kolyma Mountains (separating the present tundra race *serrirostris* from the forest race *middendorfi*).

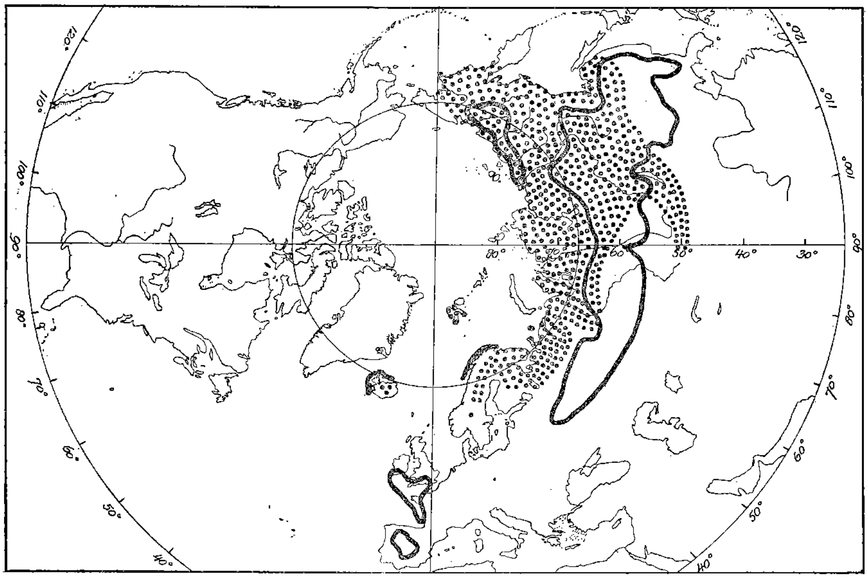


FIGURE 23. *Anser fabalis* (Latham). *Stippled area* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

(c) The lack of boreal forests in the large region between Middle Siberia and SW or SE Europe (separating the present forest race *fabalis* from all the other races).

Tundra Bean Geese probably had their refuge breeding grounds in Eurasia in the same areas as the White-fronted Geese.

RECONSTRUCTION OF GLACIAL HISTORY

The difference in morphology and ecological preference between the subspecies groups of Tundra and Forest Bean Geese are so large that the differentiation must have taken place before the Last Glacial. Therefore, it is assumed that the two groups already existed at the beginning of the Last Glacial. Within each group the development of the continental subspecies can be attributed to geographical isolation in different breeding habitats during the Last Glacial.

The insular form *brachyrhynchus*, though clearly belonging to the group of Tundra Bean Geese, differs so markedly from the other forms of Tundra Bean Geese, that its isolation must have started before the Last Glacial. The following attempt at drawing a geographical history of *A.f.brachyrhynchus* can only be tentative, but a comparison with a similar history of *A.a.flavirostris* during the Last Glacial and of *B.b.hrota* during the penultimate one, should be kept in mind.

The breeding range of *A.fabalis* in Eurasia may have extended long before the Last Glacial westwards as far as northern Scandinavian. Here the westernmost population could have adapted itself to breeding grounds in arctic-alpine areas. Presumably it could still have maintained some contact with other Tundra Bean Geese populations to the east and, possibly, with Forest Bean Geese to the south. During one of the great glaciations (Saale) this population was forced southwards and eventually found new refuge breeding grounds in the tundras of western Europe, for instance in the Channel region, where low mountains and rocky areas with steep cliffs were available. Here it was probably isolated from populations of Forest Bean Geese, though presumably it was only partly isolated from other Tundra Bean Geese populations. After this period these birds shifted their breeding grounds to isolated, probably insular, tundras in the North Atlantic area where at any rate the geographical isolation led to the geographical differentiation of *brachyrhynchus*. From here they were again driven away during a following glaciation, when, during its maximum, they possibly had found refuge breeding grounds on the shelf areas off the coasts of NW Norway and W Iceland, or again in the Channel region. As *brachyrhynchus* does not show geographical variation at present, it is assumed that the Weichselian *brachyrhynchus* population survived in one refuge area only. If it had occupied more than one refuge area, the present populations might be expected to be morphologically differentiated. On the other hand, morphological differentiation might have been prevented by an exchange of individuals between several populations in common wintering grounds.

After the Last Glacial *brachyrhynchus* shifted its breeding grounds northwards again, probably via Ireland, and Faroer to Iceland and Greenland, or from NW Norway to Spitsbergen.

However, another possibility for the origin of *brachyrhynchus* should be considered. The westernmost population of the Tundra Bean Geese occurred in northern Norway long before the Last Glacial. From here it may have been driven to Spitsbergen during the optimum of an interglacial period when all, or nearly all, Tundra Bean Geese were forced away from the Eurasiatic mainland into the arctic islands. In Spitsbergen the first stage of the geographical differentiation occurred. Its further development may have been as has been described before.

The warm Elster-Saale interglacial is the most likely period for a forced shift to Spitsbergen. If the geographical isolation took place as early as this, however, we might expect to find a greater geographical differentiation at present.

During the Last Glacial the westernmost population of the Forest Bean Geese had to retreat very far southwards, as boreal forests occurred only in the Iberian, Apennine and Balkan Peninsulas. I assume that *fabalis* retreated from Scandinavia to Spain and not to Italy or to the Balkan Peninsula, as the heavily glaciated Alps and Carpathians formed an important geographical barrier when the last boreal coniferous forests were driven from Central Europe. During the maximum of the Last Glacial the isolation between SW Europe on the one hand, and Russia and W Siberia on the other, was complete and hence *fabalis* differentiated into a clearly recognizable geographical form.

The Weichselian breading grounds of *rossicus* should be placed in the tundras of Russia and western Siberia. South of this zone there was a broad belt of forest and scrub tundra, and a narrow zone of boreal woodland in cool steppes in Kazachstan (see map in FRENZEL 1960). In these zones several pre-Weichselian geographical forms of *A.fabalis* probably could maintain contact, thus preventing further subspecific differentiation. In boreal forests in Middle Siberia Forest Bean Geese now recognized as *johanseni* may have found refuge breeding grounds during the Last Glacial. They could remain in contact with other Bean Geese populations in W Siberia, and with *middendorfi* in the eastern areas of its Weichselian breeding range. The present problematic taxonomic differentiation of *johanseni* and *middendorfi* suggests that the geographical separation of these forms during the Last Glacial was incomplete. In this connection it is noteworthy that several authors recognize one rather than two subspecies of Siberian Forest Bean Geese, using the name *sibiricus* (a.o. DEMENTIEV & GLADKOV 1960, USPENSKI 1965).

Contrary to the situation in the western palearctic the forest form *middendorfi* and the tundra form *serrirostris* occur as pure forms in extensive areas in E Siberia. This can be ascribed to partial isolation of these forms during the Last Glacial, caused by the heavily glaciated mountains in E Siberia, maintaining and strengthening the pre-Weichselian differentiation of these geese.

In postglacial times Bean Geese have all shifted their breeding grounds northwards. *A.f.fabalis* reoccupied Scandinavia and Finland. In N Russia it came into contact with other Bean Geese populations. Its mixing with northern Russian and western Siberian populations, presumably already interbreeding throughout the Last Glacial, promoted the further development of a large transitional zone of intermediate birds in this area. At present interbreeding occurs to such a degree that Russian authors do not even recognize forest and tundra races in this area. More or less pure individuals of *fabalis* occur in Finland and Scandinavia only, whereas clearly recognizable *rossicus* is only found in Novaya Zemlya and in the northernmost coastal areas of Jamal, Gyda and Taimyr Peninsulas (Delacour 1954, Johansen 1956).

The breeding ranges of *rossicus* and *serrirostris* coalesced in Middle Siberia where at present both forms intergrade (Delacour 1954).

Present intermediate forms are known between:

1. *fabalis* and *rossicus*, in forest tundra of N Russia and W Siberia (Delacour 1954, Johansen 1956); attributed to mainly postglacial secondary intergradation.
2. *fabalis* and *johanseni*, in their border areas to an unknown extent (Delacour 1954); attributed to mixing during and since the Last Glacial.
3. *rossicus* and *serrirostris*, in Middle Siberia (Delacour 1954); attributed to secondary intergradation in postglacial times.
4. *rossicus* and *johanseni*, in forest tundra of W Siberia (Delacour 1954); attributed to secondary intergradation, mainly in postglacial times.
5. *middendorfi* and *serrirostris*, at a large scale, but generally unknown where and to what extent; attributed to primary intergradation during the Last Glacial and afterwards, and partly also to secondary intergradation in those regions where they were separated during the Last Glacial and rejoined postglacially.

A.f.brachyrhynchus has remained completely isolated from the other *A.fabalis* subspecies. Intermediate forms of *brachyrhynchus* and other Bean Geese are not known.

The presence of *brachyrhynchus* in E Greenland, the only region where *A.fabalis* occurs in the nearctic, is ascribed to distribution changes during the *hypsithermal interval* when *brachyrhynchus* was probably driven from Iceland to Greenland and probably also from NW Norway to Spitsbergen. After this warmer period, part of the E Greenland populations may have returned as breeding birds to Iceland, which is on their migration route to and from W Europe.

Hypsithermal interval

During the hypsithermal interval low coastal tundras did not occur in Siberia from NE Taimyr Peninsula to Bering Strait. Through this, the populations of *rossicus* and *serrirostris* remained separated or once more became separated, which may have intensified their geographical differentiation started or continued during the Last Glacial (cf. *A.a. albifrons* versus *A.a.frontalis*, and *B.b.bernicla* versus *B.b.orientalis*). *A.f.rossicus* could still have found a breeding habitat in Novaya Zemlya, northern W Siberia, NW Taimyr Peninsula and on the islands to the north. On the adjacent mainland the slow immigration of boreal forests into the former tundra area must have promoted interbreeding between *rossicus* and Forest Bean Geese, the former still lingering on their traditional breeding grounds and adapting themselves more or less to boreal conditions. Hence, in these areas the geographical differentiation was still further diminished. Comparable to what in several instances happened during the hypsithermal interval, the differentiation into the maingroups of tundra and forest Bean Geese must have occurred during some warmer period long before the Last Glacial, when tundra forms found refuge breeding grounds in the arctic islands to the north and forest forms in mountainous areas in higher altitudes (cf. the origin of *A.erythropus*, and the relic range of *B. ruficollis*). In this connection it is noteworthy that according to DEMENTIEV and GLADKOV (1960) Forest Bean Geese, in general, have their main habitat in mountainous areas.

A.f.serrirostris could have found breeding grounds only in the New Siberian Islands, in Wrangel Island and in scattered areas in the E Siberian mountains. Here the contact with *middendorfi* may have been intensified as at that time *middendorfi* probably completely enclosed the scattered isolated mountain refuge areas of *serrirostris*.

Finally the hypsithermal interval promoted the geographical differentiation between *rossicus* and *serrirostris*, possibly also between several populations of *serrirostris* breeding in scattered areas; it maintained the isolation of *brachyrhynchus* in the North Atlantic area, but possibly diminished the separation of *middendorfi* and *serrirostris* in E Siberia and of *rossicus* and transitional southern populations in N Russia and W Siberia.

WINTERING GROUNDS

A.fabalis is a migratory bird. The following wintering grounds are known:

fabalis	— From the British Isles in the west to the Black Sea in the east.
johanseni	— From Persia to western China.
middendorfi	— Eastern China and Japan.
brachyrhynchus	— British Isles, the Netherlands, NW Germany, Denmark.
rossicus	— From Belgium in the west, possibly to China in the east.
serrirostris	— China and Japan.

The large scale interbreeding of geographical forms in this species is reflected by the geographical overlapping of wintering quarters of widely dispersed breeding populations. *A.f.brachyrhynchus*, *fabalis* and *rossicus* are synhiemic in western Europe; *A.f.johanseni* and *rossicus* are synhiemic at least in western China; *A.f. serrirostris* and *middendorfi* are synhiemic in eastern China and Japan, where they mix (DELACOUR 1954). It is not impossible that *rossicus* and *serrirostris* are also synhiemic in western China. Only *brachyrhynchus* and *fabalis* on the one hand, and *serrirostris* and *middendorfi* on the other, are allohiemic.

The populations of *brachyrhynchus* breeding in E Greenland and Iceland both winter in Scotland and England, those of Spitsbergen in Denmark, NW Germany and the Netherlands. Only very few birds ringed in Iceland during the breeding season, or in winter in Scotland, have been recorded as stragglers from the European mainland and, if so, only from sites where the Spitsbergen birds do not generally winter (WEBBE 1958). All the evidence so far collected supports the supposition that the Spitsbergen population and the Greenland-Iceland population are allohiemic units. Up till now no geographical variation has been observed (WEBBE 1958). Therefore, the separation of breeding and wintering grounds seems to be a recent development, which probably did not start until the hypsithermal interval.

22. **Anser caerulescens** LINNAEUS—Snow Goose (Fig. 24)

A panarctic species, breeding at present between the July-isotherms of 15° and 1°C. Two subspecies are recognized (DELACOUR 1954); they are isolated and clearly morphologically differentiated forms:

caerulescens	— from easternmost Siberia to Baffin Land
atlanticus	— eastern Canadian Arctic Archipelago to the Thule District in NW Greenland

Within *A.c.caerulescens* (Lesser Snow Goose) a coloured and a leucistic form occur, by some authors regarded as two sympatric species (A.O.U. CHECK-LIST 1957). According to others (DELACOUR 1954, JOHANSEN 1956, COOCH 1961, COOCH, in: LINDUSKA 1964) they are colour phases of one subspecies, in favour of which I present the following evidence:

(a) Birds of the blue phase and the white phase have the same size and proportions.
(b) They interbreed on a large scale.
(c) The offspring shows intermediate forms.
(d) The offspring is fertile.

Nevertheless I will regard the two colour phases as two incipient subspecies, which have recently come into contact, on the following grounds:

(a) The range of the white phase includes much territory where the blue phase does not occur; the blue phase has a much restricted area where it does not occur alongside the white phase; apparently the two phases have different distribution centres.
(b) The blue phase nests later in the season.
(c) The clutch size of the blue phase is 1-5, whereas that of the white phase is 4-8 or 9.
(d) The behaviour on migration is not wholly similar, the white phase birds often interrupt their migration, whereas the blue phase usually makes one long non-stop flight (COOCH, in: LINDUSKA 1964).

The populations of *A.c.atlanticus* (Greater Snow Goose) consist of white birds only.

During the Last Glacial possibilities for regular breeding grounds existed in the following refuge areas:

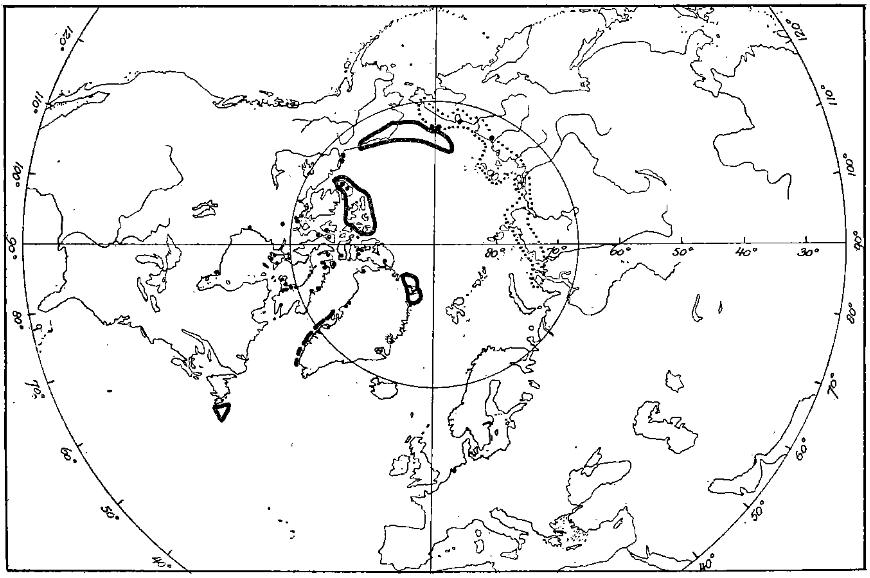


FIGURE 24. *Anser caerulescens* Linnaeus. *Dots* = present breeding distribution. *Dotted line* = borders of supposed former breeding range in Eurasia (USPENSKI 1965). *Solid lines* = borders of potential Last-Glacial breeding grounds.

caerulescens: white phase — NES, NB, NA
blue phase — CA
atlanticus — WG, NG, NF

DISCUSSION

During the maximum of the Last Glacial disjunctions in the breeding range were caused by:

(a) The Laurentide inland ice reaching the Arctic Ocean in the Mackenzie Delta area (separating the present white phase *caerulescens* and blue phase *caerulescens*; cf. *A.albifrons* and *B.bernicla*).

(b) The ice cap in NE Arctic Canada, together with Strait Davis (separating blue phase *caerulescens* and *atlanticus*).

RECONSTRUCTION OF GLACIAL HISTORY

The great similarity in morphology and life habits of the white and the blue phase *caerulescens* and of *atlanticus* suggests that their differentiation through geographical isolation occurred only recently, presumably during the Last Glacial. As the differentiation between the blue and white phase *caerulescens* is comparatively slight, they may not have come to be separated until the maximum of the Last Glacial, when the Laurentide ice sheet reached the Arctic Ocean in the Mackenzie Delta area. Before this maximum they could have maintained contact along the arctic coast of the mainland between northern Alaska and the western Canadian Arctic Archipelago.

The present distribution of white phase *caerulescens* and its former wide distribution in E Siberia (JOHANSEN 1956, USPENSKI 1965) suggest its glacial survival in NE Siberia and the Bering Sea region. Additional evidence for localizing the Wisconsin breeding grounds here is found in its present migratory routes and wintering grounds which are mainly confined to eastern Asia and western North America (cf. *A. albifrons frontalis*, *B. canadensis leucopareia*, *B.c.occidentalis*, *B.c.minima*, *B.bernicla orientalis*).

The present distribution of the blue phase suggests its Last-Glacial survival somewhere in the Canadian Arctic Archipelago. Additional evidence for localizing the Wisconsin breeding grounds here is found in its present migratory routes and wintering grounds which are mainly confined to middle and eastern North America.

The present distribution of higharctic *atlanticus* suggests its Last-Glacial survival somewhere in higharctic NE North America. The only possible higharctic refuge areas at low altitudes were situated in NE Greenland and on the emerged shelf off W Greenland. As *atlanticus* does not breed in NE Greenland at present, it presumably occupied refuge breeding grounds in western Greenland only. Additional evidence for localizing the Wisconsin breeding grounds here is found in its present migratory routes and wintering grounds which are wholly confined to eastern North America.

During the retreat of the ice sheets at the end of the Last Glacial white phase *caerulescens* had to shift its breeding grounds on the shelf in northern E Siberia and the northern Bering Sea region to the southward. Subsequently it could extend westwards, spreading possibiy as far west as Jamal Peninsula (USPENSKI 1965). Apparently its extension eastwards into the Canadian Arctic is still in progress, as new colonies have recently been established near Eskima Point, and at Cape Henrietta Maria, Ontario (COOCH, in: LINDUSKA 1964: 131). During the postglacial the white phase eventually met the blue phase, but neither the exact time, nor the place where this happened can be retraced (see also MANNING, in: MAYR 1963: 469). At present to a limited scale interbreeding is observed between Perry River and southern Baffin Land (COOCH 1961, 1963), but so far it has not given rise to a strict zone of secondary intergradation. The blue phase is increasing in numbers at the rate of two percent a year and has recently extended its breeding range westwards as far as Banks Island. The white phase is spreading eastwards (COOCH 1963). Therefore, the coalescence of the breeding ranges of blue and white phases may have taken place only recently.

At the end of the Last Glacial *atlanticus* moved northwards and westwards to its present breeding range. Probably it did not meet *caerulescens*, though COOCH (in: LINDUSKA 1964: 128) remarks that the breeding distribution of *atlanticus* partly overlaps that of *caerulescens*. However, this is contrary to what is shown on COOCH's distribution map (in: LINDUSKA 1964: 129) and to what has been published by other ornithologists (DELACOUR 1954, SNIJDER 1957, TODD 1963). At all events interbreeding between *atlanticus* and *caerulescens* has not been observed.

HYPSITHERMAL INTERVAL

During the hypsithermal interval low tundras did not occur in Siberia from NE Taimyr Peninsula to Bering Strait, and therefore the Snow Goose was expelled from this region as a breeding bird. Though it is unknown how far the tundra in North America extended during the hypsithermal interval, boreal forest, unsuitable as a breeding habitat for Snow Geese, may have locally extended to the coast of the Arctic Ocean. *A.c.caerulescens* could still have found a breeding habitat in northern W. Siberia, NW Taimyr Peninsula, the arctic islands north of Siberia, and the Canadian Arctic Archipelago (*cf. A. albifrons* and *B. bernicla*). This total range included a very large disjunction between the refuge breeding grounds in Siberia and those in the Canadian Archipelago. It is not known, whether white phase *caerulescens* had already reached the Canadian Arctic before the hypsithermal interval. However, it is possible that this interval prevented the white phase from extending into the Canadian Arctic and in this way may have postponed the coalescence of the breeding ranges of the two phases until after that period. This answers to facts mentioned before indicating that the phases have met only recently.

During the hypsithermal interval *A.c.atlanticus* could certainly have found a breeding habitat in NE North America.

WINTERING GROUNDS

A.caerulescens is a migratory bird. The following wintering grounds are known (SUTTON 1931, SNIJDER 1937, DELACOUR 1954, TODD 1963, COOCH, in: LINDUSKA 1964):

caerulescens: white phase — China, Japan, California, the Gulf Coasts from Mexico to the Mississippi, rarely east of this river.

caerulescens: blue phase — the Gulf Coasts from east of the Mississippi to Texas.
atlanticus — east coast of North America from Chesapeake Bay to
— North Carolina.

The wintering grounds of blue phase *caerulescens* and of the white phase regularly overlap along the Gulf coasts. The flocks of both forms often mix on migration and in their wintering grounds. Blue phase *caerulescens* never occur among the wintering white phase birds west of the Rocky Mountains.

Only few individuals of white phase *caerulescens* sometimes join wintering *atlanticus* on the eastcoast of North America.

23. **Anser rossii** CASSIN—Ross' Goose (Fig. 25)

A panarctic species, breeding at present between the July-isotherms of 11° and 4°C. Habitat: Island studded lakes or deltas, 8 to 40 miles inland, where the surrounding land is somewhat dry (BARRY, in: LINDUSKA 1964).

No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: CA.

DISCUSSION

In its present breeding range *A.rossii* is sympatric with *A.c.caerulescens* with which it often shares the same colony, though *rossii* seems to breed more inland than does *caerulescens*. Though resembling each other closely, they do not interbreed, not even in mixed colonies and, therefore, they have apparently passed the species limit. In this connection two questions arise:

(a) Where did the isolation of *rossii* occur?
(b) When was the species limit crossed?

RECONSTRUCTION OF GLACIAL HISTORY

I assume that a Snow Goose stock occurred in the holarctic tundras during one of the interglacial periods. During a glaciation refuge breeding grounds were restricted to the tundras of E Siberia and the Bering Sea area, and in the Canadian Arctic Archipelago. Here the geographical isolation led to geographical differentiation of western and eastern Snow Geese populations, from which respectively *A.caerulescens* and *A. rossii* would subsequently arise. The two forms, when meeting again in the Canadian Arctic during an interglacial, had passed the species limit.

During the Last Glacial *A.rossii* managed to survive in the Canadian Arctic Archipelago in approximately the same areas as those in which the geographical isolation and subspecific differentiation of blue phase

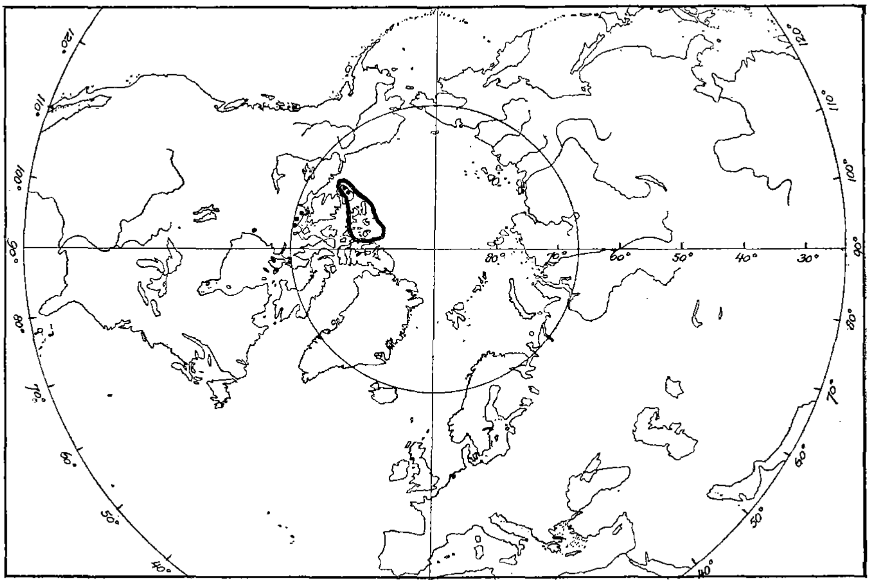


FIGURE 25. *Anser rossii* Cassin. *Dots* = present breeding distribution. *Solid line* = border of potential Last-Glacial breeding grounds.

caerulescens as well as the geographical isolation and differentiation of *A.albifrons gambelli*, *B. bernicla nigricans*, *B.canadensis hutchinsi* must have taken place.

HYPSITHERMAL INTERVAL

During the hypsithermal interval *A.rossii* may easily have maintained breeding grounds in the Canadian Arctic.

WINTERING GROUNDS

Almost the entire population of Ross' Geese (30,000 in the winter of 1962-63) winters in the interior valleys of California. A few have been observed on coasts in Louisiana and Texas in company of *caerulescens* (blue and white phases, BARRY, in: LINDUSKA 1964: 151). Ross' Geese, though often travelling together with *caerulescens* (MARSHALL 1958), are generally the earliest to leave the Arctic (BARRY, in: LINDUSKA 1964: 152). Apparently Ross' Goose is completely synhiemic with white phase *caerulescens*. In the location and restriction of its wintering grounds *A. rossii* shows a development strikingly parallel to that of *A.albifrons gambelli*.

24. **Anser canagicus** (SEWASTIANOW)—Emperor Goose (Fig. 26)

A lowarctic species, breeding at present between the July-isotherms of 10° and 7°C., on both sides of Bering Strait.

No subspecies are recognized.

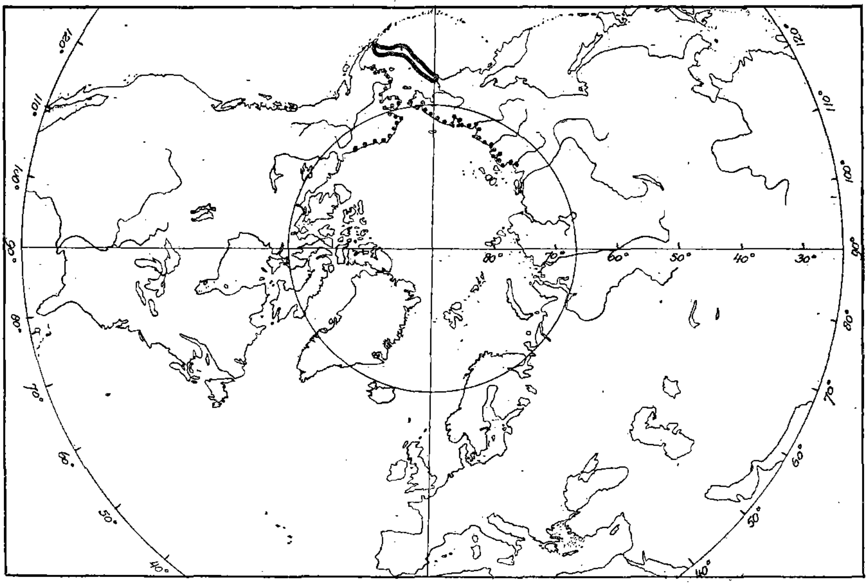


FIGURE 26. *Anser canagicus* (Sewastianow). *Dots* = present breeding range. *Solid line* = border of potential Last-Glacial breeding grounds.

During the Last Glacial possibilities for regular breeding grounds existed in: SB.

RECONSTRUCTION OF GLACIAL HISTORY

Morphologically *A.canagicus* is very similar to the snow geese and, therefore, may be more closely related to these than to any other goose species (JOHANSEN 1956). Historical details as to the origin of the species from common ancestors with the Snow Goose complex cannot be given. It is assumed that this species formation has taken place in the Early-Pleistocene and that the isolation was of the same pattern as that described for *A.rossii* and *A.caerulescens*. As several species of geese are assumed to have survived the Last Glacial in the Bering Sea area (*A.albifrons frontalis*, *A.fabalis serrirostris*, white phase *A.c.caerulescens*, *B.canadensis minima*, *B.bernicla orientalis*) inter-specific competition for breeding habitats may have occurred. According to BARRY (in: LINDUSKA 1964) these geese species nest at present in the Yukon-Kuskokwim Delta in different habitat zones, which diminishes inter-specific competition: *B.bernicla* close to shore, and then proceeding inland, *B. canadensis minima*, *A.canagicus*, and *A.albifrons frontalis*, respectively. The delineation of these zones depends upon the habitats available and the plants preferred by the species as food (Barry, in: Linduska 1964: 154). In this way the Bering Sea tundras may have harboured a large number of species of tundra birds during the Pleistocene glacial periods.

Hypsithermal interval

During the hypsithermal interval *A. canagicus* may easily have maintained breeding grounds in the northern Bering Sea area.

Wintering grounds

A.canagicus is a migratory bird, wintering from Kamchatskaya in the west to Cook Inlet, Alaska, in the east, mainly in the Aleutian Islands. At present it does not share its wintering grounds with species of the Snow Goose complex.

25. **Branta canadensis** (Linnaeus)—Canada Goose (Fig. 27)

A temperate-boreal-panarctic species, breeding at present between the July-isotherms of 25°and 3°C.

The species has a number of geographical forms, the status of which, though widely discussed, is not agreed upon. More research, especially at the breeding grounds, will be necessary to clarify the taxonomic problems (Hanson & Nelson, in: Linduska 1964). Delacour has recognized 12 subspecies. For the aim of this study I have subdivided these into four groups:

A. Eastern southern group:

canadensis
interior
maxima
moffitti
parvipes
} in North America from the eastern side of the western coastal range to the east coast, south of the subarctic region to 35°N.

The forms of this group are of continuous clinal variation.

B. Western southern group:

fulva
occidentalis
} west coast of Canada and south coast of Alaska.

The forms of this group are of continuous clinal variation

C. Aleutian group:

leucopareia
asiatica
} Kommandorski Islands and Aleutians.

The forms of this group were probably of continuous clinal variation.

D. Northern group:

minima — western Alaska.
hutchinsi — northeastern Canadian Arctic and W Greenland.

More or less isolated, morphologically differentiated forms.

B.c.taverneri is here considered an intermediate form between smaller northern and larger southern subspecies (Hanson & Nelson, in: Linduska 1964).

During the Last Glacial possibilities of regular breeding grounds existed in the following refuge areas:

Eastern southern group — south of the Cordilleran and Laurentide ice sheets east of Cascade Range and Sierra Nevada.

Western southern group — Pacific coastal region south of Cordilleran inland ice.
Aleutian group — SB
Northern group { *minima* — *B*
{ *hutchinsi* — CA

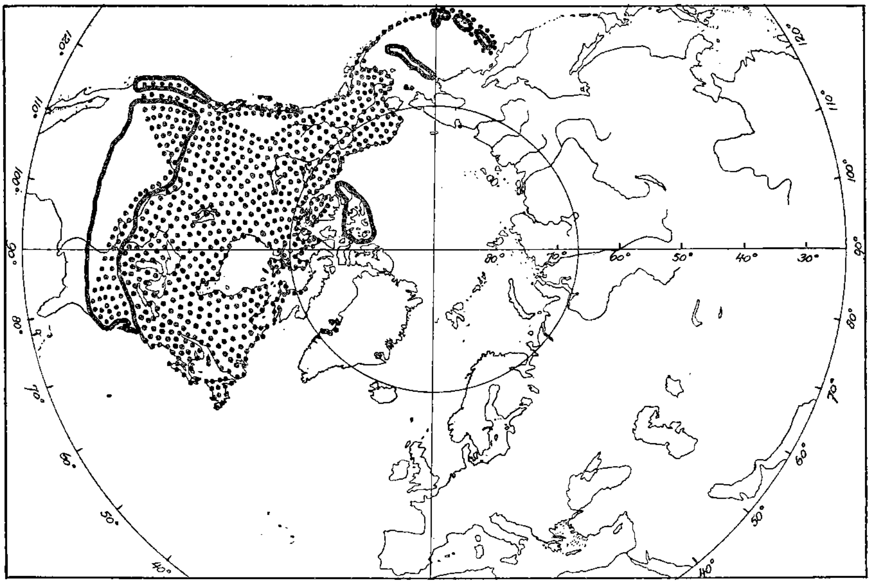


FIGURE 27. *Branta canadensis* (Linnaeus). *Stippled area* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

DISCUSSION

During the maximum of the Last Glacial ecological circumstances north of the coalescing Cordilleran and Laurentide ice sheets were certainly too severe for both southern groups to breed there regularly. South of these ice sheets there must have been ample opportunities for regular breeding in boreal and temperate climatic zones. These zones comprised different breeding habitats, ranging from coastal areas along the Pacific coast, high plateaus with numerous lakes in the Great Basin area, short and long grass prairies east of the Rocky Mountains, boreal and deciduous forests in the middle and eastern U.S.A., to marshes, sand dunes and beaches along the eastcoast. The dark rufous colour of the western subspecies may be attributed to the humid climate along the westcoast.

During the maximum of the Last Glacial cold water from the Arctic

Ocean could not penetrate southwards into the Pacific. The water of a relatively warm ocean current was concentrated along the shores of Aleutians and southern Bering Sea area. From these facts it may be inferred that a relatively mild arctic climate prevailed here even during the maximum of the Last Glacial. Hence, the Aleutian forms probably could have found refuge breeding grounds, partly in the same areas where they breed at present: the Kommandorski and Aleutian Islands.

During the maximum of the Last Glacial *minima* may have found refuge breeding grounds in the Bering Sea area, for instance in the drainage basin of the Yukon River, and *hutchinsi*, which is a panarctic subspecies, in the Canadian Arctic Archipelago.

During the maximum of the Last Glacial disjunctions were caused by:

(a) The Cordilleran and Laurentide ice sheets, separating the southern group from the Aleutian and northern groups.

(b) The remainder of the Bering sea, separating the Aleutian group from *minima*.

(c) The Laurentide inland ice reaching the Arctic Ocean in the Mackenzie Delta area and the presumed higharctic climate in northern Alaska, separating the present subarctic *minima* and panarctic *hutchinsi*.

RECONSTRUCTION OF GLACIAL HISTORY

A wide range of climates and habitats must have occurred south of the inland ice in North America during the Last Glacial, but how far they extended is still unknown and, indeed, forms a controversial issue (DEEVEY 1949, BRAUN 1951; MARTIN 1958*a*). Still this situation must inevitably have led to ecoclimatological differentiation among the boreal *B.canadensis* group. The mountain ranges in the western U.S.A. formed sharp ecoclimatological boundaries to which the relatively large morphological and ecological differences between the maritime western southern group and the continental eastern southern group may be attributed. East of the Rocky Mountains different climates and habitats, including extensive marshy and lake areas, which could have been occupied by *B.canadensis* populations, merged (see also HANSON 1965 : 46). Hence, between the geographical forms of the eastern southern group of *B. canadensis*, which have probably always been primarily ecoclimatological forms, contact was maintained and interbreeding continued. Thus the development of intermediate forms in extensive zones of primary intergradation was continued and strengthened. At present interbreeding of individuals belonging to different populations of this group is further promoted by:

(a) Different populations sharing the same migration routes and wintering quarters.

(b) Individuals and small groups tending to stray far from the normal breeding range of the subspecies.

(c) Nonbreeding birds often wandering far north of the normal breeding range of the subspecies (DELACOUR 1954, HANSON & NELSON, in: LINDUSKA 1964: 110). Interbreeding and mingling of neighbouring populations is restricted by strong family ties, return to the same breeding area every summer, and the colonial or semicolonial breeding habits (MAYR 1942: 242, DELACOUR 1954: 151).

During the retreat of the ice sheets the southern group shifted their breeding grounds northwards. The northernmost populations of the western southern group eventually met the Aleutian group in S Alaska and *minima* in W Alaska. The eastern southern group met *hutchinsi* in the central Canadian Arctic. Secondary intergradation between representatives of the southern, Aleutian and northern groups probably gave rise to the intermediate and variable form *taverneri* in large areas of Alaska. No interbreeding has been observed between the adjacent subspecies *parvipes*, which represents the eastern southern group, and panarctic *hutchinsi*.

As *asiatica* is extinct and *leucopareia* nearly so, little can be said about these subspecies of the Aleutian group. I assume this group survived the Last Glacial in refuge breeding grounds in the Bering Sea region, completely isolated from *minima*, in all likelihood in the Kommandorskie and Aleutian Islands, where they also breed at present. *B.c.minima* of the northern group also survived the Last Glacial in the Bering Sea area, possibly in the drainage basin of the Yukon River, Alaska. The complete isolation of the Aleutian and the northern group, which possibly had started already before the Last Glacial, has led to the present geographical differentiation between these groups.

When the ice sheets were waning the birds of the Aleutian group had to shift their breeding grounds just a little, to where they are at present.

The following facts may serve as evidence in favour of the assumption that *hutchinsi* survived the Last Glacial somewhere in the unglaciated western Canadian Arctic Archipelago under presumed higharctic conditions: (1) it is at present a panarctic bird; (2) it is markedly different from the other subspecies of *B. canadensis*, except *minima*, in size and proportion, indicating a long and complete isolation. If it did not survive north of the Laurentide inland ice the alternative is, that it found refuge breeding grounds south of it. In that case it would have been in continuous contact with the boreal southeastern group, which would have led to a smaller differentiation between this group and *hutchinsi* than exists at present, and besides, its panarctic character could only have developed in postglacial times, which is not likely. *B.c.hutchinsi* and *minima* resemble each other in size and proportions, and are said to show the same preference for more or less coastal habitats. Therefore, they are probably more closely related to each other than to any other form of *B. canadensis.* In the late Pleistocene history of *hutchinsi* and *minima* isolation by the Laurentide inland ice in the Mackensie Delta area must have been the prime factor for their further geographical differentiation.

Hypsithermal interval

During the hypsithermal interval all subspecies of *B.canadensis* may easily have found breeding grounds in North America. Though the extension northwards of the boreal forest during this warmer period is not known it may in some places have reached the mainland coast of the Arctic Ocean, which enabled southern boreal forms of the Canada Goose to spread as far north as this, at the expense of the ranges of *minima* and *hutchinsi.* In this way the geographical separation of *minima* and *hutchinsi* was continued and particularly the range of *hutchinsi* was considerably restricted.

The extent of present interbreeding of the races of Canada Goose in arctic Canada and Alaska is unknown.

Wintering grounds

The following wintering grounds are known (Delacour 1954, Hanson & Nelson, in: Linduska 1964, Hanson 1965):

canadensis — Atlantic Coast from Nova Scotia to Georgia.
interior — Gulf Coast from E Texas to NW Florida, and Atlantic Coast from southern New Jersey to North Carolina.
maxima — In eleven states west of Mississippi River, and in Wisconsin and Illinois.
moffitti — From southern British Columbia and NE Wyoming to California and Gulf of Mexico.
parvipes — From California to Louisiana and Mexico.
taverneri — From E Washington and E Oregon to Texas.
fulva — Non-migratory; wandering birds as far as northern California.
occidentalis — Partly non-migratory, migrating birds winter in a very restricted area in Willamette Valley, W Oregon.
leucopareia — Japan, coasts of Washington and Oregon, in California, south to NW Mexico.
asiatica — Now extinct.
minima — Mainly Sacramento and San Joacquin Valleys, California, also as far south as Mexico, occasionally in Hawaii and Japan.
hutchinsi — Oklahoma, Texas and Mexico.

The large-scale interbreeding of geographical forms in this species is reflected by the considerable geographical overlapping of wintering quarters of widely dispersed populations. Part of the *occidentals* population seems to be allohiemic in relation to all other *B.canadensis* populations. As the species comprises populations breeding from the subtropic to higharctic regions we might here have evidence of BERGMANN's rule. In the case of *B.canadensis* the smallest subspecies breed in subarctic to higharctic regions, but it should be kept in mind, that these forms spend the greater part of the year in southern areas, often to the south of forms breeding in temperate or boreal climatic zones. This applies particularly to the continental boreal form *B.c.maxima*, which is subjected to low temperatures throughout winter and therefore has attained the largest size of body.

26. **Branta leucopsis** (BECHSTEIN)—Barnacle Goose (Fig. 28)

A panarctic species, breeding at present between the July-isotherms of 7° and 2°C. No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: I and NW, SP.

RECONSTRUCTION OF GLACIAL HISTORY

The closest relative of *leucopsis* is *B.canadensis*. As the latter species is confined to North America *leucopsis* is also assumed to be of ultimate North American origin. The differences between the two species being fairly striking, the separation of *leucopsis* from the *B.canadensis* stock must have occurred a long time ago. As *B.canadensis* has no higharctic geographical forms to-day, it is assumed that *leucopsis* derives from an arctic branch of the common ancestors of *B. canadensis* and *leucopsis*. I assume that during older Pleistocene periods the Laurentide inland ice developed in the same way as during the Last Glacial. Consequently tundra birds breeding in the North American Arctic during an interglacial period could not retreat to areas south of the Laurentide ice sheet, but either survived in the Canadian Arctic Archipelago, in the Bering Sea region, or became extinct in North America. I assume that *leucopsis* developed into an arctic species north of the Laurentide ice sheet during a moderately severe ice age; that it spread from the Canadian Arctic to the North Atlantic islands during the subsequent interglacial; that it became nearly extinct in the following severe ice age, presumably during the Great Ice Age, but managed to survive that period somewhere in the North Atlantic area, where it may at least have found refuge breeding grounds in the Channel region in W Europe. After the Great Ice Age it could reoccupy the former breeding areas in the North Atlantic islands (cf. *A.fabalis brachyrhynchus*, *A.albifrons flavirostris*). During the Last Glacial

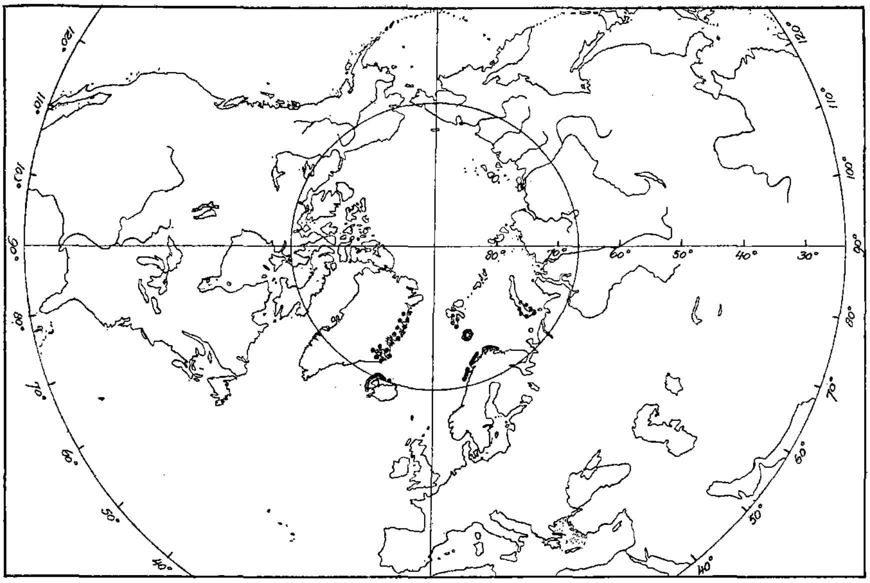


FIGURE 28. *Branta leucopsis* (Bechstein). *Stippled area* = present breeding range. *Solid lines* = border of potential Last-Glacial breeding grounds.

it managed to survive in one or more of the refuge breeding areas mentioned above and returned to the North Atlantic islands in postglacial times.

HYPSITHERMAL INTERVAL

During the hypsithermal interval *leucopsis* could still find a breeding habitat in the North Atlantic region.

The presence of *leucopsis* in E Greenland, the only region where it occurs in the nearctic, is ascribed to distribution changes during the hypsithermal interval and the time after, when *leucopsis* was probably driven from Iceland to Greenland and probably also from NW Norway to Spitsbergen (cf. *A. fabalis brachyrhynchus*).

WINTERING GROUNDS

B. leucopsis is a migratory bird. The populations breeding in E Greenland winter in Ireland and W Scotland (cf. *A.f.brachyrhynchus*), those of Spitsbergen mainly in the Solway Firth area, and the birds from the South Island of Novaya Zemlya and Vaygach in NW Germany and the Netherlands (ATKINSON-WILLES 1963, HOLGERSEN 1963). All evidence gathered so far supports the idea that the Greenland, Spitsbergen and Novaya Zemlya-Vaygach populations are generally allohiemic units. So far no geographical variation has been observed

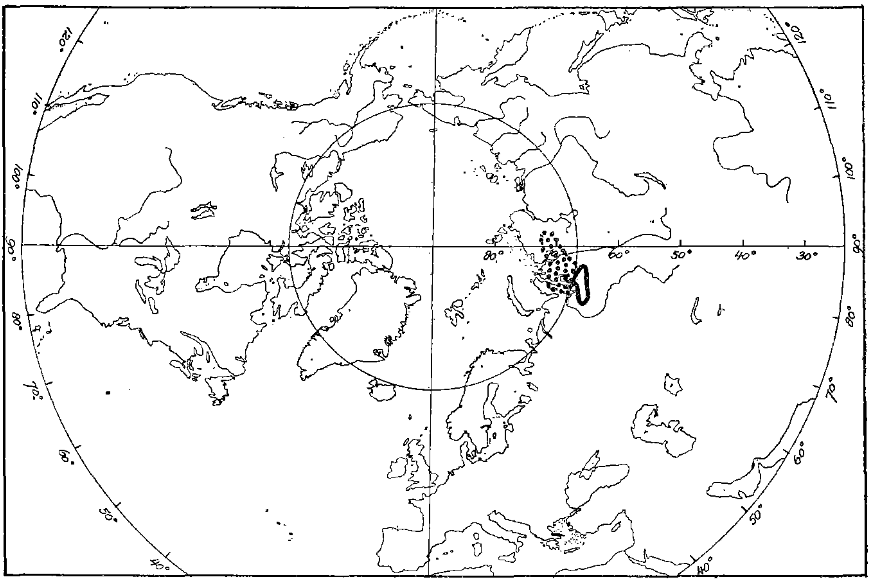


FIGURE 29. *Branta ruficollis* (Pallas). *Stippled area* = present breeding range *Solid line* = border of potential Last-Glacial breeding grounds.

(JOHANSEN 1956). Therefore, the postglacial separation of breeding grounds, and the subsequent divergence of migratory routes and wintering grounds may be a recent development, which possibly did not start before the hypsithermal interval.

27. **Branta ruficollis** (PALLAS)—Red-breasted Goose (Fig. 29)

A subarctic-lowarctic species, breeding at present between the July-isotherms of 14° and 7°C. Habitat: Scrub tundra in the neighbourhood of rivers with cliffs or steep fissured banks and bluffs (WITHERBY 1952, USPENSKI 1965).

No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: WS (south of its present breeding range).

DISCUSSION

In view of its striking morphological characters and its extremely restricted breeding range the species should be considered a relic. The total world population of *ruficollis* is estimated at 50,000 (USPENSKI 1965: 15). Its present breeding range is confined to the only area on the mainland of Eurasia where tundra and forest tundra persisted during the hypsithermal interval (FRENZEL 1960).

RECONSTRUCTION OF GLACIAL HISTORY

The morphological differences between *ruficollis* and the other *Branta* species are so large that *ruficollis* must have diverged from a common *Branta* stock, supposed to be of North American origin (see *B. leucopsis*), long before the ancestors of *B.bernicla* and those of *B.leucopsis* did so.

Nothing can be determined as to its former distribution range but it may be assumed that it used to be more widely distributed than it is at present. It may even have had a circumpolar distribution. If we assume it had acquired its present ecological preference long before the Last Glacial, different causes of its being nearly extinct can be suggested. In the nearctic it became extinct during a severe ice age, since at that time it could not find refuge breeding grounds north of the inland ice sheets (cf. *B.leucopsis*). In the palearctic it could easily survive any glacial period, as during these periods subarctic-lowarctic areas were largely available. During a warm interglacial tundras almost completely disappeared from the mainland. Hence, it could survive only in a very restricted area on the mainland (see below: hypsithermal interval.)

HYPSITHERMAL INTERVAL

During the hypsithermal interval breeding possibilities for subarctic-lowarctic birds like *B. ruficollis* and *A.erythropus* (see 20) in Eurasia were considerably limited. It is striking that the present breeding range of *B.ruficollis* nearly covers the only area where the species could have found refuge breeding grounds during the hypsithermal interval. It is generally assumed that any warm interglacial or postglacial period has played an important part in the extinction of this species and other subarctic-lowarctic breeding birds in Eurasia.

WINTERING GROUNDS

The main wintering grounds are restricted to the Kysyl-Agatsch Bird Sanctuary on the Caspian Sea in Azerbaidzjan (USPENSKI 1965). *B.ruficollis* has been fairly regularly observed on the coasts of the Sea of Azow and the Black Sea. Moreover it also used to winter in Egypt, as may be inferred from two paintings in fresco of *B.ruficollis* on the Medum panel in an Egyptian monument of 3,000 B.C. (MOREAU, in: MEINERTZHAGEN 1930: 63, 64). The Red-breasted Geese on this painting differ slightly from the present type in the colour pattern of the head and neck. From these facts it may be gathered that after the hypsithermal interval *ruficollis* still comprised two subspecies or at least had a wider distribution, the westernmost populations having since become extinct. Apart from climatological causes excessive human predation may have been another cause for its numerical decrease (USPENSKI 1965).

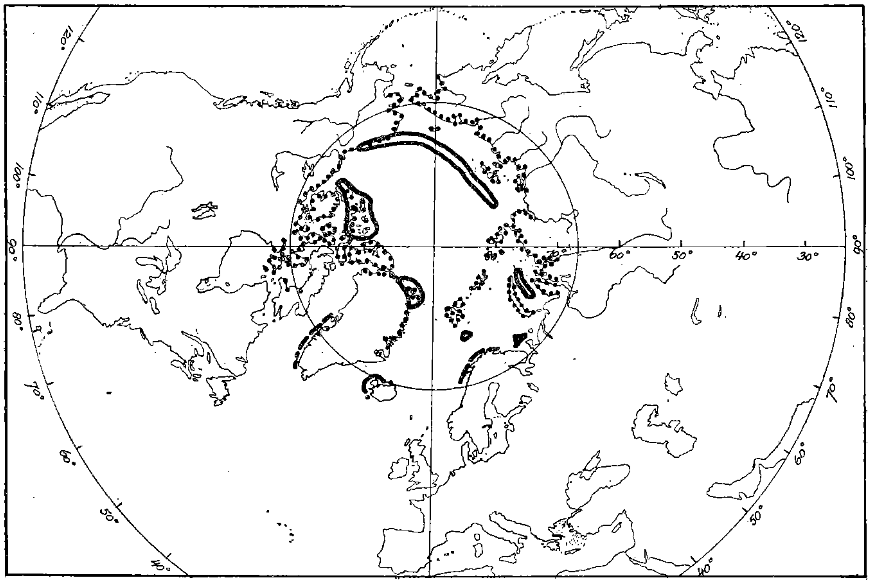


FIGURE 30. *Branta bernicla* (Linnaeus). *Dots* = present breeding range. *Solid lines* = border of potential Last-Glacial breeding grounds.

28. **Branta bernicla** (LINNAEUS)—Brent Goose (Fig. 30)

A panarctic species, breeding at present between the July-isotherms of 6° and 1°C. Four recent subspecies are recognized (DELACOUR 1954), two of which are clearly morphologically differentiated forms:

hrota — North Atlantic area, from eastern arctic Canada to northern Novaya Zemlya.
nigricans — somewhere in the Canadian Arctic, probably in the northeast of Hudson Bay, now possibly extinct.

The two other forms are of continual clinal variation:

bernicla — northernmost Russia, northern west and middle Siberia.
orientalis — northernmost east Siberia and north-west North America.

B.b. bernicla, *orientalis* and *nigricans* are dark-bellied forms; *hrota* is light-bellied.

During the Last Glacial possibilities for regular breeding grounds existed in the following refuge areas:

hrota — CA, WG, NG, I, SP, NW
bernicla — BS, KS
orientalis — NES, NB
nigricans — CA

DISCUSSION

As the species is predominantly higharctic, *B. bernicla* presumably did not breed in the relatively mild tundra regions in the southern parts of the British Isles and adjacent areas, nor along the south coast of the then emerged Bering Sea shelf.

During the maximum of eustatic lowering of sea-level the tundra extended much farther to the north on the broad northern Eurasian shelf than it does now. As *B. bernicla* is a coastal bird it was forced to shift its Eurasian breeding grounds into these unglaciated tundras, rather than to the lowarctic conditions more southward.

During the maximum of the Last Glacial the following important disjunctions in the still circumpolar breeding range were caused by:

(a) The North Atlantic.

(b) The Scandinavian inland ice reaching the Arctic Ocean between N Norway and the Barentsz Sea region (separating the present races *hrota* and *bernicla*).

(c) The coalescing ice caps on the Putorana Mountains and the Taimyr Peninsula and adjacent islands (separating the present races *bernicla* and *orientalis*; cf. *A.albifrons* and *A.fabalis*).

(d) The Laurentide inland ice reaching the Arctic Ocean in the Mackenzie Delta area (separating the present races *orientalis* and *nigricans*; cf. *A.albifrons* and *A.caerulescens*).

(e) The coalescing ice caps of Axel Heilberg, Devon and Ellesmere Island, and NW Greenland (separating *nigricans* and *hrota*).

It is assumed that Iceland and Spitsbergen did not harbour ice-free tundras of low altitude, but there may have been refuge areas on the emerged Iceland shelves and Spitsbergen Bank (See 2.2 and 6.2).

RECONSTRUCTION OF GLACIAL HISTORY

The morphological differences between the light-bellied subspecies *hrota* on the one hand and the dark-bellied forms *bernicla*, *orientalis* and *nigricans* on the other, are quite striking. Therefore, the separation between these groups must have lasted longer and therefore must have taken place earlier than that between the three dark forms. The development before the Last Glacial may have been as follows.

Within the genus *Branta* the Brent Goose is no doubt most closely related to *B.canadensis* and *B.leucopsis*. The difference between the Brent Goose and these species is so large that the former must have got separated from the common stock of the three species a long time ago and have followed an independent development since. Presumably this happened before the beginning of the independent development of *B.leucopsis*. Hence *B.bernicla* must be a descendant from an American stock which had early developed into a higharctic group and succeeded to spread westwards across the northern regions of Eurasia and eastwards to the North Atlantic during some interglacial period. As it is fairly certain that no suitable coastal refuge areas were left in N Russia and W Siberia, and possibly in the Canadian Arctic, during the Great Ice

Age the species became extinct in these areas. Evidence has been found showing that the low coasts of NE Greenland, E Siberia, the Bering Sea region, SW England and adjacent areas were never glaciated completely throughout the Pleistocene. Therefore, I assume that the ancestors of *hrota* survived the Great Ice Age in the North Atlantic region (probably in western Europe), and the common ancestor of the other subspecies in E Siberia and the Bering Sea region, both groups being completely isolated from each other. After the Great Ice Age the ancestors of *hrota* may have spread northward to the North Atlantic islands, as in *A.brachyrhynchus*, and from there westward into the Canadian Arctic. Here it may have met the geographical forms developed in E Siberia and the Bering Sea regions spreading eastward.

During the Last Glacial the ancestors of the present dark-bellied forms, originally living in the North American Arctic, survived in the Bering Sea regions (*orientalis*) and in the NW Canadian Arctic Archipelago (*nigricans*), the latter like *A.albifrons gambelli*, blue phase of *A.c. caerulescens*, *A.rossii*, *B.canadensis hutchinsi*. *B.b.hrota* managed to survive in one or more of the unglaciated areas in the North Atlantic region, where it was again completely isolated from other Brent Goose populations. This led to further divergence.

The Eurasian populations were divided by the Middle Siberian ice caps into completely separated populations, which subsequently led to the development of the western subspecies *bernicla* and the eastern form *orientalis*. A similar history is shown by *A albifrons* and *A.fabalis*. When the sea level rose again during the retreat of the ice sheets, *bernicla* and *orientalis* had to shift their breeding grounds southwards. Meanwhile they could spread eastwards and westwards and finally met in Middle Siberia. Intermediates between *bernicla* and *orientalis* have been reported among transitional or mixed populations in the Taimyr Peninsula region (DELACOUR 1954). This zone of secundary intergradiation can be located with the aid of records of breeding birds of *bernicla* eastward as far as the Chatanga River, and of *orientalis* as far westward as the Lena River (JOHANSEN 1956). A similar zone of secondary intergradation is known with regard to *A.albifrons* and *A.fabalis*.

The present breeding grounds of *bernicla* and *hrota* do not meet in N Russia. *B.b.hrota* has been observed in Kolguev Peninsula in summer, but these were summering non-breeders (SALOMONSEN 1958).

In the Canadian Arctic *orientalis* and *hrota* met in the same way after the Last Glacial. In the contact zone both forms largely keep apart but a few cases of interbreeding have been reported (DELACOUR 1954).

The rarity of interbreeding may be due to the fact that individuals of family groups are apt to keep together and do not exchange freely with individuals of other groups. Therefore, there is insufficient ground for regarding the two forms as different species as was suggested by the A.O.U. Check-list Committee (1957). Still *hrota* may be regarded to have almost reached species status in the western Canadian Arctic Archipelago.

Hypsithermal interval

During the hypsithermal interval low coastal tundras did not occur in Siberia from NE Taimyr Peninsula to Bering Strait. As a result of this the populations of *bernicla* and *orientalis* remained separated or again became separated, which may have intensified their geographical differentiation started or continued during the Last Glacial (cf. *A.a.albifrons* versus *A.a.frontalis*). *B.b.bernicla* could still find a breeding habitat in northern W Siberia and W Taimyr Peninsula and on Novaya Zemlya where it could maintain or acquire contact with *hrota.*

The extension of the tundra in North America during the hypsithermal interval is not known. But here, too, the boreal forest may have locally extended to the coast of the Arctic Ocean. This forced *orientalis* to shift its breeding grounds to Wrangel Island and to the Canadian Arctic Archipelago (as in *A.a.frontalis*), where it may have met other Brent Goose populations (*nigricans*). In N Greenland and the North Atlantic islands *hrota* could easily have maintained, or even extended, its breeding grounds.

Wintering grounds

B.bernicla is a migratory bird. The following wintering grounds are known:

hrota — Atlantic coast of North America, Ireland, England and Denmark.
bernicla — Denmark, NW Germany, the Netherlands, Belgium, France and England.
orientalis — Pacific coasts of Asia and North America.
nigricans — Atlantic coast of North America.

The *hrota* populations of the eastern North American Arctic and those of N Greenland partly follow the same migration route along the west coast of Greenland to and from Egedesminde. From there two flyways are followed, one across Davis Strait to Labrador and from there on to the eastcoast of North America, and one across the Greenland ice sheet to Angmagssalik, and via Iceland to Ireland (Lewis 1937, Salomonson 1950). Hence, these populations are allohiemic but their migration routes are partly the same. Exchange of individuals between these populations may occur on the migration route. But, as pair-formation takes place in the wintering grounds, interbreeding can only occur between birds which have lost their mates during spring migration.

The *hrota* populations of Spitsbergen and Franz Josephland seem to migrate in a nonstop flight straight to Denmark. In winter they shift their feeding grounds to NW Germany and later on to the eastcoast of England, from where they return to Denmark to start their spring migration.

The *hrota* populations of the eastern and the western North Atlantic are completely allohiemic. In combination with the separate migration routes and breeding grounds this may lead to subspecific differentiation. As this has not been observed so far, the complete isolation of the *hrota* populations may be a recent development.

B.b.bernicla migrates via the White and Baltic Seas to their wintering grounds from Denmark to France and England. In Denmark, NW Germany and in E England they occur in the same areas as *hrota*, but, at any rate in Denmark, the two subspecies keep strictly apart on separated feeding grounds (SALOMONSEN 1958). In E England they occasionally feed in mixed flocks, but in the air *bernicla* and *hrota* separate (WEBBE 1958).

In eastern North America *hrota* and *nigricans* partly followed the same spring migration route, but *nigricans* was reported to be at least two weeks earlier in spring and to be completely segregated from *hrota* (LEWIS 1937). Therefore, the two forms were presumably completely allohiemic.

B.b.orientalis migrates to the Pacific coasts of Asia and North America and is completely allohiemic with *hrota*, *nigricans* and *bernicla*.

Hence, all subspecies of *B.bernicla* are at present allohiemic (SALOMONSEN 1958).

29. **Polysticta stelleri** (PALLAS)—Steller's Eider (Fig. 31)

A lowarctic species, breeding at present between the July-isotherms of 10° and 5°C, along the arctic coast mainly from the Lena Delta to Point Barrow, Alaska. No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: SB.

DISCUSSION

The present breeding range on both sides of Bering Strait and the main wintering grounds in the Aleutian Islands indicate that the Wisconsin refuge breeding grounds should be located in the Bering Sea area. As Steller's Eider largely lives on marine food, also during the breeding season, it was essential that open coastal waters were available in its Last-Glacial breeding grounds. It is assumed that the north coast of the Bering Sea shelf area was ice-bound during the Last Glacial, whereas the south coast had open waters owing to a warm sea current from the Pacific circulation. The presumed restricted glacial breeding and wintering grounds prevented differentiation into subspecies. Though living in a relatively small area during the Last Glacial the species apparently did not lose its capacity for great wanderings outside the normal breeding and winter ranges of the species, for scattered breeding has been observed

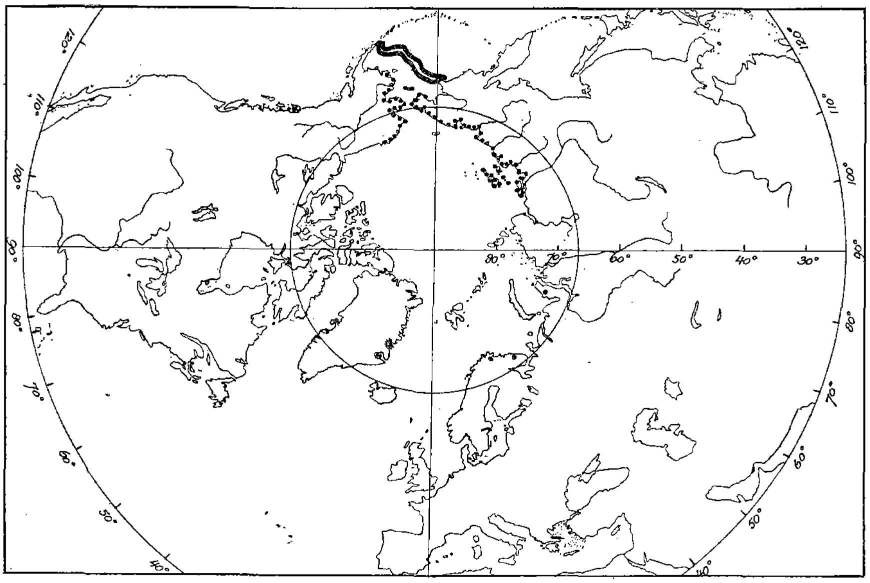


FIGURE 31. *Polysticta stelleri* (Pallas). *Dots* = present breeding range. *Solid line* = border of potential Last-Glacial breeding grounds.

as far west as Taimyr, Yamal and Varanger Peninsulas (BANNERMAN 1958, DELACOUR 1959, VAURIE 1965). Non-breeders have been regularly observed in the Varanger Fjord in summer. Outside the main wintering grounds (See below) wintering birds usually occur in the ice-free coastal waters off Kola Peninsula and N Norway, especially in Varanger and Porsanger Fjords. Most of these birds disappear in the third week of May, but their breeding grounds are still unknown (BANNERMAN 1958). These great wanderings may indicate that there was once a larger breeding range, which was considerably restricted during the ice ages, when the arctic coasts of northern Eurasia and North America were presumably ice-bound. Whenever Steller's Eider spread along these coasts during an interglacial period, it must have become extinct there in the next ice age. The only arctic coasts with open waters were in the southern Bering Sea area and possibly in the North Atlantic, but probably the species did not reach that far in interglacial periods.

The breeding range of this monotypical form indicates the same glacial refuge area as the monotypical forms *S. fischeri*, *A.canagicus*, and the subspecies *A.albifrons frontalis*, white phase *A.caerulescens caerulescens*, *B. canadensis minima*, *B.c.leucopareia*, *B.c.asiatica*, *B. bernicla orientalis*, *S.mollissima v-nigra*.

In this study the species is important because it illustrates that arctic coastal species which did not develop higharctic forms during the Pleistocene could not acquire or maintain a circumpolar breeding range but could only occupy comparatively restricted regions either in western Europe, or in Newfoundland or the Bering Sea area. During the onset of a glacial period conditions deteriorated in the far north. At the same time ice sheets developed in Scandinavia, the British Isles and North America. This prevented the species from gradually withdrawing to suitable habitats more to the south in W Europe and in Newfoundland. The only area in the northern hemisphere where a gradual southward shift of low-arctic coastal tundras occurred was in the Bering Sea shelf area.

Hypsithermal interval

The hypsithermal interval probably restricted the breeding range of *S.stelleri* to a relatively small area in the Bering Strait region, e.g. NW Alaska.

Wintering grounds

P. stelleri is a migratory bird. Its Pacific wintering grounds extend from the Kurile Islands to Kemal Peninsula in southern Alaska, mainly in the Aleutian Islands (Bannerman 1958). Its Atlantic winter resort is off the ice-free coasts of Kola and northern Norway, mainly in the Varanger Fjord, where it is fairly abundant (Bannerman 1958).

30. **Somateria mollissima** (Linnaeus)—Common Eider (Fig. 32)

A boreal-panarctic species, breeding at present between the July-isotherms of 19° and 2°C. Geographically two groups of subspecies may be recognized: an Atlantic and a Pacific group, at present completely separated from each other.

Within the Pacific group one subspecies is recognized (Delacour 1954):

v-nigra — from Chauna Bay in eastern Siberia eastward as far as Victoria Island.

The Atlantic group comprises three main subspecies with secondary intergradation in areas of recent contact:

dresseri (inclusive *sedentaria*) — mainland coasts of North America from westcoast of Hudson Bay to Maine, and New Foundland.
borealis — western and northern Atlantic, from the eastern Canadian Arctic Archipelago to Novaya Zemlya.
mollissima (inclusive *faeroensis*) — eastern Atlantic and Baltic coasts from the Netherlands to Kola Peninsula; Faeroer, Iceland and Jan Mayen.

During the Last Glacial possibilities for regular breeding grounds existed in the following refuge areas:

dresseri — NF, EA, cf. *H.h.histrionicus* (partly).
borealis — WG, I, SP, NW, BS., cf. *A.fabalis brachyrhynchus* (partly), *B.bernicla hrota*, *B.leucopsis* (partly), *H.h.histrionicus* (partly), *Bucephala islandica* (partly).
mollissima — (inclusive *faeroensis*) — WE, cf. *A.fabalis brachyrhynchus* (partly).

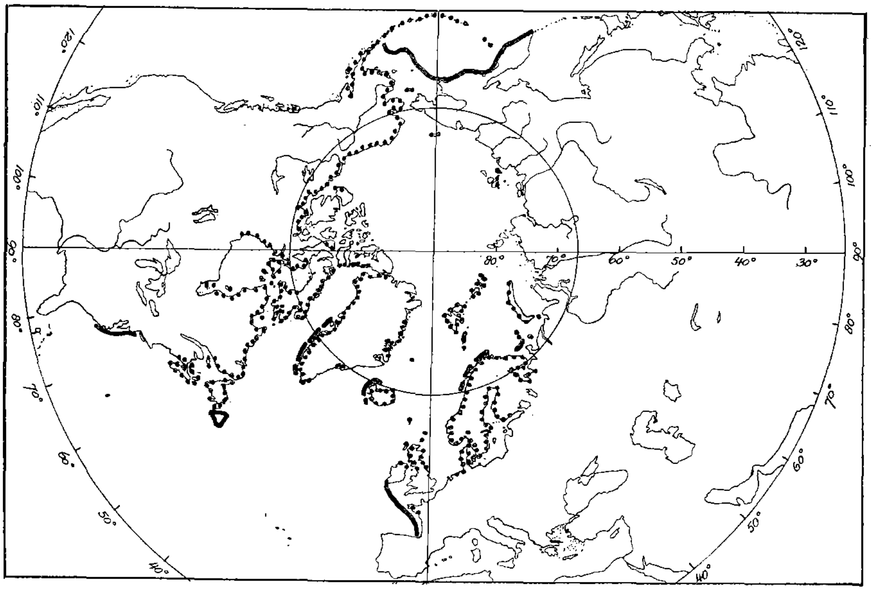


FIGURE 32. *Somateria mollissima* (Linnaeus). *Dots* = present breeding range. *Solid lines* = potential Last-Glacial breeding grounds.

v-nigra — B, cf. A.*albifrons frontalis*, A.*fabalis serrirostris*, *A.caerulescens caerulescens* (white phase), *A. canagicus*, *B. bernicla orientalis*, *B. canadensis asiatica*, *B.c.leucopareia*, *B.c.minima*, *Somateria stelleri.*

RECONSTRUCTION OF GLACIAL HISTORY

In the North Atlantic, panarctic *borealis* could find refuge breeding grounds only slightly south of the northern limit of its present breeding range. Warm sea-currents may have caused ice free coasts in these areas even during the maximum of the Last Glacial (Chapter 15).

After the retreat of the ice sheets *dresseri* spread northwards and westwards, *borealis* (eastcoast of North America) eastwards, westwards and to the south-west, ultimately meeting *dresseri* in northern Labrador (TODD 1963), where intermediate populations occur in a zone of secondary intergradation. On the European coasts *mollissima* spread northwards, subsequently meeting and interbreeding with *borealis*, which gave rise to variable intermediate forms in extensive areas of secondary intergradation in S Greenland, Iceland, N Norway and Spitsbergen. As a result of this there is a diversity of opinions among authors as regards the subspecific identity and nomenclature of the breeding birds in these areas (JOHANSEN 1951, CHECK-LIST A.O.U. 1957, DELACOUR 1954, VAURIE

1965). In the northern Pacific *v-nigra* spread westwards and eastwards, but probably did not meet the expanding subspecies of the Atlantic groups. However, according to Vaurie (1965: 126) intermediates between *v-nigra* and *dresseri* do exist, but it is not known where interbreeding occurs.

Hypsithermal interval

During the hypsithermal interval all subspecies of *S. mollissima* could have easily maintained their main breeding grounds. It was probably during this period that eastcoast *dresseri* succeeded in penetrating into the Hudson Bay region, where it was possibly isolated by expanding *borealis*, wedging in from the north, during the ensuing deterioration of the climate.

Wintering grounds

S.mollissima tends to be a sedentary bird as far as winter ice conditions permit. The following wintering grounds, outside the breeding ranges, are known (Delacour 1959, Scott 1957):

dresseri — Atlantic Coast from New Foundland to Nantucket.
borealis — Atlantic Coasts from N Labrador to Maine, SW Greenland, coastal waters of northern Norway.
mollissima — As far south as the Mediterranean and central Europe.
v-nigra — Mainly Aleutians, but also Pacific coasts of Asia, south to southern Kamchatskaya Peninsula, and of SE Alaska and British Columbia.

Though the populations of this species are mainly allohiemic, *dresseri* and *borealis* are synhiemic between New Foundland and Maine, and *borealis* and *mollissima* off northern Norway.

31. **Somateria fischeri** (Brandt)—Spectacled Eider (Fig. 33)

A lowarctic species, breeding at present between the July-isotherms of 10° and 5°C., along the arctic coast from Yana River to Point Barrow, Alaska. No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in: SB.

Discussion

The histories of *S.fischeri* and *P. stelleri* during and since the Last Glacial may have been approximately identical and they are closely bound up with the geographical history of the Bering Sea area. Therefore, I refer to the discussion under *Polysticta stelleri*. *S.fischeri* differs from *P.stelleri* in that it does not seem to make great wanderings and that it is restricted in Eurasia to eastern Siberia only. *S.fischeri* provides additional evidence that lowarctic coastal birds could not survive along the

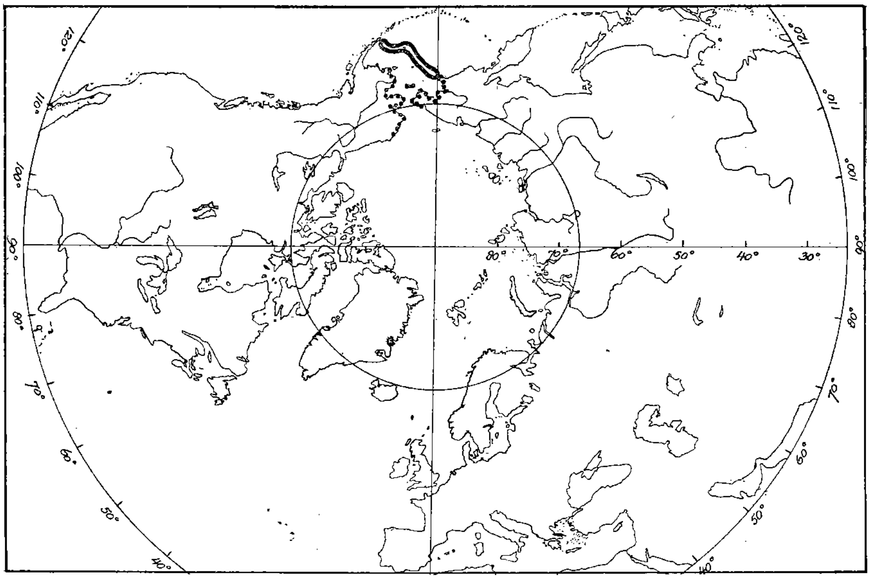


FIGURE 33. *Somateria fischeri* (Brandt). *Dots* = present breeding range. *Solid line* = border of potential Last-Glacial breeding grounds.

northern coasts of Eurasia and North America and could find refuge breeding grounds in very restricted areas in the North Atlantic and in the Bering Sea areas only.

HYPSITHERMAL INTERVAL

During the hypsithermal interval *S. fischeri* was restricted in the same way as was *P.stelleri*, for instance to NW Alaska only.

WINTERING GROUNDS

S. fischeri has a restricted migration. Its wintering grounds are not very well known, but they are mainly in the Aleutians (DELACOUR 1954).

32. **Somateria spectabilis** (LINNAEUS)—King Eider (Fig. 34)

A panarctic species, breeding at present between the July-isotherms of 10° and 2°C. No subspecies are recognized.

During the Last Glacial possibilities for regular breeding grounds existed in the following refuge areas: WG, I, NW, SP, BS, KS, NES, NB, NA, CA, cf. *B.bernicla*, *C.hyemalis*.

Hence, it has a discontinous circumpolar breeding range.

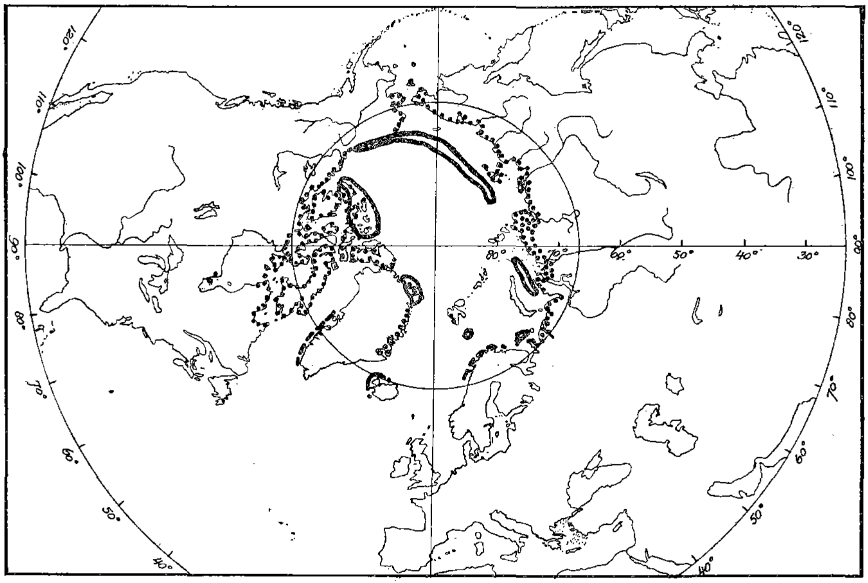


FIGURE 34. *Somateria spectabilis* (Linnaeus). *Dots* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

DISCUSSION

The lack of geographical variation may be ascribed either to gene stability or to exchange of individuals between breeding populations. According to DELACOUR (1959) the King Eider often wanders during migration. That they made great wanderings may also be concluded tentatively from the many records of King Eiders in widely scattered areas, both on sea coasts and in the interior of continents. As very few birds, adult or young, have been ringed, either in their breeding areas or in their wintering grounds, little is known about the extent of these wanderings. Presumably the King Eider has a habit of wandering about to such an extent that during the Last Glacial individuals of the species could easily have bridged the gaps in the discontinuous glacial breeding range, thus preventing geographical differentiation. This situation is contrary to that of *S.mollissima*, the populations of which are more or less sedentary and were separated in refuge breeding grounds lying very far apart, favouring subspecific differentiation.

Quite considerable congregations of wintering *S.spectabilis* are known in the North Atlantic, from NW Norway to Kolguev Island, off SW Greenland, and in the Pacific off the Aleutians and the east coast of Kamchatskaya Peninsula. Here birds of widely extended breeding areas assemble, which promotes the exchange of individuals of different breeding populations and thus preventing geographical differentiation.

Hypsithermal interval

During the hypsithermal interval *S.spectabilis* could easily find breeding grounds.

Wintering grounds

The King Eider is said to be a sedentary bird only as far as winter ice conditions permit. This implies that it is largely a migratory bird, as the greater part of the coasts of its breeding areas are ice bound during winter. Huge numbers of King Eiders have been observed migrating westwards along the north coast of Alaska.

The following wintering grounds are known, including an unknown amount of synhiemy:

(1)	Birds from the eastern Canadian Arctic, N and W Greenland	— Off the coast of SW Greenland, Atlantic coasts from Labrador south to Massachusetts
(2)	Birds from the North Atlantic islands, and W Siberia	— From Kolguev Island to NW Norway
(3)	Birds presumed to come from the western Canadian Arctic and E Siberia	— From Alaska Peninsula, off the Aleutians to east coast of Kamchatkaya Peninsula

33. **Histrionicus histrionicus** (Linnaeus)—Harlequin Duck (Fig. 35)

A boreal-subarctic-lowarctic species, breeding at present south of the July-isotherms of 5°C. Two sligtly morphologically and ecologically differentiated subspecies, geographically isolated, have been recognized:

pacificus — mountains of NE Asia and western North America.
histrionicus — Labrador, S Baffin Island, SW Greenland, areas in E Greenland, Iceland.

H.h.pacificus is a boreal-subarctic mountain bird of which the minimum July temperature in the mountain breeding areas is not known (Voous 1960). In the north this form hardly reaches the Arctic (Johansen 1956). *H.h.histrionicus* is a subarctic-lowarctic bird, breeding at present between the July-isotherms of 12° and 5°C.

During the Last Glacial possibilities for regular breeding grounds existed in the following refuge areas:

pacificus — M, the mountains south of the Cordilleran ice sheet
histrionicus — NF, WG, I

Discussion

The distribution patterns of *Histrionicus histrionicus* and *Bucephala islandica* (See next paragraph) are very similar, particularly in the separation of the ecoclimatologically different western North American and North Atlantic breeding areas. In these separated regions both species occur in the same habitat, though preferring different ecological niches.

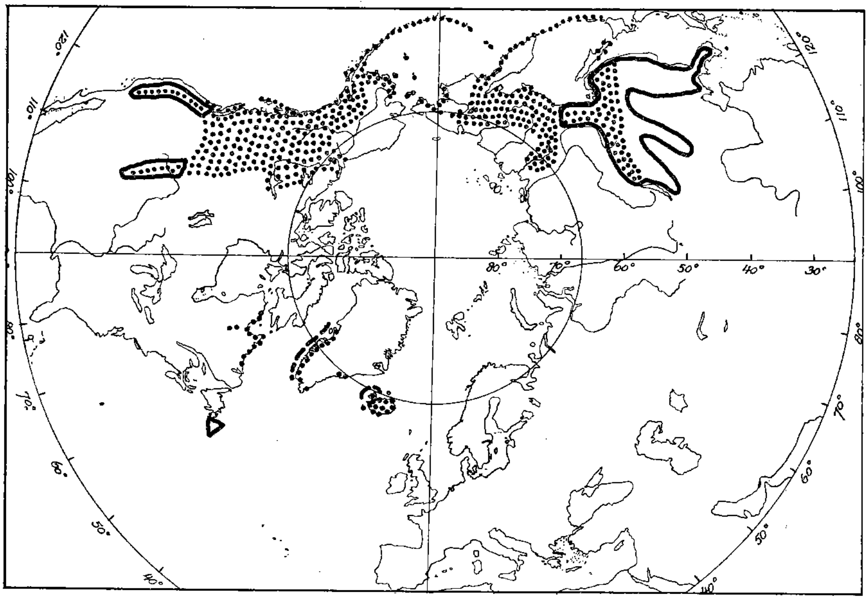


FIGURE 35. *Histrionicus histrionicus* (Linnaeus). *Stippled areas* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

Hence, it is possible that their histories during and since the Last Glacial have been similar.

It is assumed that *H.histrionicus* already occurred in NE Asia before the Last Glacial and could maintain itself south of the heavily glaciated E Siberian mountains during the Last Glacial. Its present distribution pattern, and particularly its absence from large areas on both sides of Bering Strait, contradicts the assumption of a Bering Sea refuge area. This distribution pattern equally contradicts a postglacial spreading across Bering Strait either from North America to Asia, or from Asia to North America.

Theoretically there are two possibilities of refuge areas for the western North American populations:

(a) Mountains south of the Cordilleran ice sheet.
(b) Bering Sea area.

In the boreal-alpine zone of the western mountains boreal-subarctic mountain species could spread southwards and therefore, could survive south of the Cordilleran ice sheet. As has been said above, the present absence of *H.h.pacificus* from large areas on both sides of Bering Strait contradicts the assumption of Last-Glacial refuge breeding grounds in the Bering Sea area.

The glacial histories of the North Atlantic populations of *H.h.histrionicus* and of *Bucephala islandica* are probably identical. Therefore, the following discussion applies to the North Atlantic populations of both *Histrionicus histrionicus histrionicus* and *Bucephala islandica.* For these North Atlantic populations four possibilities of Last-Glacial refuge areas must be considered:

(a) boreal forests south of the Laurentide ice.
(b) Newfoundland Bank.
(c) W Greenland and Iceland.
(d) western Europe.

The following considerations led to the assumption that the ancestors of the present North Atlantic populations of *Histrionicus h.histrionicus* and of *Bucephala islandica* survived the Last Glacial in W Greenland and Iceland.

Both forms are descendants of predominantly boreal species, breeding in coniferous forests. Together with the western North American forms, they must have had a continuous breeding range all over North America before the Last Glacial. If they had not, a greater geographical variation in these predominantly sedentary species might be expected. The extension of the Laurentide ice sheet into northern boreal forests and lowarctic tundras led to their extinction in the central part of their breeding ranges, as happened to the whole northern boreal and lowarctic bird fauna of North America. As the present distribution shows a considerable disjunction between the Pacific and Atlantic populations they apparently did not survive in boreal forests south of the Laurentide ice sheet. Moreover, the species would not have penetrated from coniferous forests into a treeless arctic zone in postglacial time without leaving population groups in the forested zone. Indeed, supposing they had done so, they would probably occur in Labrador and W Greenland, rather than in Iceland, which is the present stronghold of the species in the North Atlantic area. If both species occurred as far east as Iceland before the Last Glacial they could have retreated to refuge breeding areas in western Europe as well. If they did, however, it is not clear why at present they do not occur on the eastern side of the Atlantic.

For Newfoundland Bank I could find only two forms among all arctic species discussed in this study. Therefore, I doubt whether it actually was a refuge area.

In view of these considerations Iceland and W Greenland remain the only possible refuge breeding grounds.

As the Last-Glacial refuge breeding grounds of *H.h.histrionicus* and *B. islandica* cannot possibly be localized in other areas than those mentioned above, and both forms are at present subarctic-lowarctic, it must be concluded that in these North Atlantic refuge areas lowarctic conditions prevailed at any rate in some places.

RECONSTRUCTION OF GLACIAL HISTORY

Presumably originating from a predominantly boreal ancestor *H.histrionicus* had already developed into a boreal-lowarctic, partly alpine form before the Last Glacial, extending its breeding range from eastern Asia all over northern North America to Iceland.

Histrionicus h.pacificus could have found refuge breeding grounds south of the heavily glaciated E Siberian mountains and in North America in the mountains south of the Cordilleran ice sheet. The Atlantic populations survived the Last Glacial on the shelf areas off W Greenland and Iceland (cf. *A.caerelescens atlanticus*, *B.leucopsis*, *B.bernicla hrota*, *S.mollissima borealis*, *S.spectabilis*, *C.hyemalis*), probably in its present stronghold Iceland only, where milder circumstances may be assumed than occurring in W Greenland. On the other hand, the northern boreal and lowarctic populations on the mainland of North America east of the Rocky Mountains became extinct.

The history of the North Atlantic populations of *Histrionicus histrionicus histrionicus* and of *Bucephala islandica* (see also next paragraph) is similar to that of *Branta leucopsis* in older Pleistocene glacial periods.

After the retreat of the ice the eastern Asian and western North American *pacificus* populations spread northwards and subsequently met in the Bering Sea area; however, large potential breeding grounds are still unoccupied here.

It is certain that *H.h.pacificus* and *histrionicus* have remained separated throughout the greater part of the Last Glacial and ever since. Nevertheless their morphological differentiation is very slight, if there is any at all (CHECK-LIST A.O.U. 1957, SNIJDER 1957, TODD 1963). This slight differentiation can only be ascribed to gene stability, as the two forms are completely separated in breeding and winter seasons. This gene stability may also account for the uniformity of the Asiatic and western North American populations, which were presumably separated completely during and since the Last Glacial.

HYPSITHERMAL INTERVAL

During the hypsithermal interval the species could easily find breeding grounds, even further north, both in the Pacific and in the Atlantic areas.

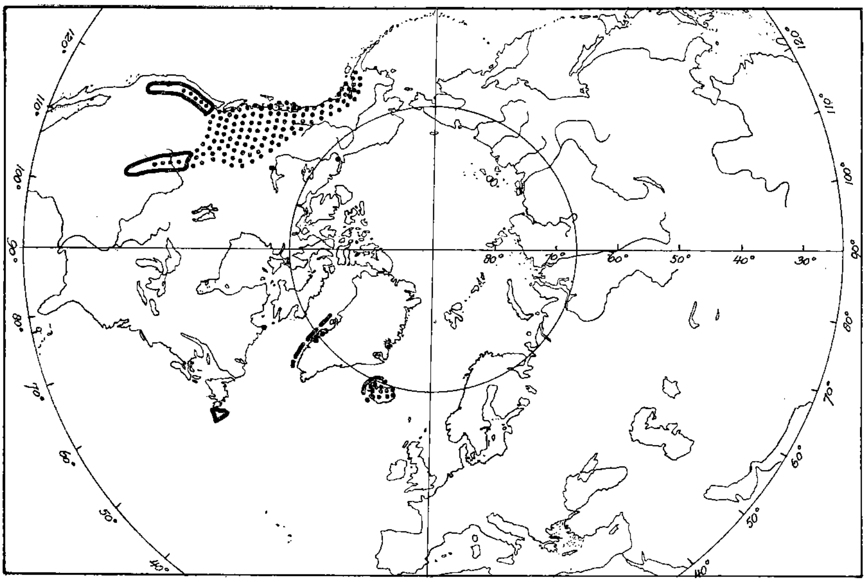


FIGURE 36. *Bucephala islandica* (Gmelin). *Stippled areas* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

WINTERING GROUNDS

In winter the Harlequin Duck is a marine bird. The populations from both sides of the Pacific are completely allohiemic. So are the populations of Labrador, Greenland and Iceland, which tend to be sedentary as far as winter ice conditions permit. Regular great wanderings that would lead to exchange of individuals of different and widely separated breeding populations, are not known. Therefore, the lack of geographical differentiation so far can only be attributed to gene stability.

34. **Bucephala islandica** (GMELIN)—Barrow's Goldeneye (Fig. 36)

A boreal-subarctic-lowarctic species, breeding at present at least north to the July-isotherms of 7°C. No subspecies are recognized.

During the Last Glacial possibilities of regular breeding grounds existed in the mountains south of the Cordilleran ice sheet and in: NF, WG, and I.

DISCUSSION

Theoretically there are two possibilities of refuge areas for the western North American populations:

(a) Mountains south of the Cordilleran ice sheet.
(b) Bering Sea area.

In the boreal-alpine zone of the western mountains boreal-subarctic mountain species could spread southwards and, therefore, could survive south of the Cordilleran ice sheet. The present absence from western and northern Alaska contradicts the assumption of a Last-Glacial survival in a Bering Sea refuge area.

As was said in the paragraph of *Histrionicus histrionicus* the glacial histories of the North Atlantic populations of *Bucephala islandica* and of *Histrionicus histrionicus histrionicus* are probably identical. For the discussion of *B.islandica*, therefore, I refer to Chapter 33.

RECONSTRUCTION OF GLACIAL HISTORY

Presumably originating from a mainly boreal ancestor, *B.islandica* had already developed into a boreal-lowarctic form before the Last Glacial. It is assumed that already before the Last Glacial its distribution range extended from the Pacific coast across North America to Iceland. The Atlantic populations survived the Last Glacial on the shelf areas of W Greenland and Iceland, probably in its present stronghold Iceland only, where circumstances milder than in W Greenland may be assumed.

In the boreal-alpine zone of the western mountains the boreal-subarctic mountains species could spread southwards and therefore could survive south of the Cordilleran ice sheet. On the other hand, the northern boreal and lowarctic populations on the mainland of North America east of the Rocky Mountains became extinct.

After the retreat of the ice the western North American Barrow's Golden Eye spread northwards; the Iceland and Greenland populations shifted their breeding grounds across a relatively small distince to their present breeding grounds and also spread to Labrador.

HYPSITHERMAL INTERVAL

During the hypsithermal interval the species could easily find breeding grounds, even further north than they do at present, both in the Pacific and in the Atlantic areas.

WINTERING GROUNDS

In winter Barrow's Golden Eye is a marine bird. The Pacific and Atlantic populations are completely allohiemic. The populations of Iceland, and possibly those of Greenland, are sedentary as far as winter ice conditions permit. Regular great wanderings that would lead to exchange of individuals of different and widely separated breeding populations, are not known.

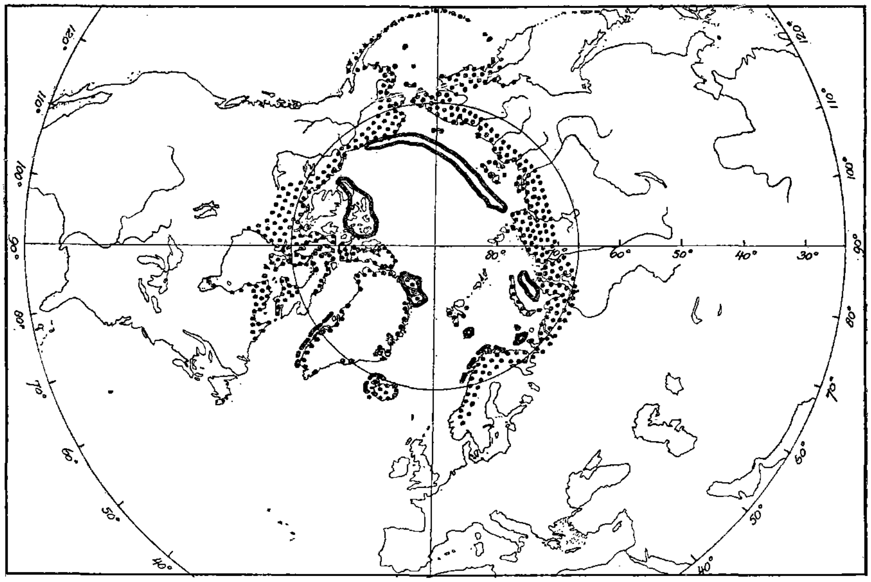


FIGURE 37. *Clangula hyemalis* (Linnaeus). *Stippled areas* = present breeding range. *Solid lines* = borders of potential Last-Glacial breeding grounds.

35. **Clangula hyemalis** (LINNAEUS)—Long-tailed Duck (Fig. 37)

A panarctic species, breeding at present between the July-isotherms of 12° and 1°C. No subspecies are recognized.

During the Last Glacial possibilities of regular breeding grounds existed in the following refuge areas: WG, NG, I, SP, NW, BS, KS, NES, NB, NA, CA, cf. *B.bernicla*.

Hence, it has a discontinuous circumpolar breeding range.

DISCUSSION

Though the breeding range must have been discontinuous the species does not at present show any geographical variation. This can be attributed either to gene-stability, or to the great wanderings of the species and the consequent exchange of individuals between populations of separate areas (SALOMONSEN 1955: 20). This situation is the reverse of that found among geese. In *B.bernicla*, for instance, which probably nested in the same glacial refuge areas as *C.hyemalis*, each subspecies follows its own migratory route to isolated wintering grounds; families keep close together and as a rule individuals do not wander about. These are all factors precluding the exchange of individuals of different breeding populations and advancing the process of subspecific differentiation. This had led to the development of four subspecies within

B.bernicla, whereas *C.hyemalis* has none. Therefore, *C.hyemalis*, being monotypical, is unsuited to the purpose of localizing higharctic refuge areas.

HYPSITHERMAL INTERVAL

During the hypsithermal interval the present circumpolar breeding range of this predominantly higharctic species must have been disrupted. Still it probably found ample opportunities for breeding in the North Atlantic islands, in northern W Siberia, NW Taimyr Peninsula, in the islands north of the Eurasian mainland, in the Canadian Arctic Archipelago and in Greenland. The total breeding population may have been considerably reduced and restricted to much smaller areas.

WINTERING GROUNDS

As individuals tend to make very great wanderings to winter quarters of synhiemic breeding populations, and mating takes place during winter, sometimes resulting in pair formation of individuals from different breeding areas, there is a large exchange of individuals.

A fine example of this habit is given by SALOMONSEN (1955: 20): Downy young of *C. hyemalis* were ringed at Disko Bay in 1947. In 1950 one of them was recovered as a breeding bird in NW Canada, not far from the Alaskan border, where the local populations move to the Pacific in winter, Another specimen was recovered in January 1951, wintering in the southern Baltic Sea. The winter visitors of this area usually breed in N Russia.

Dispersal ("*abmigration*") includes all populations, which implies that the species is a panmictic unit ranging across the entire holarctic region (SALOMONSEN 1955: 20). This precludes subspecific differentiation.

36. Summary of hypothetical Last-Glacial refuge areas of arctic *Anatidae*

SPECIES AND SUBSPECIES	CATEGORY	REFUGE AREAS [1]	PRESENT [2] DISTRIBUTION
Cygnus columbianus			
C. c. bewickii	lowarctic	E, WS, ES	P
C. c. columbianus	panarctic	CA	N
Anser albifrons			
A. a. flavirostris	lowarctic	WE	N
A. a. albifrons	panarctic, mainly lowarctic	R, WS	P
A. a. frontalis	panarctic, mainly lowarctic	ES, B	H
A. a. gambelli	unknown, probably mainly higharctic	CA	N
Anser erythropus	subarctic	R, WS, MS	P
Anser fabalis			
A. f. fabalis	boreal-subarctic	SWE	P
A. f. johanseni	boreal-subarctic	MS	P
A. f. middendorfi	boreal-alpine	M	P

Species and subspecies	Category	Refuge areas	Present distribution
A. f. brachyrhynchus	subarctic-panarctic	WE, I, NW	w.P
A. f. rossicus	panarctic	R, WS	P
A. f. serrirostris	lowarctic	ES, B	P
Anser caerulescens			
A. c. caerulescens	panartic		
(a) white phase	panarctic	NES, NB	H
(b) blue phase	lowarctic, possibly also higharctic	CA	N
A. c. atlanticus	higharctic	WG	N
Anser rossii	panarctic	CA	N
Anser canagicus	lowarctic	SB	B
Branta canadensis			
(a) eastern southern group:			
B. c. canadensis *B. c. interior* *B. c. maxima* *B. c. moffitti* *B. c. parvipes*	temperate-boreal-lowarctic	USA	N
(b) western southern group:			
B. c. fulva *B. c. occidentalis*	boreal-subarctic	w.USA	N
(c) Aleutian group:			
B. c. leucopareia *B. c. asiatica*	subarctic	SB	B
(d) northern group:			
B. c. minima	subarctic-lowarctic	B	N
B. c. hutchinsi	panarctic	CA	N
Branta leucopsis	panarctic, mainly higharctic	I, NW, SP	w.P
Branta ruficollis	subarctic-lowarctic	WS	P
Branta bernicla			
B. b. hrota	panarctic, mainly higharctic	CA, WG, NG, I, SP, NW	A
B. b. bernicla	panarctic, mainly lowarctic	BS, KS	P
B. b. orientalis	panarctic, mainly lowarctic	NES, NB	H
B. b. nigricans	unknown, probably panarctic	CA	N
Polysticta stelleri	lowarctic	SB	B
Somateria mollissima			
S. m. dresseri	boreal-subarctic	NF, EA	N
S. m. borealis	panarctic	WG, I, SP, NW, BS	w.P
S. m. mollissima	temperate-boreal-subarctic	WE	P
S. m. v-nigra	panarctic, mainly lowarctic	B	B
Somateria fischeri	panarctic, mainly lowarctic	SB	B
Somateria spectabilis	panarctic	WG, I, SP, NW, BS, KS, NES, NB, CA, NG	H H
Histrionicus histrionicus			
H. h. pacificus	boreal-subarctic-alpine	M, w. USA	H
H. h. histrionicus	subarctic-lowarctic	NF, WG, I	A
Clangula hyemalis	panarctic	WG, I, SP, NW, BS, KS, NES, NB, CA, NG	H

[1] Abbreviations: see Chapter 1.6.

[2] A = north Atlantic region, B = Bering Sea area, H = Holarctic region, N = Nearctic region, P = Palearctic region, w = western.

37. Comparison with the genus *Calidris*

37.1. INTRODUCTION

If the geographical variation and the present distribution of arctic forms of *Anatidae* were largely caused and influenced by the glacial circumstances during the Last Glacial, the same patterns of geographical variation and distribution may be expected among other arctic birds. In order to check this assumption I compared the predominantly arctic genus *Calidris* with the *Anatidae* discussed in the foregoing chapters. I mainly used the taxonomic divisions used by HARTERT (1932), JOHANSEN (1958), and VOOUS (1960). The results are summarized below.

37.2. Summary of hypothetical Last-Glacial refuge areas of *Calidris*

(ABBREVIATIONS: see Chapter 36)

SPECIES AND SUBSPECIES	CATEGORY	REFUGE AREAS	PRESENT DISTRIBUTION
minuta	subartic-panarctic, mainly lowarctic	R, WS	P
ruficollis	lowarctic	ES, SB	P, B
subminuta	boreal-subarctic	ES	P
minutilla	boreal-lowarctic	USA	N
temminckii	boreal-lowarctic	WE, R, WS, MS, EB	P
mauri	subarctic-lowarctic	SB	N
pusilla	subarctic-panarctic	CA	N
bairdii	panarctic	CA	N
fuscicollis	panarctic	CA	N
ferruginea	lowarctic	ES	P
alpina	temperate-boreal-panarctic	WE, I, SP, BS, KS, ES, B	H
maritima maritima	panarctic	WG, I, SP, NW	H
maritima ptilocnemis-group	subarctic-lowarctic	SB	B
acuminata	lowarctic	ES	P
melanotos	lowarctic	B	H
alba	panarctic, mainly higharctic	NG, SP, NW, BS, KS, NES, NB, CA	H
tenuirostris	subarctic-lowarctic	ES	P
canutus canutus	panarctic, mainly higharctic	NG, SP, NW, BS, KS, NES, NB	H
canutus rufus	higharctic	CA	N

37.3. DISCUSSION

There is less specific differentiation among the *Calidris* than among the *Anatidae* dealt with above. Instead, the number of sibling species and superspecies is relatively large. Hence, instead of subspecies, groups of closely related species seem to have survived the Last Glacial in separate refuge breeding grounds.

(a) superspecies	*minuta*	R, WS	slight distributional overlap
	ruficollis	ES	

The Last-Glacial history of this species pair was probably more or less the same as that of *Anser a. albifrons* and *A. a. frontalis*; *Anser fabalis rossicus* and *A. f. serrirostris*; *Branta b. bernicla* and *B. b. orientalis*.

(b) superspecies	*subminuta* (relic)	ES	at present no distributional overlap
	minutilla	USA	
(c) sibling species	*pusilla*	CA	at present considerable distributional overlap
	mauri	SB	

Apparently these extremely similar forms have now passed the species limit. Whether this occurred during or before the Last Glacial cannot be determined, but in any case the final differentiation may have taken place during the Last Glacial.

Two similar species survived the Last Glacial in one area:

(d) *bairdii*	CA	at present sympatric
fuscicollis	CA	

These forms must have passed the species limit before the Last Glacial. The glacial history of this species pair was probably similar to that of *Anser caerulescens caerulescens* (blue phase) and *Anser rossii*; if not at the same time, it probably happened at least in the same area.

The following relic species indicate that ES probably was their refuge breeding area (cf. *Anser albifrons frontalis*, *Anser fabalis serrirostris*, *Branta bernicla orientalis*):

(e) *subminuta*, *acuminuta*, *tenuirostris*

Three species of arctic *Calidris* show distinct subspecific variation, two of which will be discussed below.

(f) *C. maritima ptilocnemis*-group could have found refuge breeding grounds in several areas in SB, where it still occurs at present, whereas *C.m.maritima* must have survived the Last Glacial in one or more of the North Atlantic refuge areas. Both subspecies groups are still completely separated; some authors regard them as members of one superspecies.

(g) *C.canutus rufus* could have found refuge breeding grounds in CA, and *C.c.canutus* in a number of refuge areas in the northern North Atlantic and Eurasia, where it still has a wide and scattered distribution. The subspecific differentiation between nearctic *rufus* and mainly palearctic *canutus* is only slight. These subspecies are allohiemic. The migratory route of the Greenlandic population of *C.c.canatus* leads to the Palearctic (cf. *Anser albifrons flavirostris*, *Anser fabalis brachyrhynchus* and *Branta leucopsis*).

37.4. CONCLUSION

The forms of the genus *Calidris* generally show the same pattern of geographical variation, distribution, and distribution history as the *Anatidae* discussed in the preceding chapters.

38. Comparison with the genus *Tringa*

38.1. INTRODUCTION

If the geographical variation and the present distribution of arctic forms of *Anatidae* and *Calidris* were largely caused and influenced by the glacial circumstances during the Last Glacial, other patterns of geographical variation and distribution are to be expected in boreal birds. In order to check this assumption I compared the predominantly boreal genus *Tringa* with the *Anatidae* and *Calidris* discussed in the foregoing paragraphs. I mainly used the taxonomic division of HARTERT (1932). The results are summarized below.

38.2 Summary of hypothetical Last-Glacial refuge areas of *Tringa*

(ABBREVIATIONS: See Chapters 1.6 and 36; SEE = SE Europe SR = S Russia)

SPECIES AND SUBSPECIES	CATEGORY	REFUGE AREAS SOUTH OF TUNDRAS AND INLAND ICE SHEETS	PRESENT DISTRIBUTION
ochropus	boreal-subalpine	from SEE through K to M	H
solitaria	boreal-subarctic, mainly boreal	USA	
glareola	temperate-boreal-subarctic, mainly subarctic	from SWE and SEE through K to M	P
nebularia	boreal-subarctic	from WE through SR and K to southern ES	H
melanoleucus	boreal-subarctic	USA	
totanus robusta	subarctic	WE	P
totanus totanus	temperate-boreal, also steppe-desert and Mediterranean climates	from SWE and SEE to SR	P
totanus eurhinus	temperate, also steppe-desert climates	Mongolia and Manchuria	P
flavipes	boreal-subarctic	USA	N
erythropus	subarctic	from WE through SR and K to southern ES	P
stagnatilis	boreal-steppe	from SEE to K	P
guttifer	boreal	Sakhalin	P
terek	boreal-subarctic	from SEE through SR and K to southern ES	P
hypoleucos	temperate-boreal, also steppe-desert and alpine climates	from WE and SEE to ES	H
macularia	idem	USA	

The members of presumed superspecies and species groups are connected by a brace.

38.3. Discussion

Tringa totanus is the only species of its genus with a distinct subspecific differentiation. This may be attributed to its large distribution in different climatic zones, from subarctic to steppe, desert and Mediterranean climates. The other species are monotypical and have large continuous ranges in one or two bordering climatic zones with the exception of *T. stagnatilis* and *T. guttifer*, which have small and relic ranges, respectively. It is striking that six species occur in the Palearctic only, whereas, with the exception of the superspecies mentioned below, only one species is restricted to the Nearctic. This phenomenon has to be attributed to the fact that northern boreal and even predominantly subarctic palearctic *Tringa* species could easily find large continuous refuge breeding grounds in Eurasia during the Last Glacial. Possibly they also used to occur in North America, but became extinct here during one of the glaciations, when the northern boreal and subarctic zones were completely covered by inland ice.

Additional evidence corroborating this theory is the existence of two superspecies and one speciesgroup (listed above.). At present these superspecies extend their breeding ranges southward beyond the July-isotherm of 20° C and, hence, are of a more southern character than the other species. Their nearctic representatives therefore could easily have found refuge breeding grounds south of the North American inland ice during the glacial periods, which prevented them from getting extinct. The wide gap between them and their Palearctic representatives led to a considerable geographical differentiation.

38.4. Conclusion

The Pleistocene glaciations led to geographical differentiation between palearctic and nearctic boreal forms and probably to large scale extinction in North America of northern boreal and subarctic forms. Within the Palearctic and Nearctic boreal species found large continuous refuge breeding grounds, which precluded subspecific differentiation within each group.

39. **Conclusions**

39.1. General

The present distribution ranges of subspecies of arctic species of swans geese and ducks (*Anatidae*) and sandpipers (*Calidris*) coincide mainly with ice-free areas of the Last Glacial.

Some monotypical arctic species of *Anatidae* and *Calidris* have restricted ranges at present. These ranges coincide mainly with areas offering ice-free breeding grounds during the Last Glacial.

Other monotypical arctic species of *Anatidae* and *Calidris* have a circumpolar distribution. At present they are higharctic or panarctic and they may have had discontinuous circumpolar ranges in the northernmost refuge breeding grounds available during the Last Glacial. Only two species of ducks and one species of sandpiper belong to this category. These species are well-known because of their great wanderings, which advance the exchange of individuals between separate breeding populations, thus precluding geographical differentiation. No species of geese and swans known for their close family ties and their habit of returning each year to the same breeding grounds (promoting geographical differentiation),occur in this group.

The glaciated areas, forming gaps in the breeding ranges of arctic species during the Last Glacial, coincide with present disjunctions in distribution, or with present zones of secondary intergradation.

The supposed refuge breeding grounds have been mapped in Figures 19-37. A survey of the species and subspecies supposed to have survived in these refuge breeding grounds is given in the Chapters 36, 37.2, 39.2, 39.3, 40 and 41.

39.2. PREDOMINANTLY HIGHARCTIC OR PANARCTIC FORMS

The unglaciated Last-Glacial potential refuge breeding grounds of predominantly higharctic birds probably were localized in high latitudes north of inland ice sheets and of heavy local mountain glaciations.

The following regions are considered to have served as potential refuge breeding grounds:

(number of forms added; * = endemic of whole region; see also Chapters 40 and 41)

Whole North Atlantic region with 13 different higharctic forms (7 endemics)	W Greenland (WG)	— 7	*Anser caerulescens atlanticus**, *Branta bernicla hrota**, *Somateria mollissima borealis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alba*, *Calidris canutus canutus*.
	NE Greenland (NG)	— 5	*Branta bernicla hrota**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alba*, *Calidris canutus canutus*.
	Iceland (I)	— 9	*Anser fabalis brachyrhynchus**, *Branta leucopsis**, *Branta bernicla hrota**, *Somateria mollissima borealis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alpina*, *Calidris maritima maritima**, *Calidris canutus canutus*.

Whole North Atlantic region with 13 different higharctic forms (7 endemics)	Spitsbergen Bank (SP)	— 8	*Branta leucopsis**, *Branta bernicla hrota**, *Somateria mollissima borealis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris maritima maritima**, *Calidris alba*, *Calidris canutus canutus*.
	NW Norway (NW)	—10	*Anser fabalis brachyrhynchus**, *Branta leucopsis**, *Branta bernicla hrota**, *Somateria mollissima borealis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alpina*, *Calidris maritima maritima**, *Calidris alba*, *Calidris canutus canutus*.
	Barents Sea(BS)	— 6	*Branta bernicla bernicla**, *Somateria mollissima borealis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alpina*, *Calidris alba*.
	Kara Sea (KS)	— 6	*Branta bernicla bernicla**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alpina*, *Calidris alba*, *Calidris canutus canutus*.
Northern Bering Sea region with 6 different higharctic forms (2 endemics)	NE Siberia	— 6	*Anser caerulescens caerulescens* (white phase)*, *Branta bernicla orientalis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alba*, *Calidris canutus canutus*.
	North of Bering Strait	— 6	*Anser caerulescens caerulescens* (white phase)*, *Branta bernicla orientalis**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris alba*, *Calidris canutus canutus*.
	Canadian Arctic Archipelago	—14	*Cygnus columbianus columbianus**, *Anser albifrons gambelli**, *Anser caerulescens caerulescens* (blue phase)*, *Anser rossii**, *Branta canadensis hutchinsi**, *Branta bernicla hrota*, *Branta bernicla nigricans**, *Somateria spectabilis*, *Clangula hyemalis*, *Calidris pusilla**, *Calidris bairdii**, *Calidris fuscicollis*, *Calidris alba*, *Calidris canutus rufus**.

All predominantly higharctic species that have been studied appear to prefer freshwater and inland conditions during the breeding season, even though most of these species are maritime or coastal outside the breeding season. This is supposed to be an adaptation to extremely higharctic conditions, with a great survival value, because at present most of the northernmost coasts are ice-bound in summer, which may also be assumed for the Last Glacial.

The large gaps in the circumpolar breeding area were caused by the North Atlantic Ocean and the ice cap in Middle Siberia. Smaller disjunctions were caused by the ice sheets reaching the Arctic Ocean in the NE Canadian Arctic Archipelago and N Greenland, N Norway, Novaya Zemlya, and Mackenzie Delta area.

A disjunction in the present distribution still occurs in the NE Canadian Arctic Archipelago between *Anser c.caerulescens* and *A.c.atlanticus.*

A zone of secondary intergradation is known in Middle Siberia, approximately in the same area where ice sheets are supposed to have caused a distribution gap, between *Branta b.bernicla* and *B.b.orientalis.*

Higharctic and panarctic birds were probably hard-pressed by the effect of increased temperatures during the *hypsithermal interval.* The scattered circumpolar distribution of some of the higharctic birds is ascribed to this influence and to the present relatively small total area of higharctic regions on the mainland of Eurasia and North America (*Calidris alba* and *Calidris canutus*).

39.3. Predominantly lowarctic forms

In Eurasia, including the North Atlantic and the Bering Sea area, tundras were available during the Last Glacial to a considerably larger extent than at present. Generally, they were situated south of the inland ice sheets, and in E Siberia among the heavily glaciated mountains.

The following regions are presumed to have been potential refuge breeding grounds:
(number of forms added; * = endemic of whole region; see also Chapters 40 and 41)

North Atlantic area (WG, I) — 2 *Histrionicus histrionicus histrionicus**, *Bucephala islandica**.
Western Europe (WE) — 3 *Anser albifrons flavirostris**, *Somateria mollissima**, *Calidris alpina.*
Russia (R) and West Siberia (WS) — 6 *Cygnus columbianus bewickii*, *Anser albifrons albifrons**, *Anser fabalis rossicus**, *Branta ruficollis**, *Calidris minuta**, *Calidris temminckii.*
East Siberia (ES) — 9 *Cygnus columbianus bewickii*, *Anser albifrons frontalis*, *Anser fabalis serrirostris*, *Calidris alpina*, *Calidris ruficollis*, *Calidris temminckii*, *Calidris ferruginea**, *Calidris acuminata**, *Calidris tenuirostris**.
Bering Sea area (B) and coastal area of southern Bering Sea (SB) — 12 *Anser albifrons frontalis*, *Anser fabalis serrirostris*, *Anser canagicus**, *Branta canadensis minima**, *Polysticta stelleri**, *Somateria mollissima v-nigra**, *Somateria fischeri**, *Calidris ruficollis*, *Calidris mauri** *Calidris alpina*, *Calidris maritima ptilocnemis**, *Calidris melanotos**.

In North America (including the Bering Sea area) the extent of lowarctic tundras was considerably more restricted during the Last Glacial than it is at present. There were no lowarctic tundras south of the Cordilleran and Laurentide ice sheets. The Last-Glacial potential refuge breeding grounds of predominantly lowarctic birds were presumably situated in the following regions only:

Bering Sea area (B) and coastal area of southern Bering Sea (SB) — 12 *Anser albifrons frontalis*, *Anser fabalis serrirostris*, *Anser canagicus**, *Branta canadensis minima**, *Polysticta stelleri**, *Somateria mollissima v-nigra**, *Somateria fischeri**, *Calidris ruficollis*, *Calidris mauri**, *Calidris alpina*, *Calidris maritima ptilocnemis**, *Calidris melanotos**.

Newfoundland Bank (NF) — 2 *Somateria mollissima dresseri**, *Histrionicus histrionicus histrionicus*.

Four of the Bering Sea forms are still restricted to the Bering Sea area to-day (*Anser canagicus*, *Branta canadensis minima*, *Calidris mauri*, *Calidris maritima ptilocnemis*). At present six forms also occur in the coastal zones of northern East Siberia and NW North America, into which they have penetrated in postglacial times (*Anser albifrons frontalis*, *Polysticta stelleri*, *Somateria mollissima v-nigra*, *Somateria fischeri*, *Calidris alpina*, *Calidris melanotos*). The Bering Sea populations of the other two forms possibly maintained some contact with populations in East Siberia throughout the Last Glacial. At present these forms only occur west of Bering Sea (*Anser fabalis serrirostris*, *Calidris ruficollis*).

If lowarctic forms occurred in North America before the Last Glacial these must have become extinct. All present North American lowarctic forms are postglacial immigrants from the Bering Sea area and from W Greenland or Iceland.

Large disjunctions in the lowarctic circumpolar zone were caused by: the North American ice sheets, the presumed higharctic conditions in the NW Canadian Arctic Archipelago, the North Atlantic Ocean, the Scandinavian and Alpine ice sheets and the area in between, and the ice cap of Middle Siberia.

Present *disjunctions* in the North American Arctic are tabulated below:

Western form		Eastern form	
panarctic	*Anser a. frontalis*	lowarctic	*A.a. flavirostris*
panarctic	*Anser c. caerulescens*	higharctic	*A. c. atlanticus*
lowarctic	*Branta c. minima*	panarctic	*B.c.hutchinsi*
lowarctic	*Somateria m.v-nigra*	panarctic	*S.m.borealis*
		boreal-subarctic	*S.m.dresseri*
boreal-subarctic alpine	*Histrionicus h. pacificus*	subarctic-lowarctic	*H.h.histrionicus*
boreal-subarctic alpine	*Bucephala islandica in* W North America	subarctic-lowarctic	*B. islandica* in the western North Atlantic
subarctic	*Calidris m. ptilocnemis*	panarctic	*C.m.maritima*
panarctic	*Calidris c. canutus*	higharctic	*C.c.rufus*

Generally the western form are more lowarctic, the eastern more higharctic.

Secondary intergradation in the North American Arctic is tabulated below:

Western form		Eastern form	
panarctic	*Anser a.frontalis*	higharctic	*A.a.gambelli*
panarctic	*Anser c. caerulescens* (white phase)	panarctic	*A.c.caerulescens* (blue phase)
panarctic	*Branta b.orientalis*	higharctic	*B.b.hrota*

The only disjunction in easternmost Siberia occurs between lowarctic *Cygnus columbianus bewickii* and panarctic *C.c.columbianus*. This disjunction cannot be ascribed to glacial factors. No other species shows a similar disjunction. The present distribution of swans in this region is unsufficiently known.

In the scattered North Atlantic refuge breeding grounds higharctic conditions prevailed (see 39.2). However, the present distribution of the subarctic-lowarctic forms *Bucephala islandica* and *Histrionicus h. histrionicus* indicate that they cannot have found refuge breeding grounds anywhere else than in the western North Atlantic area, most probably in W Greenland, Iceland, or on Newfoundland Bank. Therefore, it is assumed that at least locally these refuge areas had lowarctic conditions. This idea is supported by the panarctic character of most other forms supposed to have survived there, e.g. *Branta leucopsis*, *Clangula hyemalis*.

Anser a.flavirostris is the only lowarctic subspecies within the otherwise panarctic *Anser albifrons*. Therefore, it would be strange, if *flavirostris* had acquired its lowarctic character in refuge areas with predominantly higharctic conditions such as W Greenland and Iceland. Consequently the supposed Last-Glacial refuge breeding grounds of *flavirostris* have been localized in western Europe.

In Eurasia the situation of the Last-Glacial disjunction is still reflected in the following distribution phenomena:

(a) Zone of secondary intergradation between:

Anser a.albifrons and *A.a.frontalis*
Anser f. rossicus and *A.f. serrirostris*

This zone is situated approximately in the same area as the Last-Glacial Middle Siberian disjunction.

(b) Two subarctic-lowarctic species are still mainly restricted to the area west of the Middle Siberian disjunction:

Branta ruficollis, *Calidris minuta*

(c) Five boreal-subarctic-lowarctic *Calidris* species are mainly restricted to areas east of the Middle Siberian disjunction:

Calidris ruficollis, *C. subminuta*, *C. ferruginea*, *C. acuminata*, *C. tenuirostris*

Anser erythropus is the only exclusively subarctic form. Its monotypical character is ascribed to its continuous Last-Glacial refuge breeding grounds. Its separation from a common *Anser albifrons-Anser erythropus* stock is ascribed to the influence of a warm interglacial period.

39.4. PREDOMINANTLY BOREAL FORMS

Within the species *Branta canadensis* temperate-boreal forms with geographical variation of a clinal type found continuous refuge breeding grounds south of the Cordilleran and Laurentide ice sheets. An eastern and western group can be recognized separated by the high mountain ranges in the western U.S.A.

The predominantly boreal genus *Tringa* also shows the influence of the Last Glacial. Contrary to arctic birds they had their breeding grounds south of the glacial disjunctions in large continuous areas, which precluded subspecies differentiation. The ice ages led to geographical differentiation between palearctic and nearctic boral forms and probably to a large scale extinction of northern boreal and subarctic forms in North America.

39.5. INTERGLACIAL PERIODS AND HYPSITHERMAL INTERVAL

Not only glacial but also warm interglacial periods and the hypsithermal interval have contributed to geographical variation and even to species formation, e.g. in *A.albifrons* and *A.erythropus.*

39.6. WINTERING GROUNDS AND MIGRATORY ROUTES

Many geese and swans have distinct migratory routes and wintering grounds, the latter often very much restricted. This, together with completely separated glacial refuge breeding grounds, close family ties and the habit of returning each year to the same breeding area, promoted geographical variation. Therefore, geese and swans are very much suited to the purpose of indicating Last-Glacial refuge breeding grounds.

The lack of geographical variation in some higharctic circumpolar ducks (*Clangula hyemalis, Somateria spectabilis*) and sandpipers (*Calidris alba*) is attributed to the relatively small disjunctions between the Last-Glacial higharctic refuge breeding grounds. These disjunctions could easily be bridged by these species, which are known to make great wanderings and migrations, leading to the exchange of individuals between different breeding populations.

39.7. FINAL CONCLUSION

The present distribution pattern and the geographical variation in the arctic *Anatidae* species and in those of *Calidris* should largely be ascribed to the physical-geographical situation during the Last Glacial.

40. SURVEY OF LAST-GLACIAL REFUGE AREAS WITH SPECIES AND SUBSPECIES OF *Anatidae* AND *Calidris* SUPPOSED TO HAVE SURVIVED THERE

Emerged shelf areas off the west coast and possible unglaciated areas on the mainland of W GREENLAND between 60° and 71°N lat. — 8 forms (1 endemic*)

*Anser caerulescens atlanticus**
Branta bernicla hrota
Somateria mollissima borealis
Somateria spectabilis
Histrionicus h. histrionicus
Clangula hyemalis
Calidris alba
Calidris c. canutus

NORTH-EAST GREENLAND — 5 forms (no endemics)

Branta bernicla hrota
Somateria spectabilis
Clangula hyemalis
Calidris alba
Calidris c. canutus

Emerged shelf areas off the coasts of ICELAND — 11 forms (no endemics)

Anser fabalis brachyrhynchus
Branta leucopsis
Branta bernicla hrota
Somateria mollissima borealis
Somateria spectabilis
Histrionicus h.histrionicus
Bucephala islandica
Clangula hyemalis
Calidris alpina
Calidris m. maritima
Calidris c. canutus

Emerged SPITSBERGEN BANK — 8 forms (no endemics)

Branta leucopsis
Branta bernicla hrota
Somateria mollissima borealis
Somateria spectabilis
Clangula hyemalis
Calidris m. maritima
Calidris alba
Calidris c.canutus

Emerged shelf areas off NORTHWESTERN NORWAY — 10 forms (no endemics)

Anser fabalis brachyrhynchus
Branta leucopsis
Branta bernicla hrota
Somateria mollissima borealis
Somateria spectabilis
Clangula hyemalis
Calidris alpina
Calidris m. maritima
Calidris alba
Calidris c. canutus

WESTERN EUROPE — 4 forms (2 endemics*)

*Anser albifrons flavirostris**
Anser fabalis brachyrhynchus
*Somateria m. mollissima**
Calidris alpina

SOUTHWEST EUROPE — 1 form (one endemic*)

*Anser f. fabalis**

Emerged BARENTS SEA shelf — 6 forms (no endemics)

Branta b. bernicla
Somateria mollissima borealis
Somateria spectabilis
Clangula hyemalis
Calidris alpina
Calidris alba

Emerged KARA SEA shelf — 6 forms (no endemics)

Branta b. bernicla
Somateria spectabilis
Clangula hyemalis
Calidris alpina
Calidris alba
Calidris c. canutus

Emerged shelf areas in Northeast Siberia — 6 forms (no endemics)

Anser c. caerulescens (*white phase*)
Branta bernicla orientalis
Somateria spectabilis
Clangula hyemalis
Calidris alba
Calidris c. canutus

Emerged shelf north of Bering Strait region and adjacent mainland — 6 forms (no endemics)

Anser c. caerulescens (white phase)
Branta bernicla orientalis
Somateria spectabilis
Clangula hyemalis
Calidris alba
Calidris c. canutus

Canadian Arctic Archipelago — 14 forms (10 endemics*)

*Cygnus c. columbianus**
*Anser albifrons gambelli**
Anser c. caerulescens (blue phase)*
*Anser rossii**
*Branta canadensis hutchinsi**
Branta bernicla hrota
*Branta bernicla nigricans**
Somateria spectabilis
Clangula hyemalis
*Calidris pusilla**
*Calidris bairdii**
*Calidris fuscicollis**
Calidris alba
*Calidris canutus rufus**

Russia and West Siberia — 7 forms (one endemic*)

Cygnus columbianus bewickii
Anser albifrons albifrons
Anser erythropus
Anser fabalis rossicus
*Branta ruficollis**
Calidris minuta
Calidris temminckii

Middle Siberia — 3 forms (no endemics)

Anser erythropus
Anser fabalis johanseni
Calidris temminckii

East Siberia — 10 forms (4 endemics*)

Cygnus columbianus bewickii
Anser albifrons frontalis
Anser fabalis serrirostris
Calidris ruficollis
*Calidris subminuta**
Calidris temminckii
*Calidris ferruginea**
Calidris alpina
*Calidris acuminata**
*Calidris tenuirostris**

Manchuria — 2 forms (one endemic*)

*Anser f. middendorfi**
Histrionicus h. pacificus

Emerged shelf area of Bering Sea — 4 forms (2 endemics*)

Anser albifrons frontalis
Anser fabalis serrirostris
*Branta canadensis minima**
*Calidris melanotos**

Coastal area of emerged Southern Bering Sea shelf area — 11 forms (9 endemics*)

*Anser canagicus**
*Branta canadensis leucopareia**
*Branta canadensis asiatica**
*Polysticta stelleri**
*Somateria mollissima v-nigra**
*Somateria fischeri**
Calidris ruficollis
*Calidris minutilla**
*Calidris mauri**
Calidris alpina
*Calidris maritima ptilocnemis**

Western U.S.A. — 3 forms (2 endemics*)

*Branta canadensis fulva**
*Branta canadensis occidentalis**
Histrionicus h. pacificus

EAST COAST of NORTH AMERICA — 1 form (no endemics)

Somateria mollissima dresseri

Emerged NEW FOUNDLAND BANK — 2 forms (no endemics)

Somateria mollissima dresseri
Histrionicus h. histrionicus

41. MAIN LAST-GLACIAL REFUGE AREAS WITH A HIGH DEGREE OF GLACIAL ISOLATION

North Atlantic region, comprising western Greenland, northeast Greenland, Iceland, northwest Norway, Spitsbergen Bank, Barents Sea, Kara Sea — 14 forms (8 endemics*)

*Anser fabalis brachyrhynchus**
*Anser caerulescens atlanticus**
*Branta leucopsis**
Branta bernicla hrota
*Branta bernicla bernicla**
*Somateria mollissima borealis**
Somateria spectabilis
*Bucephala islandica**
*Histrionicus h. histrionicus**
Clangula hyemalis
Calidris alpina
*Calidris m. maritima**
Calidris alba
Calidris c. canutus

Bering Sea region, comprising northern east Siberia, eastern Siberia, all parts of the emerged Bering Sea shelf, Aleutians, western Alaska — 25 forms (19 endemics*)

*Anser albifrons frontalis**
*Anser fabalis serrirostris**
Anser c. caerulescens (white phase)*
*Anser canagicus**
*Branta canadensis leucopareia**
*Branta canadensis asiatica**
*Branta canadensis minima**
*Branta bernida orientalis**
*Polysticta stelleri**
*Somateria mollissima v-nigra**
*Somateria fischeri**
Somateria spectabilis
Clangula hyemalis
*Calidris ruficollis**
*Calidris subminuta**
Calidris temminckii
*Calidris mauri**
*Calidris ferruginea**
Calidris alpina
*Calidris m. ptilocnemis**
*Calidris acuminata**
*Calidris melanotos**
Calidris alba
*Calidris tenuirostris**
Calidris c. canutus

Canadian Arctic Archipelago — 14 forms (10 endemics*)

*Cygnus c. columbianus**
*Anser albifrons gambelli**
Anser c. caerulescens (blue phase)*
*Anser rossii**
*Branta canadensis hutchinsi**
Branta bernicla hrota
*Branta bernicla nigricans**
Somateria spectabilis
Clangula hyemalis
*Calidris pusilla**
*Calidris bairdii**
*Calidris fuscicollis**
Calidris alba
*Calidris c. rufus**

Area west of the Middle Siberian ice sheets, comprising western Siberia, Russia — 7 forms (4 endemics*)

Cygnus columbianus bewickii
*Anser a. albifrons**
Anser erythropus
*Anser fabalis rossicus**
*Branta ruficollis**
Calidris temminckii
*Calidris minuta**

Rest of Europe, comprising west and southwest Europe — 5 forms (3 endemics*)

*Anser albifrons flavirostris**
*Anser f. fabalis**
Anser f. brachyrhynchus
*Somateria m. mollissima**
Calidris alpina

42. **Summary**

Of the non-marine arctic species of birds 45 percent show some form of geographical variation. The geographical forms of these species very frequently have their main breeding ranges in or in the vicinity of areas which were ice-free during the Last Glacial. Disjunctions in their present circumpolar breeding ranges often chiefly coincide with areas that were certainly covered by ice-sheets during the Last Glacial.

These patterns of distribution and geographical variation suggest the influence of the Last Glacial. For a detailed analysis of distribution, geographical variation, ecological preference, life habits and glacial history I selected the group of arctic swans, geese and ducks (*Anatidae*) with 18 species occurring in 38 geographical forms. During the Last Glacial time glacial conditions seriously affected the whole arctic habitat and so there is the problem as to where these birds had their breeding grounds during this period (refuge areas).

Over 38% of the species studied show some form of geographical variation. Therefore, there arises a second problem: when and where the geographical isolation preceding present geographical variation may have taken place.

The first problem is dealt with in the Physical-Geographical Part, the second in the Zoogeographical Part of this study.

A. **Physical Geographical Part**

Since at present nearly all arctic Anatidae breed in low tundras the problem may be put as follows: where did low tundra refuge areas occur during the maximum of the Last Glacial? To answer this question the Last-Glacial distribution of ice-sheets and heavy local mountain glaciations in the present arctic regions have been studied and mapped (Fig. 1a). The main lines of the extension of these ice sheets and glaciers are fairly well known. Opinions differ widely as to the questions whether in some places peripheral zones of the ice-sheets remained unglaciated and harboured an arctic flora and fauna. The most disputed of these peripheral zones are in Greenland, Iceland, northwest and north Norway, the northwest Canadian Arctic Archipelago and along the southern border of the Cordilleran and Laurentide ice-sheets in North America.

In Chapters 2, 5, 7, 11 and 12 attempts are made to answer these questions from a physical-geographical point of view, using as evidence geological, geomorphological, palynological, phytogeographical and zoogeographical data. For coastal areas of Iceland and northwest and north Norway outlet-glaciers have been reconstructed (Chapters 5 and 7); admirality charts and present geomorphological and glaciological data have been used as a basis.

Areas known to have had extensive ice-free areas with arctic tundras or subarctic woodland are briefly mentioned in Chapters 8 (North Sea area), 9 (Northern Eurasia) and 10 (Bering Sea area). Areas that probably did not offer ice-free refuge areas or about which only very fragmentary data are available are only briefly mentioned: Labrador (Chapter 3), Newfoundland Bank (Chapter 4), Spitsbergen and Spitsbergen Bank (Chapter 6).

Greenland. There is geological and phytogeographical evidence for ice-free areas in Peary Land. Other ice-free refuge areas probably existed, especially on the shelf along the west coast of Greenland south of 71° N lat. (Fig. 3) (Chapter 2).

It is unlikely that there were ice-free refuge areas along the coasts of Labrador (Chapter 3).

Newfoundland Bank probably remained ice-free (Chapter 4, Fig. 4).

In Chapter 5 (Iceland) much attention has been paid to the problem of dispersal of plants and insects from W Europe to Iceland by migrating birds. The reconstruction of outlet-glaciers has shown that fairly large emerged shelf areas off west Iceland probably remained ice-free (Fig. 5).

Spitsbergen Bank (Chapter 6) may have been partly ice-free (Fig. 6). Climatological circumstances were probably too bad to offer a refuge area for plants and animals, but this is not certain.

In Chapter 7 (Norway) a summary is given of the discussion pro and contra ice-free areas in Norway. Field-observations made by the author and the results of laboratory research convinced the author that ice-free areas existed in Andöy (Vesterålen) and Söröy (West Finmark).

Reconstruction of over 50 outlet-glaciers have shown that large emerged shelf areas may have remained ice-free off northwest and north Norway (7.2.1, Fig. 14 and 15). There is a fair agreement between the geological, phytogeographical and zoogeographical evidence for the localization of ice-free refuge areas in northwest and north Norway (Paragraph 7.4).

For the North Sea area (Chapter 8) all data fairly consistently point to predominantly subarctic to arctic conditions during the cold phases of the Last Glacial.

In Eurasia the total tundra area was much larger than it is at present (Fig. 1a). Possibly ice-free shelf areas existed in the Barents and Kara Seas (Fig. 16). As a result of the eustatic lowering of the sea-level the north coast of east Siberia shifted 1,000 km to the north. In Middle Siberia the coalescent ice caps of Taimyr Peninsula and Putorana Mountains formed an important disjunction between the western and eastern tundra flora and fauna (Chapter 9).

In the Bering Sea area Last-Glacial summer temperatures may have been only a few degrees lower than they are at present. The area was an important refuge area during the Last Glacial (Chapter 10, Fig. 17).

The northwestern Canadian Arctic Archipelago remained unglaciated during the Last Glacial. During the maximum of the Last Glacial summer temperature were perhaps not much lower than they are at present. There is some evidence that during Late-Glacial time summer temperatures were higher than they are at present. The most probable refuge area is western Banks Islands (Chapter 11, Fig. 18).

There is evidence of the presence of coniferous boreal forest or woodland along the southern border of the Laurentide ice sheet during the Last Glacial. In some areas in the NE U.S.A. a treeless landscape existed during the cold phases of the Late Glacial. Traces of permafrost have been found in many places. In extensive areas traces of periglacial frost phenomena are lacking. It is concluded that a continuous tundra zone with a permafrost and an arctic flora did not exist along the southern border of the Laurentide ice sheet during any time of the Last Glacial (Chapter 12).

The period with the maximum extent of inland ice did not necessarily coincide with the lowest temperatures in the northernmost refuge areas (Chapter 13).

During the development of inland ice-sheets the centres of ice outflow must have gradually shifted their positions. Therefore, though all large regions with inland ice-sheets may have been covered by ice during some time of the Last Glacial, this did not necessarily take place simultaneously. Consequently, refuge areas may have shifted their positions during the course of the Last Glacial. This shifting complicated the efforts made towards the reconstruction of their localization. On the other hand, however, through this shifting plants and animals must have had a much greater chance of surviving (Chapter 14).

The warm ocean currents in the North Pacific and the North Atlantic may have prevented the ocean coasts from being choked with ice-bergs (Chapter 15).

It is suggested that ice-free shelf areas off W Greenland, Iceland, Newfoundland, Spitsbergen Bank and Norway offered good breeding and feeding possibilities for arctic birds (Chapter 16).

B. **Zoogeographical Part**

In the Zoogeographical Part the Last-Glacial breeding grounds of the geographical forms and species of arctic swans, geese and ducks (*Anatidae*) are placed in the potential refuge breeding grounds found in the Physical-Geographical Part of this study.

Last-Glacial refuge breeding grounds have been searched for in the vicinity of the present breeding ranges of the species and subspecies studied. Whenever this proved to be appropriate the Last-Glacial breeding grounds were searched for along the present migration route (e.g. *Anser albifrons flavirostris*). In some species alternative possibilities for Last-Glacial breeding ranges are discussed. In these cases present-day subspecific differentiation within the species has been used to indicate which alternative should be taken as more likely.

Last-Glacial breeding ranges have been reconstructed and they are mapped alongside the present breeding ranges (Fig. 19-37).

Each of the arctic species of *Anatidae* is discussed separately.

The chapters contain paragraphs on present ecological preference, geographical forms, supposed Last-Glacial breeding grounds, reconstruction of Last-Glacial history, and the possible influences of the postglacial hypsithermal interval and of wintering grounds on the process of geographical differentiation.

The hypothetical Last-Glacial refuge areas of arctic *Anatidae* are summarized in Chapter 36.

To gain a first check of the results of this study the predominantly arctic genus *Calidris* (sandpipers) is used for the sake of comparison and it is studied along the same lines as those with arctic *Anatidae*. The results are summarized in Paragraph 37.2 and discussed in Paragraph 37.3. It is concluded that the forms of the genus *Calidris* generally show the same pattern of geographical variation, distribution, and Last-Glacial distributional history as *Anatidae*.

The glacial history of predominantly boreal birds is assumed to have been different from that of arctic species. This assumption is confirmed by means of a comparison of the predominantly boreal genus *Tringa* (Greenshank and other large sandpipers and waders) with the *Anatidae* and *Calidris*. The results are summarized in Paragraph 38.2 and discussed in Paragraph 38.3.

The conclusion is arrived at that the present distribution and the geographical variation in the arctic species of *Anatidae* should largely be ascribed to the physical-geographical situation during the Last Glacial. In some cases the postglacial hypsithermal interval seems to have advanced the geographical differentiation that existed or had started during the Last Glacial.

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44. Samenvatting

Van de arctische vogelsoorten, de zeevogels buiten beschouwing gelaten, vertoont 45% geografische variatie. De broedgebieden van de geografische vormen van deze soorten zijn zeer vaak gelegen in gebieden die gedurende de laatste ijstijd ijsvrij zijn gebleven, of in de nabijheid van deze gebieden. Disjuncties in tegenwoordige circumpolaire broedarealen vallen vaak samen met gebieden die gedurende de laatste ijstijd met ijs bedekt waren. Het lijkt waarschijnlijk, dat de omstandigheden tijdens de laatste ijstijd deze verschijnselen veroorzaakt hebben.

Voor een nauwkeurig onderzoek van verspreiding, geografische variatie, oecologische voorkeur, levensgewoonten en glaciale geschiedenis werden arctische zwanen, ganzen en eenden (*Anatidae*) uitgekozen. Deze groep omvat 18 soorten met in totaal 38 geografische vormen.

De omstandigheden tijdens de laatste ijstijd moeten grote veranderingen teweeg gebracht hebben in de arctische biotopen. De eerste vraag is, waar de genoemde vogels tijdens de laatste ijstijd broedplaatsen (refugia) hebben kunnen vinden.

Meer dan 38% van de bestudeerde soorten vertoont geografische variatie. De tweede vraag die gesteld moet worden, luidt daarom, wanneer en waar de geografische isolatie, die aan de geografische differentiatie voorafging, plaats vond.

De eerste vraag is in het Fysisch-geografische Deel behandeld, de tweede in het Zoögeografische Deel.

A. Fysisch-geografisch Deel

Bijna alle arctische Anatidae broeden in laaggelegen toendra's. Het op te lossen probleem kan daarom als volgt gesteld worden: Waar kwamen tijdens de laatste ijstijd laaggelegen toendra's voor?

De hoofdlijnen van de verspreiding van landijs en zware plaatselijke vergletsjering zijn vrij goed bekend (Fig. 1a). Er bestaat echter een groot verschil van mening over de vraag of enkele gebieden aan de rand van de landijskappen niet door ijs bedekt zijn geweest en refugia voor een arctische flora en fauna hebben gevormd. De meest omstreden perifere gebieden zijn die in Groenland, IJsland, noordwest en noord Noorwegen, de noordwestelijke Canadese Arctische Archipel en langs de zuidrand van het Noordamerikaanse landijs. In de Hoofdstukken 2, 5, 7, 11 en 12 is gepoogd een antwoord op genoemde vraag te vinden. Hierbij is gebruik gemaakt van geologische, geomorfologische, palynologische, phytogeografische en zoögeografische gegevens. Voor kustgebieden van IJsland en van noordwest en noord Noorwegen zijn de uit het binnenland komende gletsjers gereconstrueerd (Hfst. 5 en 7), waarbij zeekaarten en geomorfologische en glaciologische gegevens als basis dienden.

Gebieden die zeker door uitgestrekte arctische toendra's of door subarctisch parklandschap bedekt waren, zijn slechts kort genoemd in de Hoofdstukken 8 (Noordzeegebied), 9 (noordelijk Eurazië) en 10 (Bering Zee gebied). Gebieden die waarschijnlijk geen refugia boden of waarover zeer weinig gegevens zijn, worden slechts even aangeroerd in hoofdstuk 3 (Labrador), 4 (Newfoundland Bank), en 6 (Spitsbergen en Spitsbergen Bank).

Groenland (Hfst. 2). Er zijn geologische en phytogeografische bewijzen voor ijsvrije gebieden in Peary Land. Waarschijnlijk kwamen er meer ijsvrije gebieden voor, vooral op het toen drooggevallen deel van het continentale plat langs de westkust van Groenland ten zuiden van 71° N.B. (Fig. 3).

Het is onwaarschijnlijk, dat er ijsvrije refugia voorkwamen langs de kust van Labrador (Hfst. 3).

Newfoundland Bank is waarschijnlijk ijsvrij gebleven (Hfst. 4, Fig. 4).

In Hoofdstuk 5 (IJsland) is veel aandacht besteed aan het vraagstuk van de verspreiding van planten en dieren door trekvogels vanuit W Europa naar IJsland. Reconstructies van in zee uitkomende gletsjers tonen aan dat een betrekkelijk grote oppervlakte van het toen drooggevallen deel van het continentale plat ten westen van IJsland waarschijnlijk niet door ijs werd bedekt (Fig. 5).

Een deel van de Spitsbergen Bank (Hfst. 6) kan vrij van gletsjers of landijs gebleven zijn (Fig. 6). Het klimaat was er waarschijnlijk te ongunstig voor planten en dieren.

In Hoofdstuk 7 (Noorwegen) staat een overzicht van de argumenten pro en contra ijsvrije gebieden in Noorwegen. Veldwerk in noordwest Noorwegen en het resultaat van laboratorium onderzoek overtuigden schrijver, dat op

Andöy (Vesterålen) en Söröy (West Finmark) bepaalde gebieden tijdens de laatste ijstijd niet door ijs bedekt zijn geweest.

De reconstructie van 50 in zee uitkomende gletsjers toont aan, dat uitgestrekte gebieden van het toen drooggevallen deel van het continentale plat langs de noordwest en noordkust van Noorwegen waarschijnlijk ijsvrij zijn gebleven (7.2.1, Fig. 14 en 15). Zowel de geologische en geomorfologische, de phytogeografische en zoögeografische gegevens, als de reconstructie van in zee uitkomende gletsjers wijzen er op, dat ijsvrije refugia in de eerste plaats gezocht moeten worden in het noordwesten en noorden van Noorwegen (7.4).

Voor het Noordzeegebied (Hfst. 8) bestaat een tamelijk goede overeenkomst tussen alle gegevens. Deze wijzen op overwegend subarctische tot arctische omstandigheden tijdens de koude fasen van de laatste ijstijd.

In Eurazië was de totale toendra oppervlakte veel groter dan thans (Fig. 1a). Het is mogelijk, dat bepaalde gedeelten van het drooggevallen continentale plat in de Barents en Karo Zee ijsvrij gebleven zijn (Fig. 16). Ten gevolge van de eustatische zeespiegeldaling verschoof de kustlijn van oost Siberië 1000 km naar het noorden. In Midden Siberië vormden de samenvloeiende ijskappen van het Taimyr Schiereiland en van de Putorana Bergen een belangrijke scheiding tussen de westelijke en oostelijke flora en fauna (Hfst. 9).

In het Bering Zee gebied waren de zomertemperaturen tijdens de laatste ijstijd mogelijk slechts een paar graden lager dan nu. Dit gebied moet toen een belangrijk refugium zijn geweest (Hfst. 10, Fig. 17).

Het noordwestelijk deel van de Canadese Arctische Archipel bleef gedurende de laatste ijstijd ijsvrij. Gedurende het maximum van die tijd waren de zomertemperaturen misschien niet veel lager dan nu. Er zijn enige aanwijzingen, dat tijdens het Laat-Glaciaal de zomertemperaturen hoger waren dan nu. Het westelijk deel van Banks Eiland is het meest waarschijnlijke refugium (Hfst. 11, Fig. 18).

Er zijn bewijzen, dat gedurende de laatste ijstijd langs de zuidrand van de Laurentide ijskap een boreaal naaldwoud of een boreaal parklandschap voorkwam. In een aantal gebieden in het noordoosten van de Verenigde Staten kwam een boomloos landschap voor tijdens de koude fasen van het Laat-Glaciaal. Sporen van een permanent bevroren bodem zijn op vele plaatsen aangetroffen. Hiertegenover staat, dat in andere, uitgestrekte gebieden elk spoor van periglaciale vorstverschijnselen ontbreekt. Schrijver komt tot de conclusie dat er tijdens de laatste ijstijd langs de zuidrand van de Laurentide ijskap nooit een aaneengesloten toendra heeft bestaan (Hfst. 12).

De periode die de grootste ijsuitbreiding kende, was niet noodzakelijk ook de periode met de laagste temperaturen in de noordelijke refugia (Hfst. 13).

Gedurende de ontwikkeling van de landijskappen zijn de centra van waaruit het ijs radiaal uitvloeide geleidelijk van plaats veranderd. Daardoor is het mogelijk, dat de vroeger vergletsjerde gebieden wel geheel door ijs bedekt geweest zijn, maar niet alle delen van deze gebieden tegelijkertijd. Daardoor kan in de loop van de laatste ijstijd de ligging van de refugia veranderd zijn. Deze verplaatsing maakt de reconstructie van de ligging nog moeilijker, maar zal de overlevingskansen van planten en dieren hebben vergroot (Hfst. 14).

De warme zeestromen in de noordelijke delen van de Grote en van de Atlantische Oceaan voorkwamen mogelijk, dat de betreffende kusten volkomen door ijsbergen werden ingesloten (Hfst. 15).

De ijsvrije, drooggevallen delen van het continentale plat bij W Groenland, IJsland, Newfoundland en Noorwegen, en op de Spitsbergen Bank boden waarschijnlijk gunstige broed- en voedselbiotopen voor arctische vogels (Hfst. 16).

B. **Zoögeografisch Deel**

In dit deel worden de broedgebieden tijdens de laatste ijstijd van de geografische vormen en soorten van arctische zwanen, ganzen en eenden (*Anatidae*) gelocaliseerd in de potentiële refugia die in het Fysisch-geografische deel van deze studie werden aangewezen. Deze broedgebieden werden in de eerste plaats gezocht in de nabijheid van de huidige broedgebieden van de bestudeerde soorten en ondersoorten. Wanneer dit niet kon leiden tot een oplossing, werden de broedgebieden gezocht in potentiële refugia langs de huidige trekwegen. Bij sommige soorten worden verschillende mogelijkheden van refugia besproken. In die gevallen werd de huidige subspecifieke differentiatie binnen een soort gebruikt om aan te geven welk alternatief het meest waarschijnlijk was.

Van elke soort wordt een kaart gegeven, waarop zowel het tegenwoordige broedgebied als dat tijdens de laatste ijstijd is aangegeven (Fig. 19-37).

Aan elke soort wordt een afzonderlijk hoofdstuk gewijd. Elk hoofdstuk behandelt achtereenvolgens de tegenwoordige oecologische voorkeur, de geografische vormen, de broedgebieden tijdens de laatste ijstijd, een reconstructie van de glaciale geschiedenis van de soort, de mogelijke invloed van het postglaciale warmte-optimum en van gescheiden overwinteringsgebieden op de geografische differentiatie.

Hoofdstuk 36 geeft een samenvatting van de hypothetische refugia van de behandelde soorten gedurende de laatste ijstijd.

Het overwegend arctische genus *Calidris* (Strandloper) werd op dezelfde wijze bestudeerd. De resultaten werden vergeleken met die van de studie der *Anatidae*. Zij worden samengevat in Paragraaf 37.2 en besproken in Paragraaf 37.3. De conclusie is, dat de vormen van het genus *Calidris* in het algemeen hetzelfde patroon van geografische variatie en verspreiding vertonen, en dat de verspreidingsgeschiedenis van arctische *Calidris*- en *Anatidae*-soorten dezelfde is.

De bestudeerde arctische soorten werden voorts vergeleken met de soorten van het overwegend boreale geslacht *Tringa* (Tureluur en andere ruiters; 38.2 en 38.3). De vergelijking leidde tot de conclusie, dat de glaciale geschiedenis van de boreale soorten anders geweest moet zijn dan die van arctische soorten.

De slotconclusie luidt, dat de tegenwoordige verspreiding en de geografische variatie van de soorten van arctische *Anatidae* grotendeels dienen te worden toegeschreven aan de fysisch-geografische situatie tijdens de laatste ijstijd. Bij sommige soorten kan het postglaciale warmte-optimum de geografische differentiatie, die tijdens de laatste ijstijd bestond of begon, versterkt hebben.