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Early Holocene plant and animal remains from North-east Greenland

Ole Bennike[1], Svante Björck[2], Jens Böcher[3], Louise Hansen[4], Jan Heinemeier[5] and Barbara Wohlfarth[6] [1]*Geological Survey of Denmark and Greenland, Thoravej 8, DK-2400 Copenhagen NV, Denmark,* [2]*Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark,* [3]*Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark,* [4]*Geological Museum, University of Copenhagen, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark,* [5]*AMS ^{14}C Dating Laboratory, Institute of Physics, Aarhus University, DK-8000 Århus C, Denmark and* [6]*Department of Quaternary Geology, University of Lund, Tornavägen 13, S-223 63 Lund, Sweden*

Abstract

Aim The aim of this paper is to describe and interpret early Holocene floras and faunas.

Location The floras and faunas come from various localities in North-east Greenland.

Methods Sediment samples were wet sieved, and macrofossils picked out and dated by the AMS radiocarbon-dating method.

Results Sediments, dated to the first centuries after the last glacial stage came to an abrupt end, contain a macroflora of bryophytes and a few herbs, and we suggest that these plant remains represent a pioneer vegetation entirely without woody plants. The named species of herbs are either confined to the northern parts of Greenland at present, or they become increasingly more important towards the north. Crowberry is the oldest woody plant recovered; it was present at 10.4 cal. ka BP, and it appears to have been common during the early Holocene in East Greenland.

Main conclusions We suggest that the majority of the extant flora of vascular plants of East Greenland arrived by long distance dispersal during the Holocene. Some species may also have arrived during the late-glacial, and a few hardy species that are adapted to low summer temperatures may have survived the last glacial stage in nonglaciated areas. Some hardy animals may also have survived, but the majority of the fauna are considered Holocene immigrants. We suggest that migrating birds and storms, perhaps in combination, are under-appreciated dispersal vectors.

Keywords
Greenland, Holocene, dispersal, migration, colonization, palaeoecology, biogeography.

INTRODUCTION

It has been much discussed whether plants and animals survived the last glacial stage in unglaciated areas in the north, or whether they arrived after the last ice age came to an end. This discussion that first considered Scandinavian alpine vascular plants, is more than 100-year-old, but still vivid (Mangerud, 1973; Birks, 1993, 1996). The discussion has been expanded to other plant groups and to animals, and to other geographical regions. With regard to Greenland, the discussion was opened by Warming (1888) who suggested that a majority of the present Greenlandic flora of vascular plants had survived the ice age, whereas Nathorst (1892) suggested that only few hardy species, if any at all, had survived. Later, the botanists Gelting (1941) and Böcher (1972) supported Warmings view, whereas Hartz (1897), Ostenfeld (1926), Seidenfaden & Sørensen (1937) and Sørensen (1945) supported the view of Nathorst. These early works were primarily based on the modern day distribution of plants, and the explanations for the historical factors involved in the distribution patterns were speculative. Based on pollen analytical studies, Iversen (1953) and Fredskild (1973) could show that many plants had immigrated to West Greenland during the Holocene, and both Iversen and Fredskild supported the view by Nathorst. In North-east Greenland, pollen stratigraphical work on Holocene sequences was begun by Funder (1978, 1979, 1982). Funder showed that a number of

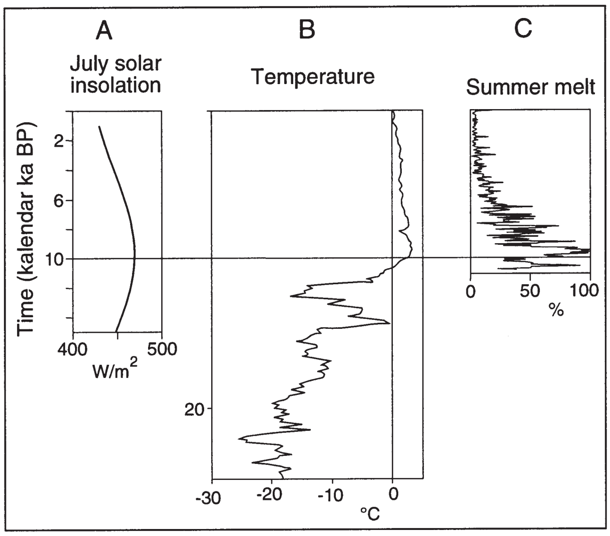

Figure 1 (A) Summer insolation at 65°N, (B) mean annual temperatures at the summit of the Greenland ice sheet (Johnsen *et al.*, 1995, (C) summer melt on the Agassiz Ice Cap, Ellesmere Island, northern Canada (Fisher *et al.*, 1995). The time scale is in calender kilo-years before present.

taxa had immigrated to NE Greenland during the Holocene, but at the same time his studies of the glaciation history indicated that rather large lowland areas remained unglaciated during the last glacial stage, and Funder also proposed that these areas housed a fairly rich flora of vascular plants. Funder suggested that it was not the hardy species that survived, but ubiquitous plants, plus some with small modern geographical ranges in East Greenland.

Glacial erratic boulders and till deposits can be found over almost all the nonglaciated onshore parts of Greenland, except for mountain peaks, and it seems likely that Greenland was almost completely ice-covered during the penultimate glacial stage (Funder *et al.*, 1989). If so, no or very few plants could have survived from the Late Tertiary, when climates were much warmer than during the Holocene (Bennike, 1990). During the last glacial stage rather large, though isolated, unglaciated areas were present in East and North Greenland (Funder, 1979 1982; Kelly & Bennike, 1992; Funder & Hansen, 1996). Rich and diverse floras and faunas lived in Greenland during the last interglacial stage (Bennike & Böcher, 1992, 1994; Hedenäs, 1994), and the majority of these species must have arrived in Greenland by long distance dispersal.

However, the question is whether summer temperatures during the last glacial stage were high enough to allow vascular plants to grow in Greenland. During the temperature minimum at 21,500 calendar years BP, mean annual temperatures over the Greenland ice sheet were *c*. 25 °C lower than those of today (Fig. 1), and little or no summer melting took place at the margin of the ice sheet (Johnsen *et al.*, 1995). It seems inescapable that very few, if any, vascular plants would be able to survive such extremely harsh conditions. On the other hand, a larger portion of other plant groups, such as bryophytes, lichens, fungi and algae, whose members are often less dependent on climatic conditions than vascular plants, may have survived (e.g. Schuster, 1988).

Those that favour the nunatak hypothesis argue that plants have poor dispersal powers, and Hultén (1937) suggested that the so-called Amphi-Atlantic plants once had circum-polar geographical ranges, and Böcher (1974) suggested that *Draba sibirica* immigrated to East Greenland from Siberia via North America. The so-called 'tabula rasa' hypothesis suggests that all plants arrived in Greenland after the last glacial stage, and that the modern geographical ranges mainly reflect modern ecological conditions. With regard to the mountain flora of Norway, Birks (1993, 1996) made statistical analyses which indicated that the modern plant distributions can be explained by climate, geology and topography. Thus the nunatak hypothesis appears to be redundant here with respect to vascular plants.

Recently, palaeoecological data have been combined with modern dispersal theory (e.g. Pitelka & the plant migration workshop group, 1997; Clark *et al.*, 1998), but these papers discuss plant migration in temperate regions. However, North American and European temperate floras and faunas are much different, and the North Atlantic has acted as a barrier to migrations at these latitudes. In the Arctic, many plants and animals show circumpolar geographical ranges, and apparently trans-oceanic dispersal is a smaller problem.

On the northern hemisphere, summer solar insolation peaked during the earliest Holocene, and proxy records from the Inland Ice of Greenland and from the Agassiz ice cap on Ellesmere Island also indicate that the earliest Holocene saw maximum summer temperatures (Fig. 1). The oldest well dated lacustrine sediments obtained so far in East Greenland extend back to about 10,000 cal. years BP (Funder, 1978, 1994b; Björck *et al.*, 1994a; Bennike & Funder, 1997). Information about the terrestrial biotas which were present during the first millennium after the last glacial stage suddenly came to an end at *c*. 11.5 ka BP, can be found in other geological archives. Here we present evidence from studies of organic detritus recovered from sediments deposited in near-shore marine environments, in fluvial and deltaic environments, in lakes and in mires. All radiocarbon dates discussed in this paper are calibrated (cal. ka BP = calibrated kilo years before the present), but the conventional radiocarbon dates appear from Table 1.

SETTING

Most of the sediment samples come from western/southern Jameson Land and Hochstetter Forland (Fig. 2) that are characterized by a thick and continuous cover of Quaternary sediments, and by gentle topography. North-east Greenland lies within the high arctic bio-climatic zone. The mean July temperature of the lowlands is 3–5 °C, and the mean annual precipitation is 300–500 mm. Permafrost is continuous. Small, isolated patches of scrub vegetation are found in the south, and dwarf shrub heaths are widespread on dry and moist soils. Fens, bogs and snow-bed vegetation characterize large areas of poorly drained ground. The uplands are characterized by fell-field vegetation.

Table 1. Radiocarbon dates

Sample No.	N. lat.	W. long.	Lab. no.	Material	Height m a.s.l.	Age, ^{14}C years BP	Calibrated age[1] years BP	δ^{13}C (‰)
Hochstetter Forland								
PBS	75°18.9′	20°2.6′	Ua-3356	*Astarte* sp. periostracum	c. 13	7470 ± 150[2]	8380–8020	
PBS	75°18.9′	20°2.6′	AAR-1193	*Betula nana* remains	c. 13	5960 ± 110[2]	6900–6670	−25[3]
94355	75°19′	19°58′	Ua-2787	*Portlandia arctica*	45	9710 ± 105[4]	10955	
G6	75°19′	19°58′	Ua-3355	Terrestrial plant remains	45	9620 ± 90	10955–10490	−25[3]
(94378)	75°14′	19°32′	Lu-3486	Marine shells	18	7890 ± 120[4]	8595	
Zackenberg, Wollaston Forland								
9201	74°28′	20°40′	AAR-1217	*Salix herbacea*	9	7140 ± 140[5]	7920	−28.4
Jameson Land								
85823	70°50.6′	24°00.5′	AAR-2540	*Polytrichum* s.l. sp.	43	10130 ± 130	11780	−24.7
85844	70°57.4′	24°06.3′	AAR-2541	?*Carex* sp.	64	9910 ± 130	11010	−27.0
100367	70°50.2′	23°57.6′	AAR-3368	*Oxyria digyna*	54	9780 ± 160	10980	−25.8
100363	70°50.2′	23°57.6′	AR-3365	*Oxyria digyna*	48	9685 ± 55	10940	−26.0
100380/81	70°50.6′	24°00.5′	AAR-3390	*Oxyria digyna, Polytrichum* s.l. sp., *Saxifraga* sp.	43	9665 ± 55	10920	−25.0
87376	70°51.3′	24°03.6′	AAR-3369	*Polytrichum* s.l. sp.	48.5	9440 ± 65	10420	−24.1
87460	70°57.6′	24°7.9′	AAR-2107	*Polytrichum* s. sl. sp., *Saxifraga oppositifolia, Oxyria digyna*	59	9420 ± 100[6]	10380	−24.9
96034	70°32′	23°36′	AAR-1121	*Empetrum nigrum*	57	8570 ± 70	9500	−27.4
85847	70°59.1′	23°59.8′	AAR-2538	*Polytrichum* s.l. sp.	62	8440 ± 120	9440	−26.0
100379	70°50.6′	24°00.5′	AAR-3366	*Empetrum nigrum, Carex bigelowii*	47	8055 ± 60	8980	−25.7
85850	70°59.1′	23°59.8′	AAR-2571	*Empetrum nigrum*	72	7920 ± 100[7]	8700–8670	−21.3
87516	71°34′	23°58′	AAR-2039	*Betula nana*	c. 250	7000 ± 390[7]	7790	−27.8

[1]Calibrated according to Stuiver & Reiner (1993), BP = before AD 1950. [2]Date from Peters Bugt Sø (PBS), Björck *et al*., 1994a. [3]Assumed value. [4]Corrected for a sea water reservoir effect by subtracting 550 years (see Björck *et al*., 1994a). [5]Christansen & Humlum (1993). [6]Funder & Hansen (1996). [7]Böcher & Bennike (1996).

MATERIALS AND METHODS

Samples were collected from lake basins and from open sections. The size of the samples from the lakes was small, while the sample size from sections varied from less than 0.5 kg of sediment to more than 10 kg of sediment. The sediments were wet sieved on 0.1, 0.21 and 0.42 mm sieves, and the residue left on the sieves were studied using a dissecting microscope. Macrofossils were identified and counted, or put into frequency classes. Material for radiocarbon dating by accelerator mass spectrometry (AMS) was dried on aluminium foil. Radiocarbon datings were performed in Århus, Denmark (AAR), in Uppsala, Sweden (Ua) and in Lund, Sweden (Lu).

RESULTS

Hochstetter Forland

The stratigraphy of the sediments in Peters Bugt Sø (Fig. 2) was discussed by Björck *et al*. (1994b). The lake became isolated from the sea around 6.8 cal. ka BP, but the chronology of the preisolation glacio-marine and marine sediments is uncertain. Björck *et al*. (1994b) suggested that the oldest sediments recovered from the lake basin are 10.5–10 cal. ka old. Simplified macrofossil and pollen data from the lake were presented by Björck *et al*. (1994b). A diagram that shows the presence/absence of all identified macrofossil taxa from the sequence is presented in Fig. 3. The dates were obtained on macrofossils.

The early flora of vascular plants around the lake was characterized by herbs, including *Papaver radicatum*, *Saxifraga oppositifolia*, *Oxyria digyna* and *Polygonum viviparum*. The only woody plant recovered from the oldest sediments is *Empetrum nigrum*, but *Cassiope tetragona* and *Vaccinium uliginosum* are found in sediments somewhat older than 8.2 cal. ka BP. A single *Saxifraga platysepala* fossil dated to 6.8 cal. ka bp is the first fossil record of this plant from Greenland. Two animals appear to occur north of their present day northern geographical range limits. The small fish *Gasterosteus aculeatus* (stickleback) and the diving beetle *Colymbetes dolabratus* have not been recorded alive north of *c*. 74°N in East Greenland (Fredskild & Røen, 1982; Böcher, 1988), which is around 100 km south of Peters Bugt Sø. Their previous occurrence on Hochstetter Forland implies slightly higher summer temperatures than at present, in accordance with results obtained further north (Fredskild, 1995).

A sequence of samples was collected from a raised delta near Peters Bugt Sø (Fig. 4), and a sample of terrestrial plant remains was dated to *c*. 10.7 cal. ka BP, whereas a sample of marine shells from the delta was dated to *c*. 11 cal. ka BP (Table 1). The samples 6–12 were collected over 2 m, but the sediments were probably deposited within only some hundred

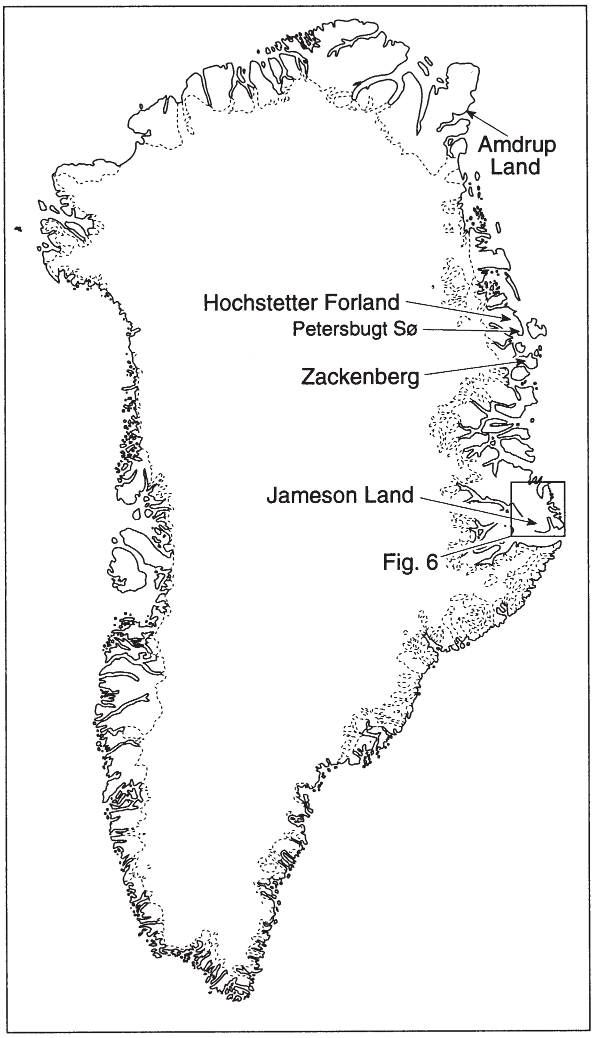

Figure 2 Map of Greenland showing the location of place names mentioned in the text.

years, and the plant remains probably also represent plant growth over a short time period. Few taxa of vascular plants are represented in the assemblages, and no woody plants were found. The only named species were *Papaver radicatum*, *Melandrium apetalum* and *Saxifraga oppositifolia*. Another sample from the delta (94355), collected by C. Hjort, contained the same three species of herbs (Table 2).

From south-east Hochstetter Forland comes another sample (94378), which is dated to 8.6 cal. ka BP on nearby marine shells (Table 1). This sample yielded a sparse flora, with only four taxa of vascular plants identified, none of which is at the species level (Table 2).

Zackenberg, Wollaston Forland

On Wollaston Forland, a raised marine delta at Zackenberg (Fig. 1) contains abundant organic detritus washed out from land. Leaves of *Salix herbacea* yielded a date of 7.9 cal. ka BP (Table 1), and the flora also contained numerous remains of *Empetrum nigrum*, in addition to fifteen taxa of nonwoody vascular plants. The *Salix herbacea* leaves are the oldest Holocene macrofossils of this plant from East Greenland, but the pollen records from the Scoresby Sund region indicate that the species was present one or two millennia earlier (Funder, 1978, 1979).

From the Zackenberg delta deposit also comes four named species of insects, of which the record of the fly *Syrphus torvus* is the first fossil record from Greenland. The enigmatic, early Holocene presence of the leaf beetle *Phratora (Phyllodecta)* cf. *polaris* in NE Greenland was discussed by Böcher & Bennike (1996). A small fragment of the ground beetle *Amara alpina* has also been recovered from the Zackenberg delta, but this fragment was probably redeposited from interglacial deposits. The *Lepus arcticus* find is the oldest Holocene record from Greenland of arctic hare (Bennike, 1997).

Jameson Land

Several lakes on Jameson Land (Fig. 1) have been cored, and macrofossil results from two of them have been published (Björck *et al*., 1994a; Bennike & Funder, 1997). In addition, pollen data from other lakes in the Scoresby Sund region have been published by Funder (1978, 1979). Macrofossil analyses of two samples were presented by Böcher & Bennike (1996). None of the lacustrine sediments on Jameson Land investigated extend back to more than *c*. 10 cal. ka BP, but during field work on Jameson Land, a number of deposits with organic remains has been located. Thirteen AMS radiocarbon dates are available (Table 1), and seven of these predate the lacustrine records. Most of the samples come from raised marine deltas, but some of them come from fluvial deposits. 85824, 85825 and 85850 represent peat deposits (Fig. 5).

The oldest analysed sample, 85823 from locality 635 (Fig. 6), yielded a radiocarbon date of 11.8 cal. ka BP. Eight taxa of herbs were found in this sample, of which *Melandrium apetalum*, *Papaver radicatum* and *Oxyria digyna* were identified at the species level (Table 2). Two amalgamated samples, 100380 and 100381 from the same locality, yielded a date of 10.9 cal. ka BP. The only named species from these samples was *Oxyria digyna*. Sample 100367 and sample 100363 from locality 702 were dated to *c*. 11 cal. ka BP. These samples also contained *Melandrium apetalum*, *Papaver radicatum* and *Oxyria digyna*.

The oldest sample with remains of woody plants is sample 87376 from locality 396. This sample which is dated to 10.4 cal. ka BP contained rare remains of *Empetrum nigrum*, in addition to one seed of *Arabis alpina*. *Empetrum nigrum* fruit stones and leaves were found in several other early Holocene samples from Jameson Land, and sample 96034 and 85850 contained numerous remains of *Empetrum nigrum*. Pollen grains of *E. nigrum* were found to be fairly common in early Holocene lake sediments from the Scoresby Sund region (Funder, 1978). Thus it appears that *Empetrum nigrum* was the first dwarf shrub that arrived in East Greenland after the last glacial stage, and the plant appears to have been more common during the early Holocene than later.

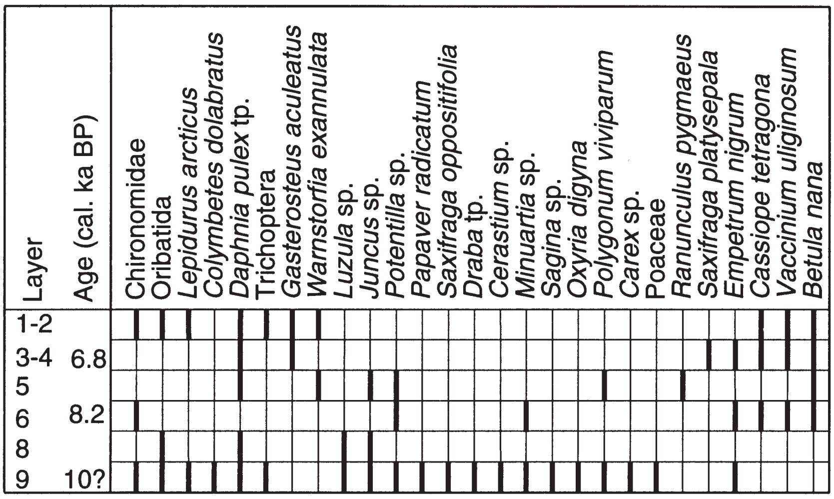

Figure 3 Macrofossil diagram from Peters Bugt Sø, amalgamated from two boring points, BP2 and BP6. See (Björck *et al.*, 1994b) for description of the stratigraphy.

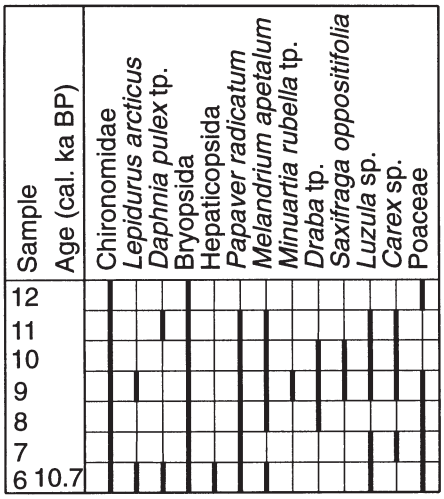

Figure 4 Macrofossil diagram from a raised delta ('50 m delta') about two km east of Peters Bugt Sø. Sample 94355 (Tables 1 and 2) comes from the same delta.

Sample 87460 which is dated to 10.4 cal. ka BP is the oldest sample from Jameson Land with *Saxifraga oppositifolia* remains, and this sample also contained one seed of *Saxifraga cespitosa*. Sample 100379 which is dated to 9 cal. ka BP contained fruits of the limnophyte *Hippuris vulgaris* and the sedge *Carex bigelowii*, but fruits of *Hippuris vulgaris* were also found in Early Holocene sediments from lake Boksehandsken (Björck *et al.*, 1994a), and the pollen record of *Hippuris vulgaris* extends back to around 10 cal. ka BP (Funder, 1978).

Sample 85850 and 87516 have been discussed by Böcher & Bennike (1996). These samples contain remains of two extralimital beetles, the ground beetle *Bembidion grapii* and the leaf beetle *Phratora (Phyllodecta)* cf. *polaris*. Sample 87516 from northern Jameson Land, dated to 7.8 cal. ka BP, contains a diverse flora, including six species of dwarf shrubs: *Betula nana*, *Salix herbacea*, *Harrimanella hypnoides*, *Vaccinium uliginosum*, *Empetrum nigrum* and *Dryas octopetala*. Non-woody, vascular plants are represented by nineteen taxa.

DISCUSSION

Much of the variation in the macrofossil assemblages may reflect differences in sample size and taphonomic processes, since samples from different types of geological archives have been analysed. However, since a fairly large material of early Holocene samples is now at hand from North-east Greenland, accidental differences between samples play a minor role. Absence of a certain taxon in a single sample may simply mean that its remains did not end up in the analysed sediments. However, if a taxon that produces abundant and robust macrofossils is not represented in a whole suite of sediment samples, it may be argued that it is unlikely that this taxon occurred in the area during the deposition of the sediments.

Only thirteen taxa of vascular plants have been identified from deposits dating to the first 500 years of the Holocene, but several of these taxa represent without any doubt several species. All taxa are herbs. The four named species of vascular plants, *Papaver radicatum* (here taken as a synonym of *Papaver* sect. *Scapiflora*), *Melandrium apetalum*, *Oxyria digyna* and *Saxifraga oppositifolia*, have wide geographical ranges in arctic and alpine regions, but they hardly extend south of or below the arctic/alpine tree line. In Greenland, *Melandrium apetalum* is confined to the high-arctic parts, whereas the other species can be found all over Greenland. However, these species become increasingly important towards the northern parts of Greenland, and they can be characterized as hardy plants that are adapted to low summer temperatures. These species are also characteristic of unstable soils, and they are often found as pioneer species on recently deglaciated terrains.

The question still remains whether these hardy plants that grew in North-east Greenland almost immediately after the abrupt warming at 11.5 ka BP immigrated (from North-west

Table 2. Macrofossils

Age (cal. ka BP)	11.0	8.6	7.9	11.8	11.0	11.0	10.9	10.9	11.0	10.4	10.4	9.5	9.4	9.0	9.0	8.7	7.8
Sample No.	94355	94378	9201	85823	85844	100367	100363	100380/81	several*	87376	87460	96034	85847	100379	85824/25	85850	87516
Plants																	
?Pyrenomycetidae	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cennococcum geophilum	–	–	r	–	–	–	–	–	–	–	r	–	–	–	–	–	c
Bryopsida	+	+	a	c	–	–	r	–	c	r	a	a	r	a	a	a	r
Polytrichum sp.	+	–	–	c	–	c	r	–	c	r	–	r	r	r	–	–	–
Distichium sp.	+	–	–	r	–	–	–	–	r	–	–	–	–	–	–	–	–
Hepaticopsida	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	r
Equisetum variegatum	–	–	c	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Equisetum sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Papaver radicatum	+	–	–	r	–	r	–	–	r	–	1	–	–	–	–	–	–
Betula nana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	a
Cerastium sp.	–	–	–	–	–	r	–	–	r	–	r	r	–	–	–	–	r
Melandrium apetalum	+	–	–	r	–	r	–	–	r	r	–	–	–	–	–	–	–
Melandrium triflorum	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Minuartia sp.	+	1	r	r	–	r	–	–	r	–	r	r	–	–	–	–	r
Armeria scabra	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oxyria digyna	–	–	r	r	–	c	r	–	c	1	r	–	–	–	–	–	c
Polygonum viviparum	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Rumex acetosella	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Draba tp.	+	1	–	r	–	r	–	–	r	–	r	–	–	–	–	–	r
Arabis alpina	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	r
Salix herbacea	–	–	c	–	–	–	–	–	–	–	–	–	–	–	–	–	c
Callitriche palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Harrimenalla hypnoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Vaccinium uliginosum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Empetrum nigrum	–	–	a	–	–	–	–	–	–	r	1	c	–	r	r	a	r
Potentilla sp.	–	1	c	1	–	–	–	–	–	r	r	r	–	1	r	–	c
Sibbaldia procumbens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	r
Dryas octopetala	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Saxifraga oppositifolia	+	–	–	–	–	–	?	–	?	–	c	–	–	–	–	–	r
Saxifraga cespitosa	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Hippuris vulgaris	–	–	–	–	–	–	–	–	–	–	–	–	2	–	r	–	–
Pedicularis hirsuta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Taraxacum phymatocarpum	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Taraxacum articum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Juncus sp.	+	+	r	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Luzula sp.	+	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Carex bigelowii	–	–	–	–	–	–	–	–	–	–	–	–	–	r	–	c	–
Carex sp.	+	–	c	r	–	r	–	–	r	r	c	r	r	–	r	r	r
Eriophorum sp.	–	–	r	–	r	–	–	–	–	–	–	–	–	–	–	–	r
Poaceae	+	–	r	r	–	r	–	–	c	1	c	–	r	–	–	–	r

Table 2. *continued*

Age (cal. ka BP)	11.0	8.6	7.9	11.8	11.0	11.0	10.9	10.9	11.0	10.4	10.4	9.5	9.4	9.0	9.0	8.7	7.8
Sample No.	94355	94378	9201	85823	85844	100367	100363	100380/81	several*	87376	87460	96034	85847	100379	85824/25	85850	87516
Animals																	
Daphnia pulex tp.	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Simocephalus vetulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r	–	–
Lepidurus arcticus	?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Candona sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Bembidion grapii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Phratora (Phyllodecta) cf. *polaris*	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	r	r
Nysius groenlandicus	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	r	–
Hymenoptera	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	r	–
Nematocera	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	r
Syrphus torvus	–	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chironomidae	+	1	r	–	–	–	–	–	–	1	–	r	–	–	–	r	r
Oribatida	+	–	r	–	–	–	–	–	–	–	–	–	–	–	r	r	r
Lepus arcticus	–	–	c	–	–	–	–	–	–	–	–	–	–	–	–	–	–

r: rare; c: common; a: abundant; +: present; –: absent; 1–9: absolute numbers. Nomenclature for vascular plants follows Böcher *et al.* (1978)
*100352, 100362, 100364–100367, 199382–100384 that are *c.* 9.7 ka old are included here

Europe?) or survived the temperature minimum of the last glacial stage. And if they immigrated, would they be able to immigrate to NE Greenland during the late glacial period when the recession and thinning of the Inland Ice had begun? That could explain their widespread presence in NE Greenland in the earliest Holocene.

Woody plants require fairly high summer temperatures, with a mean July temperature above 3 °C (Edlund & Alt, 1989), and it seems most unlikely that they should have been able to survive the exceedingly severe climatic conditions of the last glacial stage in NE Greenland, or even the late glacial. From the data presented here it appears that *Empetrum nigrum* was the first dwarf shrub to arrive in NE Greenland, but this species certainly is not a cold resistant species; and it does not grow in the northern parts of Greenland at the present. The berries of this plant are eaten by birds, and endozoic transport of the fruit stones by birds seems to be the most likely mechanism for dispersal of diaspores of this plant across wide expanses of water.

The next woody plants to colonize NE Greenland could be *Salix herbacea* and *Dryas octopetala*. Funder (1979) found frequent pollen grains of these species in lake sediments that are now dated to *c.* 10 cal. ka BP, but the macrofossil record of these species only extends back to around 7.9 cal. ka BP (Fig. 7). Like *Empetrum nigrum*, *Salix herbacea* is not particularly cold adapted, whereas *Salix arctica* which is widespread in the northern parts of Greenland today, appears to be a late immigrant to NE Greenland, arriving around 6.8 cal. ka BP (Funder, 1978), even though it was present on Ellesmere Island at 8.6 cal. ka BP (Blake, 1993). Pollen analysis indicate that *Cassiope tetragona* arrived in central East Greenland around 6.8 cal. ka BP (Funder, 1979), but macrofossils of this species are present in somewhat older lake sediments from Peters Bugt Sø on Hochstetter Forland (Fig. 3) and from Jameson Land (Bennike & Funder, 1997).

With respect to arthropods, five named species of insects and three named species of crustaceans have been reported from the early Holocene of North-east Greenland. The presence of the leaf beetle *Phratora (Phyllodecta)* cf. *polaris*, the ground beetle *Bembidion grapii and* the seed bug *Nysius groenlandicus* in NE Greenland was discussed by Böcher & Bennike (1996). The records of *Phratora (Phyllodecta)* cf. *polaris* are especially enigmatic, since this species has not been recorded from Greenland alive, even though the fossil records show that it was widespread in NE Greenland in the early Holocene. The species was undoubtedly favoured by the warmer climates that prevailed then (Fig. 1), but how the species was transported to NE Greenland, presumably from north-west Europe, is hard to understand. However, it appears that both vascular plants and beetles are much more mobile, even across the North Atlantic Ocean, than earlier assumed (Coope, 1986; Birks, 1991). Thus the small volcanic island Jan Mayen in the Greenland Sea, which has never been connected to the mainland, houses sixty-two species of vascular plants (Lid, 1964), all of which must have arrived by long distance chance dispersal.

Aerial transport is presumably the principal means of dispersal of algae (Kristiansen, 1996), fungi, bryophytes,

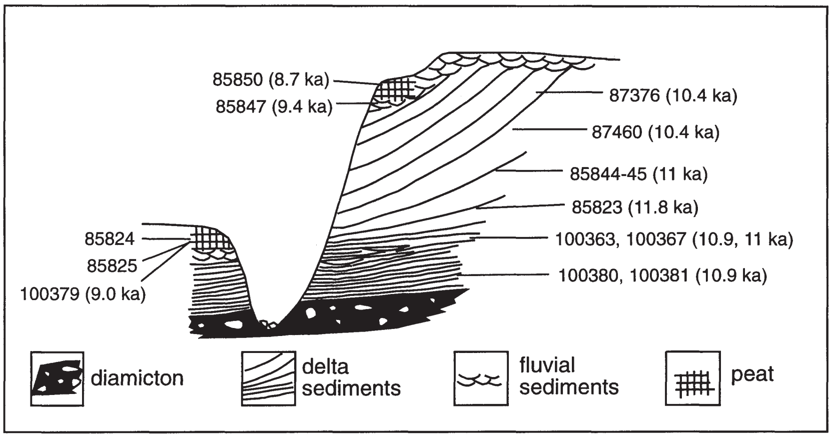

Figure 5 Schematic diagram showing a composite section across a river flanked by delta terraces in western Jameson Land. A diamicton (interpreted as a debris flow deposit) is overlain by prograding delta sediments, fluvial sediments and locally peat. Note that the oldest plant remains do not always come from the oldest sediments, showing that some reworking of plant remains has occurred.

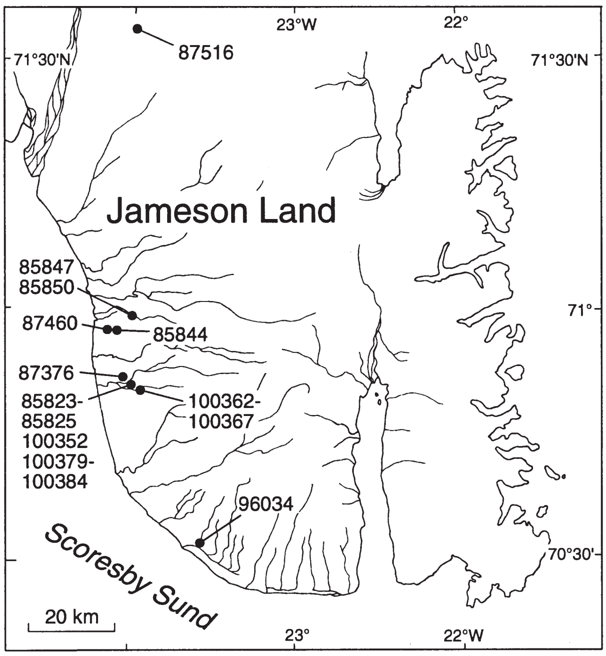

Figure 6 Map of Jameson Land showing fossil localities. For the location of Jameson Land in Greenland see Figure 2.

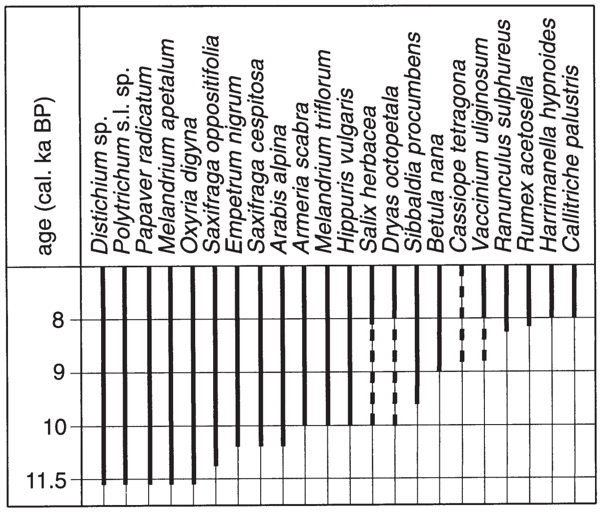

Figure 7 Diagram showing the early Holocene record of some North-east Greenland plants in order of oldest record, based on this study, Funder (1978, 1979), Björck *et al.* (1994a), Fredskild (1995) and Bennike & Funder (1997).

pteridophytes, small insects (Felt, 1928; Holzapfel & Harrell, 1968), spiders (Brændegaard, 1938) and many freshwater organisms, e.g. (Wesenberg-Lund, 1895). Wind dispersal may also be effective for some angiosperms that have either small diaspores or diaspores adapted to wind dispersal. In this context it should be noted that unexpectedly large mineral grains are blown across the Pacific Ocean (Betzer *et al.*, 1988). Other transport agencies could be driftwood (Ingvarson, 1903), ice bergs, ice islands and sea ice (Hultén, 1962; Coope, 1986). When Dusén (1901) first decribed *Draba sibirica* from Jameson Land, he suggested that it had arrived from Siberia with the Transpolar Drift. On the other hand, Böcher (1974) suggested that the species spread to East Greenland via northern North America and North Greenland before the last glacial stage and achieved a circumpolar range, but died out over its North American range during the last glacial stage. In Jameson Land the species survived in a local refugium. However, given the species narrow ecological amplitude in Jameson Land (Fredskild *et al.*, 1986), we consider it unlikely that it could survive the harsh conditions of the last glacial stage. We follow Dusén and suggest that *Draba sibirica* was dispersed from Siberia to East Greenland by sea ice during the Holocene.

Birds may also be an important tranport medium (Cruden, 1966; DeVlaming & Proctor, 1968; Gillham, 1970). At the present, about 250,000 pink-footed geese *Anser brachyrhynchus* and 38,000 barnacle geese *Branta leucopsis* migrate to central East Greenland from North-west Europe (J. Madsen, pers. comm. 1997). A small population of Brent goose *Branta bernicla* migrate from Norway to eastern North Greenland, and recent satellite tracking of two birds showed that this nonstop flight of *c.* 3500 km was accomplished in 83 h (Clausen & Bustnes, 1997). Geese may have immigrated to NE Greenland in the early Holocene, and we suggest that these large, migrating birds constitute a main vector for the dispersal of plants and animals to Greenland. Many nonbreeding geese arrive in Greenland after the summer season, and postbreeding northwards dispersive movements are also common.

Ice rafting was suggested as the primary mode of dispersal for beetles and other animals and plants from Europe to Greenland, shortly after 11.5 ka BP (Coope, 1986; Buckland, 1988). One argument supporting this scenario was that surface ocean currents were thought to have followed a short course from Europe to Greenland at this time, but newer palaeoceanographic results appear to indicate that the currents in the North Atlantic were not much different from those of today at this time (Koc *et al*., 1993; Hald & Aspeli, 1997). In addition, deglaciation of the ice free parts of Greenland had scarcely begun at 11.5 ka BP.

Another argument that supports a young age for the Greenland flora and fauna is the very low number of endemic species. Among vascular plants most endemic taxa are classified as subspecies, varieties or forms, which might well have formed during recent millenia (Nordal, 1987). One species endemic to central East Greenland, *Saxifraga nathorstii*, is probably a hybrid between *Saxifraga oppositifolia* and *S. aizoides* (Böcher, 1983), but we suggest that it could have formed during the Holocene. Among vertebrates, the east Greenland reindeer and wolf have been described as separate subspecies. However, the extinct East Greenland *Rangifer tarandus eogroenlandicus* is probably a synomyn of *Rangifer tarandus pearyii* from northernmost Canada (Meldgaard, 1986), and the Greenland wolf *Canis lupus orion* is considered a synonym of *Canis lupus arctos* because *C. lupus orion* was described on a North-west Greenland specimen that was undoubtedly a straggler from Canada (Pocock, 1935; Bennike *et al*., 1994). Both reindeer and wolf remains from North Greenland have been dated to the early or mid Holocene (Bennike, 1997), and these species were presumably also present in NE Greenland this early.

CONCLUSIONS

Only few taxa of vascular plants have been recovered from NE Greenland sediments that date to the first 500 years of the Holocene. The macrofossil floras comprise only four named species, which can be classified as hardy species that may have immigrated to NE Greenland during the late-glacial. We suggest that all woody plants are Holocene immigrants, and that the first immigrants came from north-west Europe by chance dispersal. The main agent for dispersal of vascular plants to NE Greenland was probably migrating geese. By 8 ka BP diverse floras suggest that a major part of the modern species of vascular plants had immigrated. We also consider all vertebrates Holocene immigrants, and this may also apply to a major part of the NE Greenland invertebrate fauna. It may be speculated that some species of sporophytes and some animals that can endure short summers with low temperatures, and which can live in geographically small areas, could have survived the last glacial stage in nonglaciated areas.

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BIOSKETCHES

Ole Bennike is a research geologist. His fields encompass Quaternary geology, biology and climatology in the North Atlantic region. **Svante Björck** is professor in Quaternary Geology and has worked with stratigraphic and palaeoclimatic problems of the last glacial cycle around the N Atlantic, in N America and Antarctica. **Jens Böcher** is a zoologist. He studies modern and Quaternary Greenlandic insect faunas, and his main areas are ecology, biogeography and palaeoentomology. **Louise Hansen** is a Ph.D. student. She works with sedimentology and Quaternary stratigraphy in East Greenland. **Jan Heinemeier** is a research physicist and director of the Aarhus AMS ^{14}C Dating Laboratory. He specializes in methodological studies of calibration and ^{14}C reservoir effects. **Barbara Wohlfarth** is associate professor in Quaternary Geology. Her research focuses mainly on high-resolution records and palaeoclimate variations during the past 15,000 years.

Appendix. Nomenclatural authorities for the species mentioned in this paper

Cennococcum geophilum Fries
Warnstorfia exannulata (B., S. & G.) Loeske
Equisetum variegatum Schleich.
Ranunculus sulphureus Sol. in Phipps
Ranunculus pygmaeus Wbg.
Papaver radicatum Rottb.
Betula nana L.
Melandrium apetalum (L.) Fenzl
Melandrium triflorum (R. Br.) J. Vahl
Minuartia rubella (Wbg.) Hiern
Armeria scabra Pall.
Oxyria digyna L.
Polygonum viviparum L.
Rumex acetosella L.
Draba sibirica (Pall.) Thell.
Arabis alpina L.
Salix herbacea L.
Salix arctica Pall.
Callitriche palustris L.
Cassiope tetragona (L.) D. Don
Harrimanella hypnoides (L.) Coville
Vaccinium uliginosum L.
Empetrum nigrum L.
Sibbaldia procumbens L.
Dryas octopetala L.
Saxifraga oppositifolia L.
Saxifraga nathorstii (Dusén) Hayek
Saxifraga aizoides L.
Saxifraga cespitosa L.
Saxifraga platysepala (Trautv.) Tolm.
Hippuris vulgaris L.
Pedicularis hirsuta L.
Taraxacum phymatocarpum J. Vahl
Taraxacum arcticum (Trautv.) Dahlst.
Carex bigelowii Torr.
Daphnia pulex (De Geer)
Simocephalus vetulus (O. F. Müller)
Lepidurus arcticus (Pallas)
Bembidion grapii Gyllenhal
Amara alpina (Paykull)
Phratora (Phyllodecta) cf. *polaris* (Sparre-Schneider)
Colymbetes dolabratus (Paykull)
Nysius groenlandicus (Zetterstedt)
Syrphus torvus Osten Sacken
Portlandia arctica (Gray)
Gasterosteus aculeatus L.
Anser brachyrhynchus Baillon
Branta leucopsis (Becht.)
Branta bernicla (L.)
Lepus arcticus Ross
Canis lupus L.
Rangifer tarandus (L.)