The Quaternary arthropod fauna of Greenland: a review with new data

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Arthropod fossils from Quaternary deposits in Greenland are considered. The few occurrences of Early and Middle Pleistocene age have yielded only three species of barnacles. This contrasts sharply with the last interglacial stage which is represented by many sites, from which a range of marine, lacustrine and terrestrial crustaceans and insects are reported. The only secure late glacial sediments from Greenland are found in the far south, and only a few taxa of arthropods have so far been identified from these. The best dated and richest faunas come from the Holocene. Most records of insects are from the late Holocene, but there are also a number of finds from the early and mid Holocene. Arthropods are considered good palaeoclimate indicators, because they are generally dispersed quicker, for example, than vascular plants. This group of animals is also highly useful for reconstructing former ecological conditions, because they occupy such a wide range of biotopes. A total of about 105 taxa have been reported so far, but several groups of arthropods, such as marine ostracodes, chironomids and oribatids, have received little attention, and many more taxa can be expected when these groups are being studied in the future.

Key words: Greenland, Quaternary, biogeography, palaeoecology, Arthropoda, Insecta, Crustacea, Cladocera, Ostracoda.

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Arthropoda is by far the largest phylum within the animal kingdom, with millions of species that have adapted to almost all biotopes on Earth. The arthropods are characterized by a chitinous exoskeleton, which covers the whole body, and which is divided into segments. In many species the chitinous exoskeleton is impregnated with calcium carbonate. Amongst geologists, the most famous group of arthropods is the trilobites, but this group became extinct already during the Permian. Other groups of arthropods, such as ostracodes and insects, are also abundant in pre-Quaternary deposits.

In Greenland, the mean summer temperature declines from more than 11°C in the south to 3°C in the north, and the mean winter temperature from –6°C to –35°C. Scrub and heath vegetation is widespread in the lowlands of Greenland, but in the far south, at 60°N, small areas of birch forest are present. Polar deserts, without woody plants, are found in the far north. In North Greenland, permanent sea ice is found, but further south the period with open water increases. West Greenland is strongly influenced by the relatively warm northward flowing West Greenland Current, whereas East and South Greenland are influenced by the cold, southward flowing East Greenland Current.

The modern arthropod fauna of on-shore Greenland comprises about 700 species of insects, of which 35 are beetles, *c.* 50 are butterflies and moths, *c.* 60 species of spiders and *c.* 60 species of non-marine crustaceans (Røen 1962, Heide-Jørgensen & Johnsen 1997). These are rather small numbers considering the 410,000 km^2 of ice-free land, but it mainly reflects the cold climates of Greenland.

The most common groups represented in Quaternary deposits are insects and crustaceans, but other groups, such as mites and spiders, are also present, although the latter groups have received little attention. Among the insects, those with heavily sclerotised skeletons, such as beetles and non-biting midges, are most common, but other groups are also well represented.

Table 1. List of localities with remains of non-marine arthropods

Loc. No.*	Locality	N. lat.	W. long.	Sediments	Reference
1	Vølvedal	83°02′	34°21′	Peat	Bennike 1983
2	Klaresø	82°10′	30°34′	Gyttja	Fredskild et al. 1975
3	Lake on Amdrup Land	80°49′	15°00′	Gyttja	Fredskild 1995
4a	Hovgaard Ø	79°44.9′	18°51.6′	Marine delta	This study
4b	Hovgaard Ø	79°44.4′	18°48.3′	Marine delta	This study
5	"Midgårdsormen"	79°38.9′	21°08.1′	Marine delta	This study
6a	Lake near Blåsø	79°32.9′	23°53.1′	Gyttja	This study
6b	Section near Blåsø	79°38.3′	22°49.2′	Fluvial sed.	This study
7	Lambert Land	79°15.7¢	19°09.2′	Marine delta	This study
8a	Peters Bugt Sø	75°18.9¢	20°02.6′	Gyttja	Bennike et al. 1999
8b	G6	75°19′	19°58′	Marine delta	Bennike et al. 1999
9	Zackenberg	74°28′	20°40′	Marine delta	Bennike et al. 1999
10	Coloradodal	71°34′	23°58′	Fluvial sed.	Böcher & Bennike 1996
11a	"Boksehandsken"	70°44′	24°03′	Gyttja	Björck et al. 1994
11b	Lake near Lollandselv	70°55.3′	24°07.7′	Gyttja	Bennike & Funder 1997
11	Holocene sites			Peat, deltas	Bennike et al. 1999
11	Interglacial sites			Deltas	Bennike & Böcher 1994
11c	Interglacial site	70°28.9′	23°28.6′	Delta	This study
12	N5	59°54.69′	43°55.30′	Gyttja	Bennike & Björck 2000
13	Drepanocladus Dam	60°20′	44°16′	Gyttja	Fredskild et al. 1975
14a	Isoëtes Sø	59°58′	44°21′	Gyttja	Fredskild et al. 1975
14b	Spongilla Sø	59°58′	44°21′	Gyttja	Fredskild et al. 1975
14c	Kløftsø	60°03′	44°14′	Gyttja	Fredskild et al. 1975
15a	N1	60°08.20′	45°18.27′	Gyttja	Bennike & Björck 2000
15b	N16	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15c	N17	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15d	N18	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15e	N19	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15f	N21	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15g	N22	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15h	N23	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
15i	N24	60°02.20′	44°55.37′	Gyttja	Bennike & Björck 2000
16	N14	59°58.84′	44°58.79′	Gyttja	Bennike & Björck 2000
17a	Comarum Sø	61°08′	45°32′	Gyttja	Fredskild et al. 1975
17b	Galium Kær	61°10′	43°31′	Peat, gyttja	Fredskild et al. 1975
17c	Qassiarsuk	61°09′	45°31′	Peat	Fredskild 1978
18	Saarlluk Qaaqaa	64°24′	51°41′	Gyttja	Fredskild 1983
19	Terte, Lake A	64°28′	51°35′	Gyttja	Fredskild 1983
20a	Gården under sandet	64°06.1′	50°05.4′	Culture layers	Buckland et al. 1998
20b	Nipaaitsoq, V54	64°06.8′	50°07.1′	Culture layers	Buckland et al. 1983
20c	Niaquussat, V48	64°12.8′	50°22.7′	Culture layers	McGovern et al. 1983
21	Johs. Iversen Sø	64°24′	50°12′	Gyttja	Fredskild 1983
22	Karra	64°46′	50°35′	Gyttja	Fredskild 1983
23a	SFL 17	67°04.9′	50°27.5′	Gyttja	Eisner et al. 1995, Willemse pers. comm.
23b	Lille Saltsø	66°59.3′	50°38.6′	Gyttja	Bennike 2000
23c	Store Saltsø	66°59.4′	50°35.9′	Gyttja	Schmidt 1976, Bennike 2000
23d	Delta, Saaningassoq	67°06′	50°14′	Delta	Van Tatenhove et al. 1996, this study
24	Qeqertasussuk	68°35′	51°07′	Peat	Böcher & Fredskild 1993
25	Sermermiut	69°12′	51°11′	Peat	Haarløv 1967
26	Brændevinsskær	69°04′	53°32′	Peat	Bennike 1992
27	Fortunebay Lake	69°16′	53°50′	Gyttja	Bennike 1995
28	Qivittut Lake	69°26.5′	53°40′	Gyttja	Bennike 1995
29	Lake on Nuussuaq	70°28′5	4°01.6′	Gyttja	Bennike 2000
30	Lake on Svartenhuk	71°0.3′	53°59.6′	Gyttja	Bennike 2000
31a	Tuttulissuaq, Langesø	75°22′	58°36′	Gyttja	Fredskild 1985
31a	Tuttulissuaq, Rundesø	75°22′	58°36′	Gyttja	Fredskild 1985
32	Narsaarsuk	76°27′	69°35′	Marine deposit	Bennike & Böcher 1992
33	Qeqertat	77°30′	66°39′	Gyttja	Fredskild 1985
34	Kap Inglefield Sø	78°31.8′	72°21′	Gyttja	Blake et al. 1992
35	Washington Land W	80°24.5′	67°00.6′	Org. detritus	This study
36	Washington Land S	80°0.3′	61°55.2′	Peat	Bennike & Jepsen 2000
37	Warming Land N	81°57′	53°38′	Org. Detritus	Meldgaard & Bennike 1989
38	Wulff Land SW	81°21′	48°55′	Peat	Kelly & Bennike 1992
39	Wulff Land N	81°23′	49°10′	Pond deposit	Frey 1991

*See Fig. 1

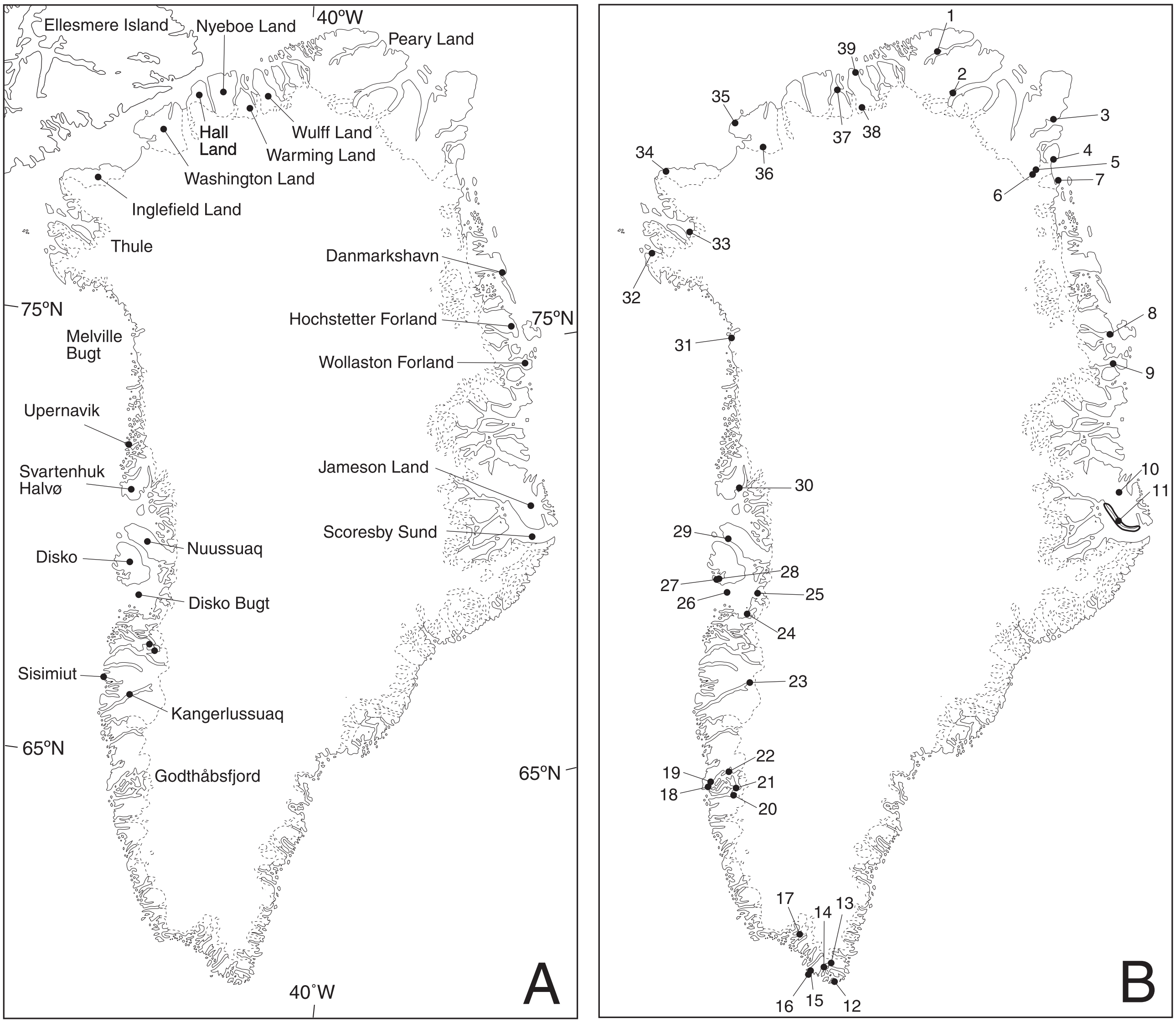


Figure 1. Maps of Greenland and northernmost Canada showing the locations of place names mentioned in the text (A) and sites with records of non-marine arthropods (B). The numbers refer to Table 1.

In Greenland, the first record of arthropods from Quaternary deposits dates back to the 17th century (Spengler 1790). During the past decades much data have been added to our knowledge of arthropod remains in Late Cenozoic deposits in Greenland, and the knowledge of arthropod remains is increasing at an accelerating rate. Rich faunas of beetles and other insects, lacustrine crustaceans and marine ostracodes have been reported from the Kap København Formation (Røen 1988, Brouwers, Jørgensen & Cronin 1991, Penney 1993, Böcher 1995), and marine ostracodes have been reported from the Lodin Elv Formation in East Greenland (Penney 1993). However, it is beyond the scope of this paper to review this evidence, because the age of these formations is believed to be 2 to 3 million years, and these formations can be considered to be of pre-Quaternary age (Bennike 1990, Símonarson, Petersen & Funder 1998). The information on Quaternary arthropods is highly scattered in the literature, and in addition to reviewing this information, a large amount of unpublished data is included in this outline. Reviews on Greenland Quaternary vertebrates and Holocene macro-limnophytes have been published by Bennike (1997) and Fredskild (1992), and the last review on the Quaternary geology of Greenland was published by Funder (1989).

The ages reported here are based on radiocarbon dates, which have been calibrated using the INTCAL98 calibration dataset (Stuiver, Reimer, Bard, Beck, Burr, Hughen, Kromer, McCormac, Plicht & Spurk 1998). This means that ages younger than 11,500 years BP are of Holocene age, and all dates thus refer to calibrated years before present when dealing with Holocene records. Marine dates have been corrected for the marine reservoir age before calibration (Bennike 1997). Pre-Holocene records are mainly dated or correlated by thermoluminescence and optically stimulated luminescence dating, and by amino acid analyses. The terms early, mid and late Holocene are here used as "loose" terms, and the term late glacial is used for the time period between Greenland stadial 2 and the Holocene (Björck, Walker, Cwynar, Johnsen, Knudsen, Lowe, Wohlfarth & INTIMATE members 1998). Thus the latter term is used only in areas where pre-Holocene sediments from the latest part of the last glacial stage are found. The last glacial stage corresponds to oxygen isotope stages 2–5d, and the last interglacial stage corresponds to oxygen isotope stage 5e.

Arthropod remains come from diverse settings. By far the most numerous remains are found in Holocene lake sediments, which may contain thousands of Cladocera remains per ml. Remains of terrestrial species are also often found in lake deposits. Peat deposits are dominated by terrestrial species, and deltaic and fluvial deposits can sometimes also contain arthropod remains. Raised marine, deltaic and littoral deposits provide a rich source for marine species, and reworked specimens are occasionally found in till. In addition, archaeological sites are often rich in arthropod remains (Buckland, Sveinbjarnardóttir, Savory, McGovern, Skidmore & Andreasen 1983, Böcher & Fredskild 1993). A list of localities with fossils of non-marine arthropods is provided in Table 1, and the locations appear on Figure 1.

When naming remains of arthropods from Quaternary deposits, identification keys are of limited value, because the characteristics used in the keys usually are missing. Therefore it is essential to compare the fragments found with reference material of whole animals collected alive and housed in museum or private collections (e.g., Elias 1994). However, in some cases, illustrations can be of some value, such as those of Cladocera presented by Frey (1958, 1962). Scanning electron microscope photographs of ostracode shells may also be diagnostic, and egg sacs of copepods were identified, although tentatively, by comparisons with line drawings published by Røen (1957).

Table 2. Non-marine arthropods in interglacial deposits

Taxon	Jameson Land	Thule area	Washington Land	Warming Land	Zackenberg
CRUSTACEA					
Lepidurus cf. *arcticus*	+	+	-	+	-
Daphnia cf. *pulex*	+	+	+	+	-
COLEOPTERA					
Elaphrus tuberculatus Mäklin	+	-	-	-	-
Amara alpina (Paykull)	+	+	+	-	+
Cymindis vaporariorum (Linnaeus)	+	-	-	-	-
Hydroporus morio Aubé	+	-	-	-	-
Hydroporus cf. *planus* (Fabricius)	+	-	-	-	-
Colymbetes dolabratus (Paykull)	+	-	-	-	-
Agabus bipustulatus (Linnaeus)	+	-	-	-	-
Eucnecosum cf. *tenue* (LeConte)	+	-	-	-	-
Olophrum consimile (Gyllenhal)	+	-	-	-	-
Stenus carbonarius Gyllenhal	+	-	-	-	-
Byrrhus fasciatus (Forster)	+	-	-	-	-
Simplocaria metallica (Sturm)	+	-	-	-	-
Coccinella cf. *hieroglyphica* (Linnaeus)	+	-	-	-	-
Nephus bisignatus (Boheman)	+	-	-	-	-
Otiorhynchus arcticus (O. Fabricius)	+	-	-	-	-
Otiorhynchus nodosus (Müller)	+	-	-	-	-
Lepyrus arcticus Paykull	+	-	-	-	-
Lepyrus nordenskioeldi Faust	+	-	-	-	-
Isochnus arcticus (Korotyaev)	-	+	-	-	-
HYMENOPTERA	+	-	-	-	-
Bombus sp.	+	-	-	-	-
HEMIPTERA					
Nysius groenlandicus Zetterstedt	+	+	+	-	-
DIPTERA	+	+	+	+	-
ORIBATIDA	+	+	+	+	-

Annotated list of selected taxa

This list comprises notes on species and higher taxa. It focuses on Holocene records and on new data. Complete lists of the taxa recorded are found in Tables 2–6.

Crustaceans

Lepidurus arcticus (Pallas) (Conchostraca) – The known modern geographical range in Greenland of the arctic tadpole shrimp *Lepidurus arcticus* covers West Greenland between 66° and 79°N and East Greenland between 66° and 77°N, in addition to an isolated, high elevation occurrence in South Greenland (Fredskild & Røen 1982). Recently, the species was also found in a few ponds in western North Greenland, at 80°15′N (O. Bennike, unpublished, material deposited in the Zoological Museum, Copenhagen). The species is common on northern Ellesmere Island (Røen 1981), and may well be found in other parts of North Greenland in the future.

The mandibles of *L. arcticus* are highly distinctive, and although these can only be identified to the genus level, all fossil records from Greenland are referred to this species. Other parts of the exoskeleton are also encountered, including the species diagnostic supra anal plates. Eggs are also found, often being attached to water mosses.

Lepidurus cf. *arcticus* remains have been found in last interglacial sequences in Warming Land in North Greenland (Meldgaard & Bennike 1989), in the Thule area, Northwest Greenland (Bennike & Böcher 1992) and in Jameson Land in East Greenland (Bennike & Böcher 1994) (Table 2). The record from Warming Land was believed to lie north of the species' northern range limit, but considering the occurrence of the species on northern Ellesmere Island (Røen 1981), and the recent record from Washington Land, this may be questionable.

The oldest apparent record to post-date the last deglaciation comes from Wulff Land in central North Greenland. The deposit is dated to around 12500 years BP (GU-2588), but this date is probably subject to a considerable hard water effect (Kelly & Bennike 1992). Based on the regional deglaciation chronology, an early Holocene age, somewhat less than 11500 years BP seems more likely.

In South and West Greenland, several lake sequences show an early maximum of *L. arcticus* remains, followed by extinction or decline (Fredskild et al. 1975, Fredskild 1983, Bennike 2000a). This was assigned by Fredskild (1983) to early cold climates followed by warming, or a consequence of the ontogenetic development of the lakes (Bennike 2000a). Tadpole shrimps are important prey for fishes, and it is also possible that the species became extinct after the arrival of char or sticklebacks to the lakes (E. Jeppesen, pers. comm. 1999). A similar decline has not been reported from East Greenland (Bennike & Funder 1997). The oldest record in West Greenland is around 10300 years old (Bennike 2000a) and in East Greenland it is around 10700 years old (Bennike, Björck, Böcher, Hansen, Heinemeier & Wohlfarth 1999). Thus it appears that the species was widespread in Greenland in the early Holocene.

Daphnia pulex (De Geer) (Cladocera) – *Daphnia pulex* is a planktonic species of circum-Greenlandic distribution. It is eurytopic and found in many different lakes and ponds in Greenland (Røen 1962, 1968, 1981, 1994, Fredskild 1995).

Daphnia ephippia have been recorded from many sites in Greenland. Interglacial records are found in Meldgaard & Bennike (1989), Bennike & Böcher (1992, 1994), and Holocene records are found in Fredskild et al. (1975), Fredskild (1978, 1983, 1985, 1995), Bennike (1992, 1995, 2000a), Kelly & Bennike (1992), Björck, Bennike, Ingólfson, Barnekow & Penney (1994a), Björck, Wohlfarth, Bennike, Hjort & Persson 1994b), Bennike & Funder (1997), Bennike et al. (1999), Bennike & Björck (2000). The identification of *Daphnia* remains from early Holocene (?) sediments in North Greenland was discussed by Frey (1991) who concluded that the species present was *Daphnia pulex*. Other *Daphnia* ephippia have been referred to as *Daphnia pulex* type (Bennike 1995). Ephippia are the most common remains found, but shells and head shields (Fig. 2) were reported from the North Greenland deposit studied by Frey (1991), and head shields have later proved to be locally rather common in lake sediments

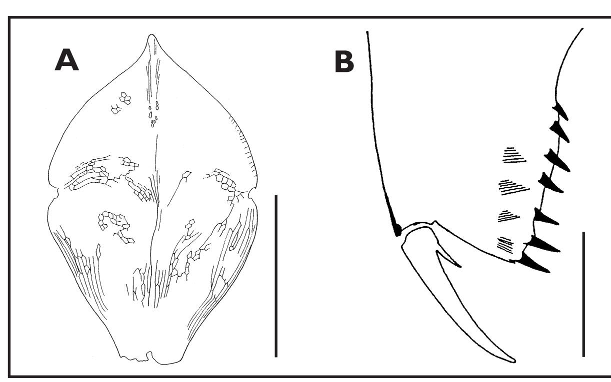


Figure 2. A: Head shield of *Daphnia pulex* (Crustacea: Daphniidae). Scale bar 600 µm; B: Postabdomen and postabdominal claw of *Alona guttata* (Crustacea: Chydoridae). Scale bar 30 µm. Modified from Frey (1991).

from both East, West and South Greenland (Björck et al. 1994a, Bennike 2000a, Bennike, unpublished).

With regard to isolation basins, a very marked peak in the abundance of *Daphnia* ephippia is often seen just after isolation (Björck et al. 1994a, Bennike 1995), which is believed to reflect the presence of nutrient-rich waters following emergence from the sea. In non-isolation basins, decreasing concentrations of *Daphnia* ephippia have been reported (Fredskild 1983), which is interpreted as an effect of oligotrophication.

D. pulex is one of the first species to colonize newly formed lake basins, whether this is a result of local deglaciation or a result of land uplift. However, in South Greenland, the species did not arrive until around 12500 years BP, more than 1000 years after the onset of lake sedimentation (Bennike & Björck 2000).

Simocephalus vetulus (O.F. Müller) (Cladocera) – All fossil ephippia of *Simocephalus* have been referred to the species *Simocephalus vetulus*, which is planktonic, common and widespread in the low-arctic parts of Greenland (Røen 1962, Fredskild et al. 1975). Another *Simocephalus* species, *S. serrulatus* (Koch), has only been found in two ponds in southernmost Greenland (Røen 1994). *S. vetulus* has been recorded from a number of Holocene sequences in South and West Greenland (Fredskild et al. 1975, Eisner, Törnqvist, Koster, Bennike & van Leeuwen 1995, Bennike & Björck 2000), with the oldest record dated to about 12400 years BP.

Bosmina sp. (Cladocera) – *Bosmina* spp. are planktonic fresh water animals that are widespread in Greenland (Røen 1962, 1968). Published accounts of *Bosmina* sp. remains come from Kap Inglefield Sø in western North Greenland, where the taxon was found in small numbers in a single sample dated to *c.* 8000 years BP (Blake, Bourcherle, Fredskild, Janssens & Smol 1992), and from Svartenhuk Lake where the species occurs back to around 9500 years BP (Bennike 2000a). Considering the wide geographical range in Greenland, it is surprising that there are not more records. Presumably, more works dedicated to studies of fossil Cladocera would yield more records.

Eurycercus glacialis Liljeborg (Cladocera) – This is a rather thermophilous species that is common only in South and Southwest Greenland, with the northernmost records from Svartenhuk Halvø and Scoresby Sund (Røen 1962).

Remains of this large cladoceran have been recorded from three lake sequences in South Greenland and from seven lake sequences in West Greenland (Fredskild, Jacobsen & Røen 1975, Fredskild 1983, Bennike 1995, 2000a, Eisner et al. 1995). The species appears to be a rather late immigrant to Greenland, with the earliest record dated to around 8000 years BP. The species mostly lives among macrolimnophytes, and its recent increase in a lake at the head of Kangerlussuaq corresponds to an increase in the macro-algae *Nitella* and *Cladophora* (Eisner *et al.* 1995).

Acroperus harpae (Baird) (Cladocera) – Fossil remains of this cladoceran were first reported from two lake basins in South Greenland by Fredskild et al. (1975), where it was present from *c.* 8700 ^{14}C years BP. It has later been recorded from a single lake sequence in central East Greenland where it did not appear until *c.* 6000 ^{14}C years BP (Bennike & Funder 1997), but until more East Greenland Holocene lake sequences are analysed, it cannot be determined if the species was such a late immigrant to East Greenland. In West Greenland, the species has been reported from two lake basins near the head of Kangerlussuaq (Eisner et al. 1995, Bennike 2000a). At one of the sites, a clear correspondence is seen between *A. harpae* and charophytes, and it appears that the species, which is highly dependent on submerged macro-limnophytes, lived among the charophytes. Further north in West Greenland, *A. harpae* has been reported from two isolation basins on Disko, from a basin on Nuussuaq, a basin on Svartenhuk Halvø, and two basins in Melville Bugt (Fredskild 1985, Bennike 1995, 2000a). A marked mid Holocene peak occurrence in the sequence from Svartenhuk Halvø indicates that the species was much more common during this period than before or after, but farther north in West Greenland it seems that the species was most common in the late Holocene. The northernmost records from West Greenland come from the Thule area where it seems to be rare (Røen 1981). Recent studies of lake sediments from southernmost Greenland show that the species was already present here around 13500 years BP, then became extinct during the Younger Dryas cold period, and re-immigrated about 10800 years BP (Bennike & Björck 2000). In this context it can be noted that *A. harpae* was one of only two cladocerans that persisted in Kråkenes Lake in western Norway during the harsh conditions of the Younger Dryas (Duigan & Birks 2000).

Alona guttata Sars (Cladocera) – Exoskeleton fragments and ephippia of the cladoceran *Alona guttata* Sars have been recovered from pond deposits in central North Greenland (Frey 1991, Fig. 2). The deposit was dated to *c.* 12500 years BP, but this dating, which was based on lacustrine macrofossils, is probably subject to some hard water effect, and the deposit may come from the earliest Holocene, around 11500 years BP. Postabdomens of *Alona guttata* were also found in three samples from a peat deposit in eastern North Greenland. The oldest of these samples was dated to 5600 years BP (K-3494, Bennike 1983). The species is very rare in the Arctic, and in Greenland the northernmost record is at 76°45'N (Røen 1962, 1992). However, it should be emphasised that the present day invertebrate fauna of North Greenland is poorly known, and whether the species has died out here or is still extant is unknown.

Alona affinis (Leydig) (Cladocera) – This species is in Greenland found up to *c.* 73°N (Røen 1992). Shells of it have been identified from two lakes in South Greenland, with the oldest record at around 7400 years BP (Fredskild et al. 1975).

Alona rustica Scott (Cladocera) – This species is unknown from the extant fauna of Greenland, but in South Greenland, a closely related species, *Alona fabricii* (Røen) was described by Røen (1992). The recent specimens from South Greenland were first referred to as *A. rustica* (Røen 1975).

A single shell was found in sediments dated to around 6300 years BP from Spongilla Sø in South Greenland (Fredskild et al. 1975). Even though all extant specimens from this area were referred to the new species *A. fabricii* by Røen (1992), the fossil specimen was retained as *Alona rustica*.

Chydorus arcticus Røen (Cladocera) – This species was erected by Røen (1987), but the distinction between this taxon and other taxa within the *Chydorus sphaericus* complex is not clear. However, all fossil *Chydorus* remains from Greenland are here referred to *C. arcticus*. The species is the most common cladoceran in Greenland, being very widespread in Greenland, both geographically and ecologically. Fossil remains have been reported from a lake in western North Greenland (Blake et al. 1992), a lake in central East Greenland (Bennike & Funder 1997), and from several lakes in South and West Greenland. In larger lakes, the species mostly lives in the littoral zone, but its remains are also common in profundal gyttja. The species was probably the first Cladoceran immigrant to Greenland, and the oldest remains of it in South Greenland are around 13800 years old. The species was even able to endure the harsh conditions of the Younger Dryas in southernmost Greenland (Bennike & Björck 2000).

Table 3. Marine ostracodes from Quaternary deposits in Greenland

Taxon	Pleistocene	Holocene
Acanthocythereis dunelmensis (Norman)	+	
Cytheretta teshekpukensis Swain	+	
Cytheroptoron montrosiense Brady, Crosskey & Brady		+
Cytheroptoron nodosoalatum Neale & Howe	+	
Finmarchinella barentzovoensis (Mandelstam)	+	
Hemicythere emarginata (Sars)		+
Roberrsonites tuberculatus (Sars)	+	
Sarsicytheridea bradii (Norman)	+	
Sarsicytheridea macrolaminata (Elofson)	+	
Sarsicytheridea punctillata (Brady)	+	
Xestoleberis depressa (Sars)		+

Sources: Brady 1878; Penney in Bennike et al. (1994)

Limnocythere sanctipatricii (Brady & Robertson) (Ostracoda) – This fresh water ostracode have been found in very few localities in Greenland. The finds are highly scattered and indicate a widespread,

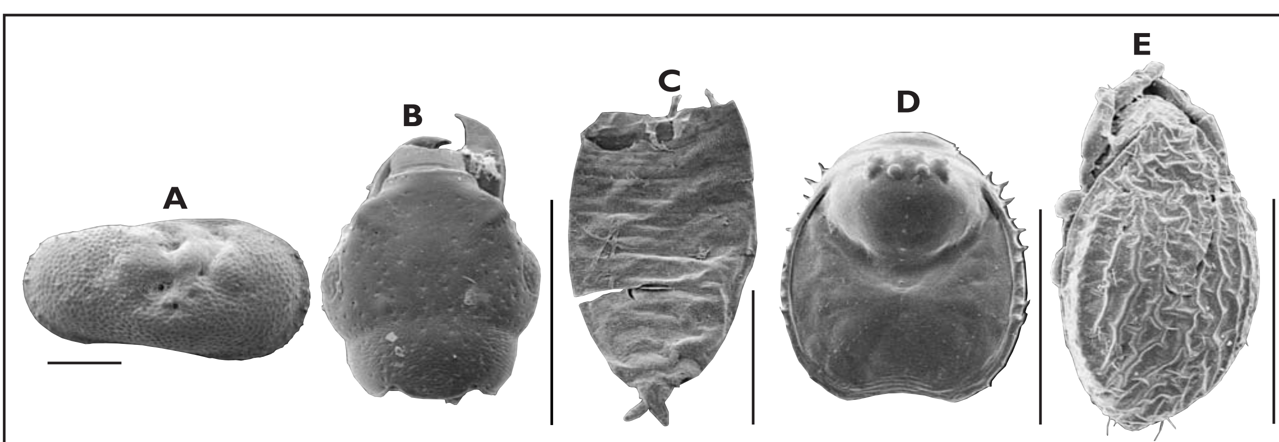


Fig. 3. A: Shell of *Ilyocypris bradyi* (Crustacea: Ostracoda), scale bar: 200 ìm ; B: Head of *Micralymma brevilingue* (Insecta: Coleoptera), scale bar: 0.5 mm; C: Puparium of Cyclorrapha indet. (Insecta: Diptera), scale bar: 1 mm; D: Cephalothorax of *Erigone* sp. (Araneae), scale bar: 1 mm; E: Exoskeleton of *Ameronothrus lineatus* (Acarina: Oribatida), scale bar: 0.5 mm.

circum-Greenlandic distribution (Røen 1962, 1968). Shells of the species have been found in sediments from Store Saltsø, dating back to *c.* 7000 years BP, and in late Holocene sediments in Lille Saltsø (Bennike 2000a). In addition, shells of *L. sanctipatricii* have been recovered from a lake sequence near Blåsø in northern East Greenland. Here the oldest sediments with the species present are around 7500 years old (Bennike unpublished).

Candona subgibba Sars (Ostracoda) – This species appears to have a markedly northern distribution in Greenland, being collected only in the Thule area and in Peary Land (Røen 1962, 1981). *C. subgibba* was originally described from arctic Canada, but in Delorme's monograph on the freshwater ostracodes of Canada, the species is not mentioned (Delorme 1970b). The name is probably a junior synonym of *C. pedata* Alm, 1914, which has been collected in arctic Canada (L. Denis Delorme, pers. comm., 2000).

As a fossil, *C. subgibba* has been reported from Klaresø in Peary Land (Fredskild et al. 1975), where the oldest shells were *c.* 3000 years old. Shells of the species have been tentatively identified from the early Holocene of northern Wulff Land (Kelly & Bennike 1992) and from Holocene lake sediments near Blåsø (loc. 6a, Table 1) in northern East Greenland, where the oldest sediments with the species present are around 7500 years old (Bennike unpublished). In addition, a single poorly preserved *Candona* sp. carapace found in Holocene deposits in Jameson Land could belong to this taxon (Böcher & Bennike 1996).

Ilyocypris bradyi Sars (Ostracoda) – There are no records of this ostracode from the modern day fauna of Greenland, but surprisingly shells were found over a short interval in Store Saltsø at the head of Kangerlussuaq. This spectacular occurrence, which was documented by (Bennike 2000a) (Fig. 3) is dated to around 7000 years BP. It is the first example of a non-marine species that apparently lived in Greenland during the peak of the Holocene warm period, and which later became extinct on the sub-continent.

Cypris pubera O.F. Müller (Ostracoda) – Shells of this large ostracode have only been recorded from two lake basins, both situated near the head of Kangerlussuaq (Bennike 2000a). In both lake sequences shells were rare, and the oldest shells were found in sediments dated to *c.* 4000 years BP. The finds are too few to determine if this represents the first occurrence of the species in Greenland. Extant populations of the species are known from only three localities in Greenland (Røen 1962).

Tonnacypris glacialis (Sars) (Ostracoda) – *T. glacialis* is of northern circumpolar distribution (Griffiths, Pietrzeniuk, Fuhrmann, Lennon, Martens & Evans 1998), and in Greenland it appears to be most common in the northern parts (Røen 1962).

Fossil records of the species come from Peary Land and Wulff Land in North Greenland (Fredskild et al. 1975, Kelly & Bennike 1992). The latter record is probably of earliest Holocene age (see above).

Heterocypris incongruens (Ramdohr) (Ostracoda) – The species is known as *Cyprinotus incongruens* from scattered localities throughout Greenland, except North Greenland (Røen 1962). However, the species was found to be fairly common in ponds in northern Ellesmere Island, and it may also be found in North Greenland in the future (Røen 1981).

Shells of the species were reported from Comarum Sø and Kløftsø in South Greenland by Fredskild et al. (1975). The oldest record is dated to *c.* 9000 years BP.

Potamocypris parva Schmidt (Ostracoda) – This is one of the few arthropod species that is considered endemic to Greenland. The species was erected on the basis of live specimens from Lille Saltsø and shells collected from peat deposits from fossil shorelines at Store Saltsø, both near the head of Kangerlussuaq (Schmidt 1976). During analysis of a sediment core from Store Saltsø, shells of this species were found in sediments dating back to *c.* 6000 years BP (Bennike 2000a). Shells of the species has also been recovered from late Holocene deposits of one of the other oligohaline lakes in this area, designated SS6, and it is presumably quite widespread in this area.

Sarscypridopsis aculeata (Costa, 1847) (Ostracoda) – There are no extant records of this species from Greenland, but it has been recorded from Iceland (Enckell 1980) and from Canada (Delorme 1970a). Thousands of decalcified shells of the species were recovered from isolation basins in South Greenland. However, it was not present in those basins that became isolated from the sea already in the Younger Dryas, only in those (N16, N18, N21, N22, N24) that became isolated in the early Holocene. The oldest dated record is about 10400 years old. The species is a non-marine species that is typical of lakes and ponds with elevated salinity.

Marine ostracodes – There are few reports of marine ostracodes from the Quaternary of Greenland, apart from those of the Kap København and Lodin Elv Formations mentioned above. *Cytheropteron montrosiense* Brady, Crosskey & Robertson has been reported from

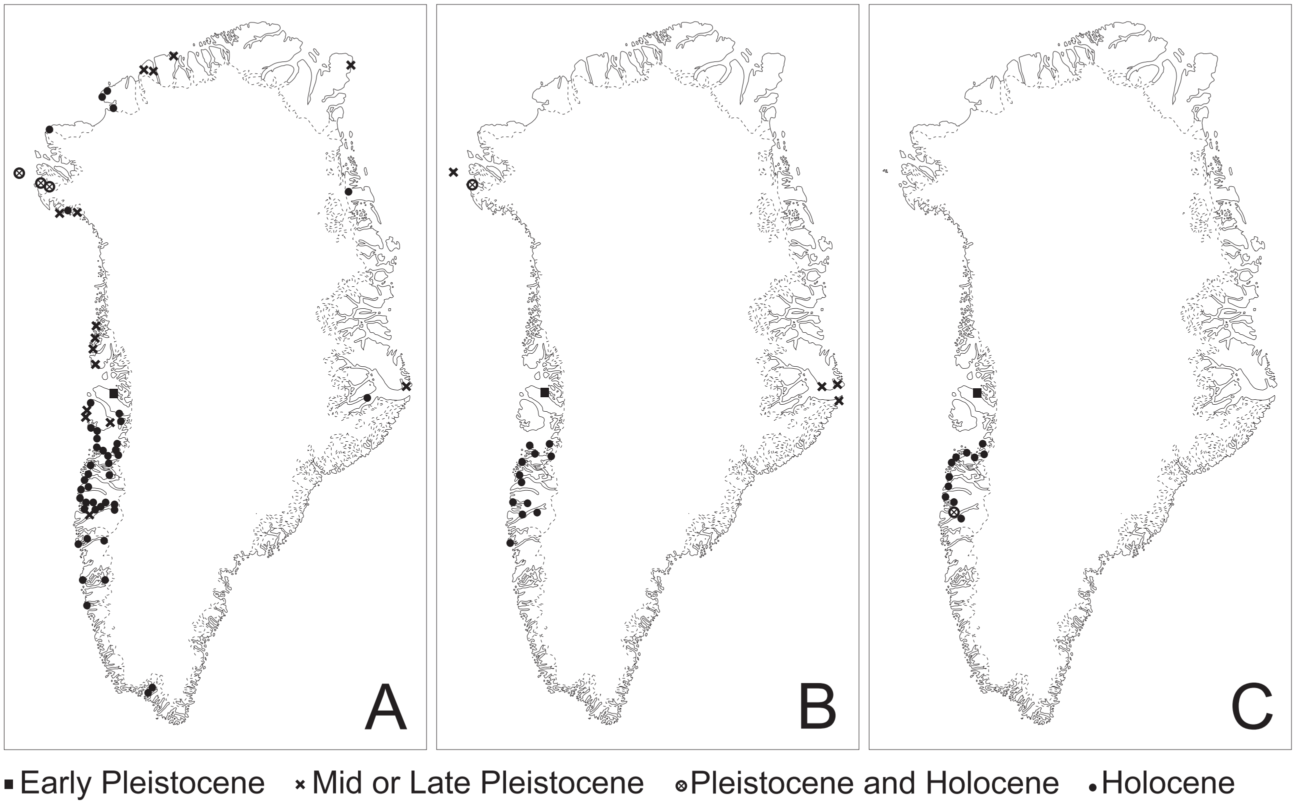


Figure 4. Maps of Greenland showing locations for Quaternary records of barnacles. A: *Balanus balanus*, compiled from Helland (1876), Kornerup (1879), Steenstrup (1881), Steenstrup (1883), Holst (1886), Hammer (1889), Jensen (1917), Quervain & Mercanton (1925), Laursen (1944, 1950), Harder et al. (1949), Weidick (1968, 1972a, 1972b, 1972c, 1973, 1975), Kelly (1973, 1975, 1979, 1980, 1986), Blake (1975, 1977, 1987), Funder (1978, 1979, 1990), Símonarson (1981), Funder & Símonarson (1984), Hjort (1987), Frich & Ingóflsson (1990), Kelly & Bennike (1992), Bennike et al. (1994), Mangerud & Funder (1994), Kelly *et al.* (1999) and Bennike (unpublished). B: records of *Balanus crenatus* based on Quervain & Mercanton (1925), Laursen (1944, 1950), Harder et al. (1949), Weidick (1968), Kelly (1973), Símonarson (1981), Funder (1990), Kelly et al. (1999), Mangerud & Funder (1994), Vosgerau et al. (1994). C: records of *Balanus hammeri*, compiled from Quervain & Mercanton (1925), Jensen (1942), Laursen (1944, 1950), Harder *et al.* (1949), Sugden (1972), Kelly (1973, 1986), Weidick (1974) and Símonarson (1981).

North Greenland by Brady (1878). This early record probably refers to Holocene deposits.

The only recent record of marine ostracodes is that of Penney in Bennike et al. (1994), who recorded two species from mid Holocene deposits, and eight species from Late Pleistocene deposits in West Greenland (Table 3). No doubt, Quaternary deposits in Greenland offer a large potential for studies of marine ostracodes.

Diaptomus castor (Jurine) (Copepoda) – Copepods play a large role in limnic ecosystems, but their exoskeleton does not normally preserve in Quaternary sediments (Frey 1964). However, copepod egg sacs, tentatively referred to as *Diaptomus castor*, have been reported from sediments from a single Greenland lake (Bennike 1998). The membrane of *Diaptomus castor* egg sacs which contain resting eggs is unusually thick, and can apparently be preserved. However, the species usually lives in ponds whereas it is rare in lakes, and the only Greenland record comes from a small, shallow lake.

Balanus hammeri (Ascanius) (Cirripedia) – The name of this barnacle is often spelt *B. hameri*, but since the species was named after G. Hammer, the correct spelling is *B. hammeri* (Jensen 1942). At present, the species occurs in the North Atlantic. Its distribution is mainly boreal, but a single live specimen was collected in West Greenland in 1911 around 68°N (Stephensen 1914, Jensen 1942). This is apparently the only live specimen collected in Greenland waters, and we suggest that this may represent a small population that has survived the cooling that followed after the mid Holocene warm period. Weidick (1976) considered *B. hammeri* a high arctic species, apparently because it was present in West Greenland already in the earliest Holocene, and Dyke, Dale & McNeely (1996, p. 175) suggested that it lives along the whole western coast of Greenland, but this is apparently not supported by extant records. The species normally occurs at water depths over 40 m (Stephensen 1933).

There are several fossil records from the last century of this species in West Greenland, but at least some of these appear to refer to *Balanus balanus* or *B. crenatus*. Thus the barnacles of Middle Pleistocene and Holocene deposits in western Disko are *B. balanus*, not *B. hammeri* as listed by Steenstrup (1883), see Bennike et al. (1994). The same probably applies to records by Hammer (1889), Jensen (1889) and Pjetursson (1898).

Fossil shell plates, sguta and terga occur rarely in the early Pleistocene Pattorfik beds in West Greenland (Símonarson 1981), and remains of the species are abundant at Eqalugsugssuit, a sequence in West Greenland considered to be of Middle Pleistocene age (Kelly 1986). Funder (1989) also recorded it from the last interglacial in West Greenland, but without information on the source. The species is known from Holocene raised marine deposits in West Greenland (Fig. 4), and it is fairly common in sediments from the classic locality at Orpigsooq in the southeastern part of Disko Bugt (Quervain & Mercanton 1925, Jensen 1942, Laursen 1944, 1950, Harder, Jensen & Laursen 1949, Sugden 1972). Samples of *B. hammeri* shells have been radiocarbon dated to *c.* 7900 and 8400 years BP (Weidick 1972a: K-1817, Kelly 1973: K-1557). Other dated samples from the region south of Disko Bugt that include the species gave ages between 10200 and 6400 years BP (Sugden 1972, Weidick 1974, Kelly 1979). It is apparent from this that the species was an early Holocene immigrant to the outer coast of West Greenland, and the documented temporal range of the species covers 4 millennia. The Holocene geographical range of the species was limited to a fairly small area (Fig. 4). The species immigrated earlier than another boreal species, the bivalve *Zirphaea arctica* (Linnaeus) (Jensen & Harder 1910, Funder & Weidick 1991). This species was for almost a century assumed to be extinct in Greenland waters, but a small extant population has now been found (Bennike 2000a). The early presence of *B. hammeri* shows that warm Atlantic water entered Baffin Bay in the early Holocene, in accordance with the early presence of subarctic species in the Thule area, at their present northern limit (see below).

Balanus balanus (Linnaeus) (Cirripedia) – The present day range of *B. balanus* is circumpolar, and it is very common in the northern Pacific and Atlantic Oceans. In Greenland waters, it is the most widely distributed species of *Balanus*. Thus it has been sampled northwards to Danmarkshavn in Northeast Greenland and in Nares Strait between Greenland and Canada (Miers 1877,1881, Stephensen 1943). It lives in depths from a few metres down to several hundred metres (Stephensen 1933).

B. balanus is by far the most widespread and common barnacle present in Quaternary marine deposits in Greenland. In the older literature, the synonym *B. porcatus* is normally used, and the species has also been reported under the name *B. sulcatus*. The species is abundantly present in the Pattorfik beds (Símonarson 1981), and it has been reported from Middle Pleistocene deposits on Disko (Funder & Símonarson 1984, Bennike et al. 1994), and elsewhere in West Greenland (Kelly 1986). *B. balanus* is recorded from the Ymer Formation (Middle Pleistocene) in Northeast Greenland (Hjort 1987). It is also reported from a number of sites in West, Northwest and East Greenland that are correlated with the last interglacial stage (Kelly 1986, Bennike et al. 1994, Mangerud & Funder 1994, Funder, Hjort, Landvik, Nam, Reeh & Stein 1998, Kelly, Funder, Houmark-Nielsen, Knudsen, Kronborg, Landvik & Sorby 1999), and in reworked, Late Pleistocene (?) faunas from Hall Land and Nyeboe Land in central North Greenland (Kelly & Bennike 1992).

There are numerous records of *B. balanus* from Holocene deposits in West Greenland, and it is the only barnacle species that has been found in Holocene sediments in East and North Greenland (Fig. 4). The oldest Holocene record comes from Disko and is around 11000 years old (Bennike, Hansen, Knudsen, Penney & Rasmussen 1994).

Balanus crenatus Bruguière (Cirripedia) – This species is widely distributed in the North Pacific and North Atlantic Oceans. In Greenland it extends all along the west coast up to the Thule area, whereas there is only one highly dubious record from East Greenland (Stephensen 1943). A specimen from Nares Strait has also, tentatively, been referred to this species (Miers 1881). Thus the interglacial finds from central East Greenland are considered southern extralimital records (Mangerud & Funder 1994). This barnacle is most common in shallow waters (Stephensen 1933).

The zoologists Reinhardt (1857), Lütken (1875) and Stephensen (1913) identified Spengler's *Lepas foliaceae* (Spengler 1790) as *Balanus crenatus*, a viewpoint followed here, although Pjetursson (1898) thought that the name refers to *B. hammeri*. It appears that Spengler was the first to report on a Quaternary invertebrate fossil from Greenland. During the 19th century, the species had been reported from the Pattorfik beds (Símonarson 1981), from pre-Holocene deposits in the Thule area (Funder 1990, Kelly et al. 1999) and from last interglacial deposits at Scoresby Sund in central East Greenland, where it was common near the mouth of the fjord (Mangerud & Funder 1994, Vosgerau, Funder, Kelly, Kronborg, Madsen & Sejrup 1994, Funder et al. 1998). The species also occurs in Holocene deposits in Southwest Greenland (Nordmann in Quervain & Mercanton 1925, Laursen 1944, 1950, Harder *et al.* 1949, Weidick 1968, Kelly 1973). The latter author reports on two radiocarbon dated samples that each included one *B. crenatus.* These were dated to 7600 and 8200 years BP (K-1550, K-1552). The species was also recorded from several Holocene faunas in the Thule area, Northwest Greenland, dated to between 9000 and 10200 years BP (Blake 1975, Funder 1990: GSC-2079, K-4781). These dates show that the species already occurred at its present northern range limit in the early Holocene, similar to the subarctic bivalve *Mytilus edulis* (Funder 1990).

Balanus balanoides (Linnaeus) (Cirripedia) – This barnacle lives in inter-tidal littoral waters, and it is often so abundant that it forms a white band on rocky shores. It is confined to areas where the coastal waters are ice free for several months during the summer, and its northern range limit in West Greenland is around Upernavik (Stephensen 1936, Madsen 1940, Vibe 1950). There is a single, maybe doubtful fossil record of this species from West Greenland by Steenstrup (1883). Apart from that, remains of the species are locally common in pre-Holocene deposits in the Thule area. The deposits belong to the Qarmat marine event that is correlated with the last interglacial stage (Funder 1990, Kelly *et al.* 1999). The fossil finds are located around 600 km north of the modern northern range limit.

Isopoda – The isopod *Saduria sabini* (Kröyer) (reported as *Idothea sabinei* Kröyer) was mentioned from Holocene marine deposits in West Greenland by Nordenskiöld (1871) and Harder et al. (1949). The species is circumarctic and has been recorded from West and East Greenland (as *Mesidothea sabini*) (Stephensen 1936, 1943, Kusakin 1982). The species lives on soft and rocky bottoms. Hammer (1889) has reported on *Idothea* sp., also from Holocene deposits in West Greenland. This find presumably refers to the same species.

Decapoda – The hermit crab *Pagurus* sp. was reported by Steenstrup (1883) from Holocene deposits in West Greenland, and the spider crab *Hyas* sp. was reported by Weidick (1972c) from Holocene deposits in southwest Greenland.

Table 4. Insects from Holocene deposits in Greenland

Taxon	Pre-Eskimo	Palaeo-Eskimo	Norse
PSOCOPTERA			
Liposceles sp.	-	+	-
ANOPLURA			
Damalinia ovis Linnaeus	-	-	+
Damalinia caprae (Gurlt)	-	-	+
Pediculus humanus Linnaeus	-	-	+
P. humanis/capitis Linnaeus	-	-	+
HEMITERA			
Nysius groenlandicus (Zetterstedt)	+	+	+
Chlamydatus pullus (Reuter)	-	+	-
Nabis flavomarginatus Scholz			
Psylla cf. *groenlandica* Sale	-	+	-
Psylla ?alni Linnaeus	-	+	
?Deltocephalus/Macrosteles sp.	-	+	
Aphidoidea	-	+	-
TRICHOPTERA			
Apatania zonella Zetterstedt	+	-	-
Limnephilus sp.	+	-	+
COLEOPTERA			
Bembidion grapii Gyllenhal	+	+	+
Trichocellus cognatus (Gyllenhal)	-	+	+
Hydroporus morio Aubé	+	+	+
Colymbetes dolabratus (Paykull)	+	+	+
Gyrinus opacus Sahlberg	+	-	-
Micralymma marinum (Ström)	-	+	-
M. brevilingue Schiödte	-	+	-
Atheta islandica (Kraatz)	-	-	+
Atheta hyperborea Brundin	-	+	-
Euaestethus laeviusculus Mannerheim	-	+	+
Eusphalerum sorbi (Gyllenhal)	-	-	+
Xylodromus concinnus (Marsham)	-	-	+
Quedius mesomelinus (Marsham)	-	-	+
Philonthus politus (Linnaeus)	-	-	+
Cryptophagus sp.	-	-	+
Atomaria sp.	-	-	+
Caenoscelis ferruginea (Sahlberg)	-	-	+
Simplocaria metallica (Sturm)	+	+	+
Simplocaria elongata Sahlberg	-	-	+
Byrrhus fasciatus Forster	-	+	+
Nephus redtenbacheri (Mulsant)	-	-	+
Coccinella transversoguttata Falderman	-	+	+
Phratora cf. *polaris* (Sparre-Schneider)	+	-	-
Lathridius pseudominutus Strand	-	-	+
Lathridius minutus Linnaeus	-	-	+
Corticaria linearis (Paykull)	-	-	+
Corticaria cf. *rubripes* Mannerheim	-	+	-
Otiorhynchus arcticus (O. Fabricius)	-	-	+
Hypera diversipunctata (Schrank)	-	-	+
Rutidosoma globulus (Herbst)	-	-	+
Dorytomus imbecillus Faust	-	+	-
HYMENOPTERA indet.	+	+	+
SIPHONAPTERA			
Ceratophyllus cf. *vagabundus* Boheman	-	+	-
DIPTERA			
Tipula arctica Curtis	-	+	-
Limonia sp.	+	-	-
Chironomidae indet.	+	+	-
Aedes cf. *nigripes* Zetterstedt	-	+	-
Heleomyza serrata (Linnaeus)	-	-	+
Neoleria ?septentrionalis Coll.	-	-	+
Leptocera sp.	-	-	+
?Delia sp./Calythea micropteryx Thoms.	-	-	+
Scatophaga sp.	-	-	+
?Piophila sp.	-	-	+
Syrphus torvus Osten-Sacken	+	-	-
Protophormia terraenovae (Robineau-Desvoidy)	-	+	-
Melophagus ovinus (Linnaeus)	-	-	+

Sources: see text

Insects

Nysius groenlandicus (Zetterstedt) (Hemiptera) – Remains of the seed bug *Nysius groenlandicus* (Zetterstedt) have been reported from several interglacial and Holocene sites (Tables 2, 4). The first pre-Holocene record was from the Thule area in Northwest Greenland, from near-shore marine sediments first dated to 70–105 ka BP (Funder 1990), but now correlated with the last interglacial stage, at 115–130 ka BP (Kelly et al. 1999). From central East Greenland, a few remains of the species have also been found in a sediment sample that is dated to the last interglacial (Bennike & Böcher 1994), and in North Greenland it was found at a site that has yielded non-finite radiocarbon dates, and a last interglacial age is tentatively also suggested for this site (Bennike & Jepsen, in press, Bennike, unpublished).

N. groenlandicus is a terrestrial species, and remains of it have only been found in a single lake sequence, from Svartenhuk Halvø in West Greenland (Bennike 2000a). The oldest remain was found in sediments dated to *c.* 9800 years BP. There are also two early Holocene records from East Greenland, one from a peat deposit on Jameson Land dated to *c.* 8700 years BP, and one from a raised delta deposit on Wollaston Forland dated to *c.* 7900 years BP (Bennike et al. 1999). There is no doubt that the species has lived in Greenland continuously since the early Holocene, and there are some mid Holocene records from the lake basin on Svartenhuk Halvø mentioned above, as well as from the archaeological site on Qeqertasussuk in Disko Bugt, where frequent remains of *N. groenlandicus* were found in layers dated to approximately 3000–4000 years BP (Böcher & Fredskild 1993). Near Sisimiut, a few remains of the species dated to *c.* 3000 years BP were found at another archaeological site (Böcher 1997, 1998). In addition, the species was represented by a single fragment in a sample from Norse layers in Godthåbsfjord (Buckland et al. 1983).

Psylla spp. (Hemiptera) – A few remains of *Psylla* sp. were found in lake sediments from Lille Saltsø, dated to between 3000 and 3500 years BP (Bennike 2000a). *Psylla* cf. *groenlandica* has been recorded from a Palaeo-Eskimo site (Böcher & Fredskild 1993), and *Psylla ?alni* has been found in Norse ruins (Buckland *et al.* 1983) (Table 4).

Apatania zonella Zetterstedt (Trichoptera) – Larval cases of Trichoptera (caddis fly) have been reported from different parts of Greenland (Fredskild et al. 1975). Two types were described, one with almost the same diameter along its axis, and another broadest at the middle, which were tentatively referred to *Limnophilus* sp. and *Apatania zonella*, respectively. Sclerites of Trichoptera larvae are also commonly encountered in lake deposits (Williams, Westgate, Williams, Morgan & Morgan 1981), but so far such remains from West Greenland have not been identified (Bennike 1995, Eisner et al. 1995, Bennike 2000a). Unidentified Trichoptera larval cases have been reported from late Holocene layers in South Greenland (Fredskild 1978).

A. zonella can be found all over Greenland, and it is the only Trichoptera species found in Northwest, North and Northeast Greenland (Stoltze 1981). Thus Holocene records of Trichoptera larvae from these parts of Greenland most likely represent *A. zonella* (Fredskild et al. 1975, Fredskild 1985, 1995, Bennike et al. 1999, Bennike, unpublished). The earliest Greenlandic record of Trichoptera remains referred to *A. zonella* comes from South Greenland, and is dated to around 10400 years BP (Fredskild et al. 1975).

Limnophilus sp. (Trichoptera) – In addition to caddis fly larval remains, a single head of an adult animal of *Limnophilus* sp. was found in Svartenhuk Lake (Bennike 2000a). The head was found in a sample dated to *c.* 3000 years BP. There are no modern records of *Limnophilus* spp. this far north in Greenland, but this may reflect lack of collections (Stoltze 1981). Thus during field work around Svartenhuk Lake in 1996, one charophyte species and two freshwater mollusc species were found that had not previously been recorded this far north in Greenland (Anderson & Bennike 1997).

Lepidoptera – Pupae of the butterfly *Agrotis occulta* (now *Eurois occulata* (Linnaeus)) were found in abundance in a layer in two peat sections situated near Norse ruins in the Godthåbsfjord area by Iversen (1934), and the layer also contained large concentrations of butterfly scales. Iversen suggested that the butterfly larvae had eaten much of the vegetation in large areas, and thus were a contributing factor for the extinction of the Norsemen in Greenland, because their domestic animals would be starving.

Other remains of butterflies, mostly larval mandibles, have been reported from the late Holocene of West Greenland (Fredskild & Humle 1991, Böcher & Fredskild 1993). None of these remains have been identified.

Amara alpina (Paykull) (Coleoptera, Carabidae) – This is the most cold adapted of all ground beetles, being present as far north as *c.* 75°N in arctic Canada. Thus it is surprising that the species is not a member of the extant Greenland fauna. However, remains of the species are known from deposits of the last interglacial stage near Thule Air Base in Northwest Greenland

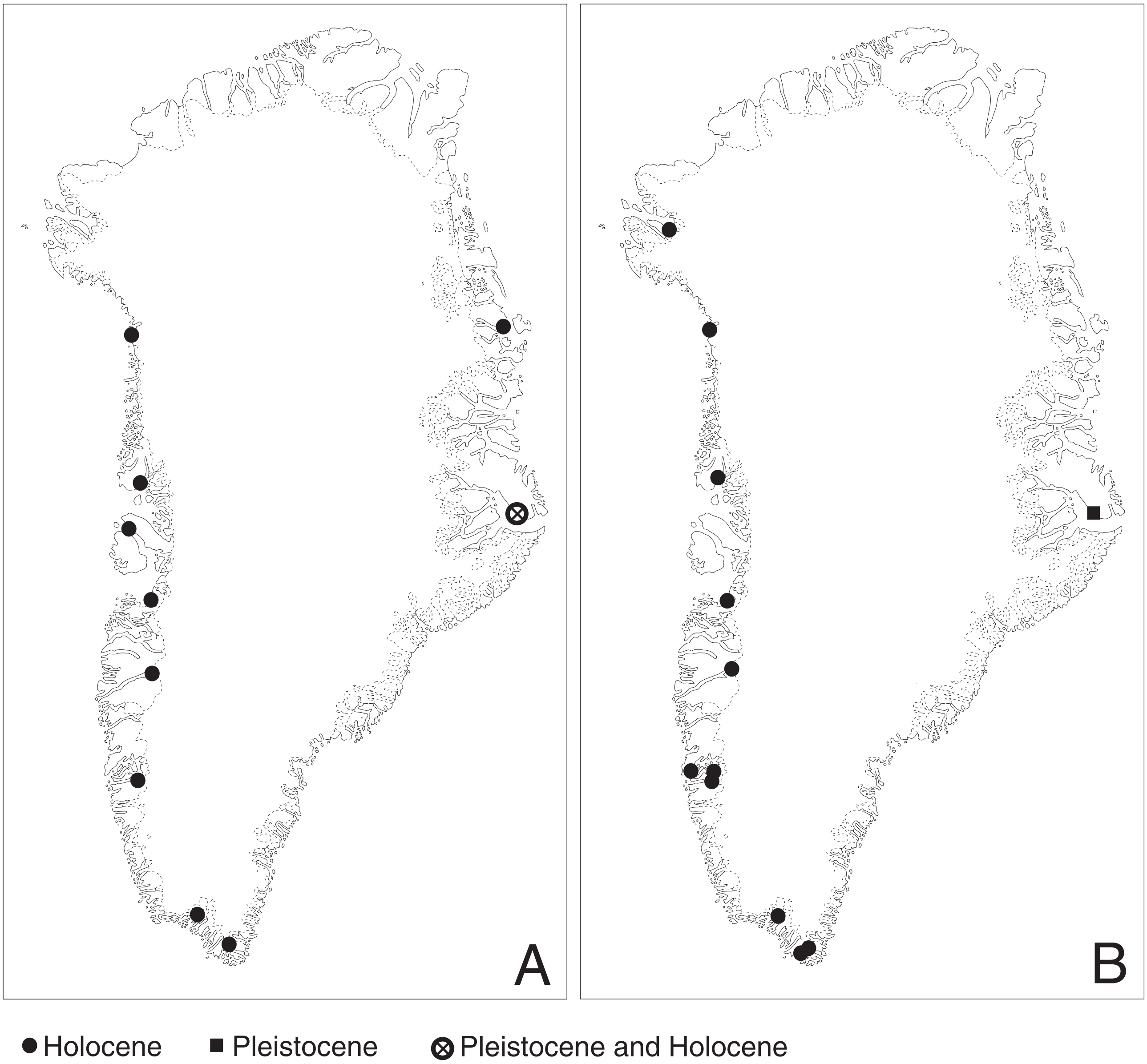


Figure 5. Maps of Greenland showing locations for Quaternary records of diving beetles. A: *Colymbetes dolabratus, c*ompiled from Fredskild et al. (1975), Buckland et al. (1983), Fredskild (1985), Böcher & Fredskild (1993), Bennike & Böcher (1994), Björck et al. (1994a), Bennike (1995, 2000, unpublished), Eisner et al. (1995), Bennike & Funder (1997) and Bennike *et al.* (1999). B. *Hydroporus morio*, compiled from Fredskild et al. (1975), Fredskild (1983, 1985), Buckland et al. (1983), Böcher & Fredskild (1993), Bennike & Böcher (1994), Bennike (1995, 2000, unpublished) and Eisner et al. (1995).

(Böcher 1989, Bennike & Böcher 1992, Kelly et al. 1999) and in central East Greenland (Bennike & Böcher 1994). *Amara alpina* remains were also found in a single sample from East Greenland from a layer that was correlated with oxygen isotope stage 5c, but it may have been reworked from the interglacial deposits. There is also a record from early Holocene deposits at Zackenberg on Wollaston Forland in Northeast Greenland, but redeposition from interglacial layers is likely (Bennike et al. 1999). Finally, a few fragments were recently found in an undated deposit in Washington Land, North Greenland (Bennike 2000b). Although undated, a last interglacial age for the fragments is a possibility (Table 1). These records show that the species was formerly widespread in North and East Greenland.

Bembidion grapii Gyllenhal (Coleoptera, Carabidae) – The range of this ground beetle is circumpolar, boreal and low-arctic. *B. grapii* has been recovered in fluvial deposits from central East Greenland, at a locality that is somewhat north of its present northern range limit in East Greenland (Böcher & Bennike 1996). The record is dated to *c.* 7800 years BP. In West Greenland the oldest record of the species is represented by two elytra that were recovered from organic detritus present in sandy lake deposits northeast of the Kangerlussuaq airport. The detritus is dated to *c.* 5800 years BP (van Tatenhove, Van der Meer & Koster 1996: UtC-2534). Rare remains of the species were also found in the Disko Bugt area, in layers dated to between *c.* 4000 and 3400 years BP (Böcher & Fredskild 1993).

Hydroporus morio Aubé (Coleoptera, Dystiscidae) – The predaceous diving beetle *Hydroporus morio* is commonly encountered in West and Southeast Greenland, and there is also a single, isolated record from North Greenland (Böcher 1988). It occurs in small ponds as well as larger lakes. Remains of this species have been reported from last interglacial deposits in central East Greenland (Bennike & Böcher 1994), which is outside the modern range of the species. Within its modern range, it has been recorded from a number of lake and mire sequences in South and West Greenland (Fredskild et al. 1975, Fredskild 1983 1985, Böcher & Fredskild 1993, Bennike 1995, 2000a, Eisner et al. 1995, Bennike, unpublished (Fig. 5). The oldest record of the species is dated to about 9500 years BP (Fredskild et al. 1975).

Colymbetes dolabratus (Paykull) (Coleoptera, Dystiscidae) – The other Greenlandic predaceous diving beetle *Colymbetes dolabratus* (Paykull) is widely distributed in West and East Greenland (Böcher 1988). The elytron shows a distinct striation, and even small fragments are easily identified. Other parts of the exoskeleton of the adult animal are also found, and larval heads are also diagnostic. Since this species lives in lakes, at least during the winter, its remains often end up in lake deposits, and fossil remains of the species have been reported from many lake basins and some other geological deposits (Fig. 5). Two of these basins, one in West and one in East Greenland, are situated north of the species' present known northern range limit (Fredskild 1985, Bennike et al. 1999), and it appears that it lived somewhat farther north during the Holocene temperature optimum than at present. These extralimital occurrences are dated respectively to around 8000 and 10000 years BP. The earliest known occurrences are dated to *c.* 9500 years BP (West Greenland: Fredskild (1983) and to *c.* 10800 years BP (East Greenland: Björck et al. 1994a). In addition, the species is known from interglacial deposits in East Greenland (Bennike & Böcher 1994).

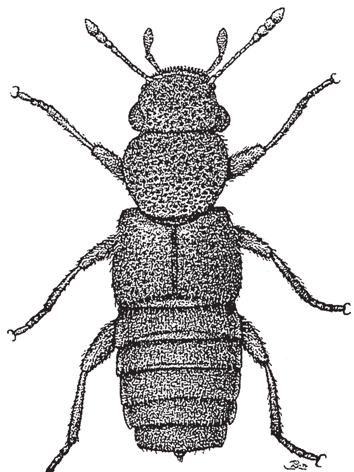


Fig. 6. Drawing by Birgitte Rubæk of a modern specimen of *Euaestethus laeviusculus* (Coleoptera: Staphylinidae). The total length is 1.8 mm.

Gyrinus opacus Sahlberg (Coleoptera, Gyrinidae) – The whirligig beetle *G. opacus* is in Greenland confined to the southern and southwestern parts (Böcher 1988). The species is most common in ponds and small lakes.

Rare remains of *Gyrinus opacus* have been found in Holocene lake sediments from two lakes at Kangerlussuaq (Eisner et al. 1995, Bennike 2000a). The oldest remains are around 5200 years old, but because of the scarcity of finds, we do not know if the species immigrated to Greenland earlier. The fossil localities are situated near the present northern range limit. The species' preference for ponds may explain why fossil remains are so rare in lake sediments.

Phratora (Phyllodecta) cf. *polaris* (Sparre-Schneider) (Coleoptera, Chrysomelidae) – The presence of this leaf beetle in early Holocene deposits in East Greenland was discussed by Böcher & Bennike (1996) and Bennike et al. (1999). It was found at three localities spanning about 400 km from south to north, and separated by wide fjords. The finds are dated to between 7900 and 8700 years BP. There are no extant records of the species from Greenland, and it seems highly unlikely that it still lives there. It probably disappeared from Greenland after the early to mid Holocene warm period ended *c.* 5000 years ago (Funder 1978, Bennike & Weidick 1999).

Micralymma spp. (Coleoptera, Staphylinidae) – The small rove beetle *Micralymma brevilingue* Schiödte is widespread in Greenland up to around 74°N (Böcher 1988), and it lives in humid places, often near the sea.

Remains of this species occurred abundantly in peat layers at an archaeological site on the small island Qeqertasussuk in Disko Bugt (Fig. 1). The remains were found in layers dated to *c.* 3000–4000 years BP (Böcher & Fredskild 1993). Fossils of the species were also present in cultural layers from another palaeo-Eskimo site dated to *c.* 3000 years BP near Sisimiut

(Böcher 1997), in a peat sequence from Brændevinskær, a small island in Disko Bugt. Here the oldest peat layers were around 1500 years old (Bennike 1992).

Micralymma marinum Ström is of more limited range, being confined to south and southwest Greenland (Böcher 1988). It lives at sea shores. At Qeqertasussuk, a single abdomen of *M. marinum* was also found (Böcher & Fredskild 1993). The find is around 4500 years old.

Atheta hyperborea Brundin (Coleoptera, Staphylinidae) – The rove beetle *Atheta hyperborea* is rare in Greenland, where it is confined to the southwestern part (Böcher 1988). Fossils of it were found in a single sample from the peat section on Qeqertasussuk, dated to around 3300 years (Böcher & Fredskild 1993). A few remains of *Atheta* sp. were found in a fen section from Southwest Greenland. The finds date from this millennium (Fredskild & Humle 1991).

Euaestethus laeviusculus Mannerheim – This rove beetle is unknown from the modern day fauna of Greenland, but due to its extremely small size, with a total length of 1.8 mm, it may well have been overlooked (Fig. 6). A few finds of it, dated to around 3000 years BP, come from palaeo-Eskimo cultural layers near Sisimiut (Böcher 1997, 1998), and it has also been recovered from a Norse ruin in Godthåbsfjorden (Böcher 1999).

Simplocaria metallica (Sturm) (Coleoptera, Byrrhidae) – The geographical distribution of the pill beetle *S. metallica* is circumpolar, boreal and low-arctic, and the species is rather common in southwest Greenland (Böcher 1988). A fragment of an elytron of this species was found in the sandy lake deposits northeast of Kangerlussuaq, which as mentioned above is around 5800 years old. Remains of the species were also found on Qeqertasussuk, with the oldest around 4000 years old (Böcher & Fredskild 1993), near Sisimiut (3000 years old: Böcher 1997), and in Norse layers in the Godthåbsfjord region (Buckland et al. 1983).

Hymenoptera – Heads of Hymenoptera are often found in fossil assemblages, but no identifications below the family level have been attempted. There are interglacial and Holocene records from Greenland (Fredskild & Humle 1991, Böcher & Fredskild 1993, Bennike & Böcher 1994, Böcher & Bennike 1996, Bennike et al. 1999, Bennike 2000a). From interglacial deposits in East Greenland, *Bombus* sp. (a bumblebee) was recorded (Bennike & Böcher 1994).

Chironomidae (Diptera) – Larval head capsules of

Table 5. Chironomidae and other invertebrates in sample 87511 (Jameson Land)

Taxon	number
Lepidurus cf. *arcticus*	rare
Coleoptera	rare
Cyclorrhapha	rare
Tipulidae	rare
Diamesa	117
Cricotopus/Orthocladius	54.5
cf. *Orthocladius lapponicus*	2.5
subtribe Tanytarsina	43
Chironomus	7
Metriocnemus	3
Psectrocladius	2
Eukiefferiella/Tvetenia	1.5
Sergentia	1
Paracladopelma type.	1
Brillia/Euryhapsis	1
Doithrix/Pseudorthocladius	0.5
Simuliidae	5
Oribatida	common

Chironomidae (non-biting midges) are very common in Holocene lake deposits, and detailed studies of fossil Holocene chironomids from lake sequences in West Greenland are currently being carried out (Brodersen & Anderson 2000). There are a few published records of the two subfamilies Chironominae and Tanypodinae, and there are also a few records of chironomid larval houses (Fredskild 1983, 1985). Thoraces of adult animals are also regularly found (Bennike, unpublished). Larval head capsules and adult thoraces have also been reported from interglacial sites (Meldgaard & Bennike 1989, Bennike & Böcher 1992, 1994, Bennike & Jepsen, in press).

A detailed study of chironomids has been conducted at a single interglacial site in Jameson Land, central East Greenland (Table 5). Twelve chironomid taxa were identified, together with *Simulium* (black fly) remains. Like the black flies, one chironomid taxon, *Diamesa,* is restricted to streams. Among the many analysed interglacial samples from East Greenland, this is the only sample that provides direct palaeoecological evidence for streams.

Danks (1981) lists five *Diamesa* species (*D. aberrata* Lundbeck, *D. arctica* (Boheman), *D. bohemani* Goetghebuer, *D. geminata* Kieffer, *D. simplex* Kieffer) as part of the extant Greenland fauna. The high percentage of *Diamesa* suggests that the stream was likely fed by permanent snow-fields or glacial meltwater.

The interglacial faunas and floras comprise a number of extra-limital taxa. For example, among the chironomids, *Brillia* and *Euryhapsis* are wood-mining taxa, widely distributed south of arctic tree-line

(Oliver & Roussel 1983). They have never been reported from the extant arctic fauna (Danks 1981, Walker & MacDonald 1995, Walker et al. 1997). However, given the limited data available for the arctic, many Chironomidae may occur farther north than indicated by current literature.

Simulium sp. (Diptera) – As mentioned above, head capsules of Simuliidae have been reported from an interglacial deposit at Jameson Land in East Greenland. From Holocene deposits, a few pupal houses of *Simulium* sp. were reported from South Greenland. The age of this find was around 7500 years BP (Fredskild et al. 1975). Rare pupal houses of *Simulium* were also reported from Norse layers from Qassiarsuk (Fredskild 1978). *Simulium* larvae are restricted to streams. Danks (1981) lists three species (*S. tuberosum* Lundström, *S. venustum* Say, *S. vittatum* Zetterstedt) as part of the extant Greenland fauna.

Limonia sp. (Tipulidae) – A single head of *Limonia* sp. found in Holocene lake deposits in NE Greenland (loc. 6) is dated to *c.* 6000 years BP. The genus is represented by several species in Greenland, and the head could not be identified to species.

Acalyptratae (Diptera) – Small puparia of unidentified Acalyptratae flies were identified from a late Holocene peat deposit from Disko Bugt, West Greenland (Bennike 1992).

Cyclorrapha (Diptera) – Puparia of Cyclorrapha flies are rather common in peat deposits, and can also be found in lake sediments and in samples of organic detritus (Fig. 3). Haarløv (1967) identified some from Disko Bugt to the family Agromyzidae, and Böcher & Fredskild (1993) noted that Anthomydae, Muscidae and Calliphoridae dominated their material, also from Disko Bugt. The latter authors identified the blowfly *Protophormia terranovae*, the larvae of which live on carcasses. *Syrphus torvus* Sacken from an early Holocene deposit in Northeast Greenland is the only specifically identified fly remain from Northeast Greenland (Bennike et al. 1999).

Table 6. Oribatida in Holocene deposits

Achiptera coleoptrata (Linnaeus)
Ameronothrus lineatus (Thorell)
Diapterobates notatus (Thorell)
Epidamaeus spp.
Hermannia reticulata Thorell
Hermannia scabra (Koch)
Hydrozetes confervae (Schrank)
Liebstadia similis (Michael)
Melanozetes meridianus Sellnick
Mycobates consimilis Hammer
Oromurcia lucens Koch
Platynothrus peltifer (Koch)
Platynothrus punctatus (Koch)
Trichoribates trimaculatus (Koch)

Araneae

Spiders are soft-bodied arthropods, but nevertheless their remains are found in peat deposits, but few identifications have been made. The genera *Pardosa* (Lycosidae) and *Erigone* (Linyphiidae) were reported from mid to late Holocene layers from Disko Bugt (Bennike 1992, Böcher & Fredskild 1993, Fig. 3).

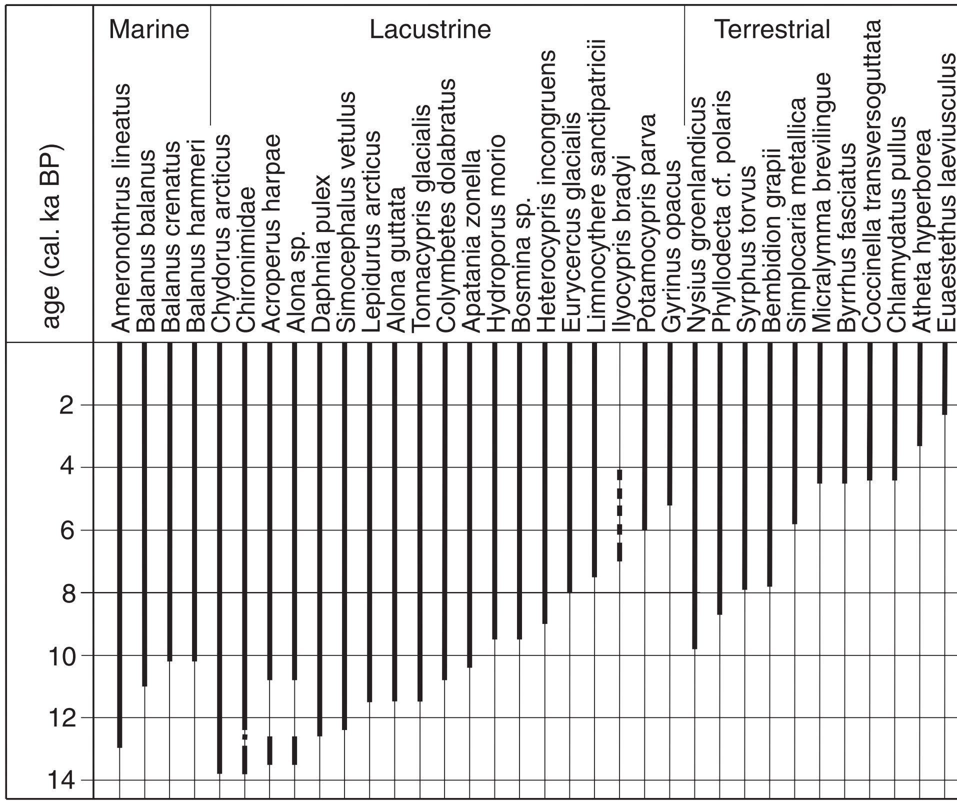
Acarina

Among the mites, the soil mites (Oribatida) are characterised by a heavily sclerotised exoskeleton, and being abundantly present in soils, their remains are common in mire deposits. Nine species were identified from undated Holocene peat collected in Southwest Greenland (Graversen 1931), and seven species were identified from a peat section in Disko Bugt, West Greenland (Haarløv 1967) (Table 6). The oldest peat from Disko Bugt with mites was dated to *c.* 2800 years BP (Tauber 1960, Fredskild 1967: K-516). Unidentified oribatid remains from peat deposits in West Greenland have been reported by Fredskild & Humle (1991).

Ameronothrus lineatus (Thorell) has been reported from several sites in South and West Greenland (Graversen 1931, Bennike 1992, 1995, unpublished, Fig. 3). This oribatid lives at or near the sea shore (Hammer 1944), and it is often found in sediments from isolation basins deposited during the period when the basin became isolated from the sea as a consequence of relative land uplift.

Oribatid remains are also common in lake sediments. Most of these remains probably come from the genus *Hydrozetes*, which is one of the few oribatid mites that lives in lakes. Fredskild et al. (1975) and Fredskild (1995) have reported on Hydrachnidae (water mite) remains from Holocene lake sediments in South and Northeast Greenland. However, because (1) Hydrachnidae are rare in Greenland, (2) their exoskeletons are only lightly sclerotised and (3) oribatid mite remains were not reported in these studies, we feel that these reports on fossil Hydrachnidae need to be documented. Furthermore, we are not aware of any other records of Hydrachnidae from Quaternary sediments (Frey 1964).

Figure 7. Diagram showing the temporal range of selected taxa. The transition from the Holocene to the last glacial stage is dated to *c.* 11,500 cal. years BP (Björck et al. 1998).



Remains of *Eugamasus* sp. (Acarina, Gamasides) were found in late Holocene peat deposits in Disko Bugt, West Greenland (Haarløv 1967, Bennike 1992). The genus is unknown from the modern Greenland fauna, but considering the young age of the finds, there can be little doubt that the animal lives in Greenland.

Brief chronological review and discussion

Early and Middle Pleistocene

A number of Early and Middle Pleistocene marine deposits have been located in Greenland. Three species of barnacles were reported from the Early Pleistocene Pattorfik beds (Símonarson 1981), and barnacles have also been reported from several sites referred to the Middle Pleistocene, but the chronology and correlation of these sites are uncertain. Most of them are located in West Greenland, but a single site in Northeast Greenland has also yielded a species of *Balanus*. The presence of barnacles is indicative of sea water temperatures similar to those of the present interglacial stage, rather than cold stages.

The last interglacial stage (oxygen isotope stage 5e)

A few species of barnacles and marine ostracodes have been reported from Greenland deposits assigned to the last interglacial stage. A fairly diverse fauna of non-marine arthropods from sites that are more or less securely referred to the last interglacial stage has been reported from central East Greenland (Tables 2, 5). It is especially noteworthy that the majority of the beetles are not members of the extant Greenland fauna. All the beetle species are presently found in the subarctic zone of the boreal region (Bennike & Böcher 1994). Faunas from other sites in Greenland are less diverse, but this could, to some degree, reflect the fact that far less material was available for study. The interglacial faunas are dominated by palaearctic species, as is the modern day beetle fauna of Greenland.

The last glacial stage

A single fragment of the beetle *Amara alpina* from isotope stage 5c could be reworked from interglacial deposits. In southernmost Greenland, a few lake records extend back into the later part of the last ice age. These late glacial lake sediments contain a fauna that include some Cladocera in addition to non-biting midges (Fig. 7). It appears that three taxa of Cladocera immigrated very early, but two of them apparently became extinct during the Younger Dryas cold period, and re-immigrated during the early Holocene.

The Holocene

Holocene deposits are widespread in Greenland, and have received much more attention than older deposits, partly because they can be securely dated using radiocarbon. Figure 7 shows the temporal range of a number of species. Some of these, especially the terrestrial species, are only sparingly represented, which means that their temporal distribution in Greenland is highly uncertain. Cladocerans on the other hand, can be represented by thousands of specimens per ml of lake sediment, and their temporal distributions are thus much better constrained. The chitinous remains of Cladocera may even constitute a major part of lake sediments, and the term chitin gyttja was proposed by Wesenberg-Lund (1901).

Insect remains from Norse ruins have been studied by Buckland et al. (1983), Buckland, Buckland & Skidmore (1998), McGovern, Buckland, Savory, Sveinbjarnardóttir, Andreasen & Skidmore (1983) and Buckland (1988) who found a diverse fauna that includes several beetles that no longer live in Greenland. It seems that the Norse farms provided biotopes for anthropocorous species that disappeared together with the Norsemen. Not surprisingly, the fauna included ectoparasites such as lice (*Pediculus* and *Damalinia*), fleas (*Pulex*) and ked (*Melophagus*) (Table 4).

Survival or immigration

The discussion about whether the fauna of Greenland survived the Quaternary ice ages (or at least the last ice age) in Greenland, or whether the species immigrated after the last temperature minimum at around 22000 years ago, has been reviewed by Bennike (1999). It was concluded that most animals, except some cold-adapted hardy species, could not survive the last glacial stage in Greenland. This would also apply to most arthropods. This conclusion is mainly based on palaeotemperature reconstructions modelled from temperatures in the GRIP bore hole on the Greenland ice sheet, which indicate a mean annual temperature depression of around 25°C. Larvae of marine species could spread to Greenland by ocean surface currents. Some species of insects such as butterflies could fly actively to Greenland, and others could be blown there by strong winds. Aerial dispersal was no doubt also the main mechanism for spiders, as young spiders are carried along by a thread. Many freshwater animals are generally believed to be dispersed epizoically by migrating birds, and parasites such as lice, fleas and mites were no doubt brought to Greenland by birds, mammals and invertebrates. The majority of Greenland’s beetle fauna, arrived from Northwest Europe, and it is enigmatic how and when this dispersal came about, especially since beetles are rather heavy insects and some of them are unable to fly. It has been suggested that the beetles were transported to Greenland from northwest Europe on ice floes at the Pleistocene-Holocene transition (Coope 1986, Buckland 1988, Böcher 1988). Unfortunately, the Holocene record of beetles is still too meagre to allow the arrival date for the different species to be established. However, it appears that the sea surface currents would tend to move ice floes up along the northwest European coast, rather than across the ocean, both during the last termination and during the Holocene (e.g. Hald & Aspeli 1997). One should not forget that the Greenland beetle fauna is much impoverished when compared to other arctic regions, and it may be that the few species that made it to Greenland arrived by long-distance chance dispersal over the course of the Holocene. If transport on ice floes is discounted, migrating birds may be the only feasible alternative. Many thousands of geese migrate from northwest Europe to Greenland every year, whereas much smaller numbers of geese migrate to Greenland from eastern USA/Canada. Perhaps this difference, operating over a long time period, could account for the dominance of palaearctic beetles in the Greenland fauna. Certainly the importance of migrating birds as transport agents of arthropods to Greenland should not be under-appreciated.

Fredskild (1992) concluded that the first immigrants among the Greenland macro-limnophytes were species that are currently widespread in Greenland. These were followed by more warmth-demanding species, and finally the most warmth-demanding species arrived. With respect to arthropods, the marine arthropods arrived early (Fig. 7). Some of the lacustrine arthropods are very well represented in the fossil record, so their history can be elucidated in some detail. Some species immigrated already during the late-glacial, but most species did not arrive until the Holocene (Fig. 7). Two of the late-glacial immigrants, *Acroperus harpae* and *Simocephalus vetulus*, only live in low-arctic parts of Greenland, and thus the earliest fauna did not entirely consist of the most cold-adapted species. The terrestrial species are only represented by rare casual finds, and little concrete evidence is available about the timing of their immigration.

Another argument for postglacial immigration to Greenland is the dearth of endemic species, in contrast to the situation on islands further south in the Atlantic Ocean, where the species could survive during the glacial stages. However, some endemic arthropod species have been described from Greenland, but all these are closely related to other species, and it is often a matter of debate whether they should be ranked as species rather than sub-species. It was concluded by Sadler (1998) that all the Greenland non-marine invertebrate endemic species are equivocal. The small differences found may have evolved in the course of some millennia, especially if the Greenland population was founded by a single or a few individuals. The lack or rarity of true endemic species in Greenland must mean that the fauna is young.

Final remarks

The study of chironomids, oribatids and especially marine ostracodes should be rewarding and could bring a wealth of data on the Quaternary history of these groups to light. Chironomids are also being increasingly used as palaeoclimate indicators, and the chironomid faunas from two Holocene lake sequences in West Greenland are currently being studied (Brodersen & Anderson 2000).

The purpose of this paper has been to compile our current knowledge about the Quaternary history of arthropods on Greenland. Thus the emphasis is on Quaternary zoogeography. But it should be stressed that many species of arthropods are characterised by narrow ecological amplitudes, and these are therefore excellent indicators of past environmental changes. For instance, some species are suited for palaeosalinity reconstructions, and can be used to locate the boundary between marine - brackish - lacustrine deposits from isolation basins. Many arthropods have narrow climatic amplitudes, and can be used as indicators of past climatic changes. The most secure interpretations can be achieved by integrated studies of various plant and animal remains, combined with non-biological proxies.

Acknowledgments

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Dansk sammendrag

Leddyrene eller arthropoderne, som er den mest artsrige række indenfor dyreriget, omfatter velkendte dyregrupper såsom insekter, krebsdyr og edderkopper. Alle leddyr har et ydre kitinskelet, der hos nogle arter er imprægneret med kalk. Rester af leddyrenes skelet træffes ofte i aflejringer fra Kvartærtiden, der omfatter de sidste ca. 2,5 millioner år. Aflejringer fra søer, moser, floder, deltaer og havet kan rumme rester af leddyr, og i forbindelse med arkæologiske udgravninger er der ligeledes gjort rige fund.

Fra Kvartære aflejringer på Grønland foreligger der fund af arktisk damrokke, otte forskellige dafnier, otte forskellige ferskvandsostracoder, 11 forskellige marine ostracoder, en copepod, fire forskellige rurer, tre storkrebs, næsten 90 forskellige insekter, få edderkopper og 15 mider. Alle fund er henført til nulevende arter, og størstedelen af fundene er bestemt til artsniveau ved sammenligning med recent referencemateriale. En del fund har det dog ikke været muligt at bestemme til artsniveau, fordi artsdiagnostiske dele ikke er bevaret.

Tidsmæssigt spænder fund af marine rurer (*Balanus*) over hele kvartærtiden, mens fund af insekter og ferskvandskrebsdyr er dateret til sidste mellemistid samt sen- og postglacialtid. Fra lag afsat under sidste mellemistid kendes en rig insektfauna, der omfatter en række varmekrævende arter der ikke længere lever på Grønland. Middeltemperaturen for årets varmeste måned var ca. 5°C højere end i dag.

Ifølge resultater fra iskerneboringerne på Grønlands Indlandis var årets middeltemperatur under den koldeste del af sidste istid ca. 25°C lavere end i dag. Hvis det er korrekt, er det tvivlsomt, om leddyr kunne overleve på Grønland, og vi foreslår at alle arter er indvandret efter sidste istid. Mange arter kan være fløjet eller blæst til Grønland, det gælder for eksempel myg, fluer og sommerfugle. Andre arter, så som dafnier og ferskvands-ostracoder er formentlig transporteret til Grønland med trækkende vandfugle. Biller er forholdsvis tunge dyr, hvoraf flere der er ankommet fra Nordvesteuropa ikke kan flyve. Hvorledes disse arter har kunnet finde vej til Grønland er noget af en gåde, men det må huskes, at en enkelt gravid hun i princippet er nok. Det har været foreslået, at disse arter er transporteret af sted på isflager, men det er svært at forlige med havstrømmenes forløb. Den eneste anden realistiske mulighed synes at være tilfældig transport med trækfugle, og i denne forbindelse må det ikke glemmes, at tusindvis af gæs hvert forår trækker fra Nordvesteuropa til Grønland, hvorimod langt færre gæs trækker fra det østlige USA og Canada til Grønland. Måske kan denne forskel til dels forklare, hvorfor den grønlandske billefauna domineres af palaearktiske arter.

De marine leddyr giver informationer om havtemperaturer og vandmasser. I denne forbindelse er det vigtigt at bemærke, at fund af den varmekrævende rurer *Balanus hammeri* viser, at Atlantisk vand allerede var begyndt at strømme op langs kysten af Vestgrønland for 10200 kalenderår siden, hvilket er i god overensstemmelse med daterede fund af *Mytilus edulis* skaller fra Thule området.

References

Anderson, N. J. & Bennike, O. 1997: Holocene lake sediments in West Greenland and their palaeoclimatic and palaeoecological implications. Geology of Greenland Survey Bulletin 176, 89–94.

Bennike, O. 1983: Palaeoecological investigations of a Holocene peat deposit from Vølvedal, Peary Land, North Greenland. Rapport Grønlands Geologiske Undersøgelse 115, 15–20.

Bennike, O. 1990: The Kap København Formation: stratigraphy and palaeobotany of a Plio-Pleistocene sequence in Peary Land, North Greenland. Meddelelser om Grønland, Geoscience 23, 85 pp.

Bennike, O. 1992: Paleoecology and paleoclimatology of a late Holocene peat deposit from Brændevinsskær, central West Greenland. Arctic and Alpine Research 24, 249–252.

Bennike, O. 1995: Palaeoecology of two lake basins from Disko, West Greenland. Journal of Quaternary Science 10, 149–155.

Bennike, O. 1997: Quaternary vertebrates from Greenland: a review. Quaternary Science Reviews 16, 899–909.

Bennike, O. 1998: Fossil egg sacs of Diaptomus (Crustaceae: Copepoda) in Late Quaternary lake sediments. Journal of Paleolimnology 19, 77–79.

Bennike, O. 1999: Colonisation of Greenland by plants and animals after the last ice age: a review. Polar Record 35, 323–336.

Bennike, O. 2000a: Palaeoecological studies of Holocene lake sediments from West Greenland. Palaeoecology, Palaeoclimatology, Palaeogeography 155, 285–304.

Bennike, O. 2000b: Notes on the late Cenozoic history of the Washington Land area, western North Greenland. Geology of Greenland Survey Bulletin 186, 29–34.

Bennike, O. & Björck, S. 2000: Lake sediment coring in South Greenland in 1999. Geology of Greenland Survey Bulletin 186, 60–64.

Bennike, O. & Böcher, J. 1992: Early Weichselian interstadial land biotas at Thule, Northwest Greenland. Boreas 21, 111–117.

Bennike, O. & Böcher, J. 1994: Land biotas of the last interglacial/ glacial cycle on Jameson Land, East Greenland. Boreas 23, 479–487.

Bennike, O. & Funder, S. 1997: Macrofossil studies of Holocene lake sediments from Jameson Land, East Greenland. Geology of Greenland Survey Bulletin 176, 80–83.

Bennike, O. & Jepsen, H. F. in press: A new interglacial sequence from Washington Land, North Greenland. Polar Research.

Bennike, O. & Weidick, A. 1999: Observations on the Quaternary geology around Nioghalvfjerdsfjorden. Geology of Greenland Survey Bulletin 183, 57–61.

Bennike, O., Hansen, K. B., Knudsen, K. L., Penney, D. N. & Rasmussen, K. L. 1994: Quaternary marine stratigraphy and geochronology in central West Greenland. Boreas 23, 194–215.

Bennike, O., Björck, S., Böcher, J., Hansen, L., Heinemeier, J. & Wohlfarth, B. 1999: Early Holocene plant and animal remains from North-east Greenland. Journal of Biogeography 26, 667–677.

Björck, S., Bennike, O., Ingólfsson, O., Barnekow, L. & Penney D. N. 1994a: Lake Boksehandsken's earliest postglacial sediments and their palaeoenvironmental implications, Jameson Land, East Greenland. Boreas 23, 459–472.

Björck, S., Wohlfarth, B., Bennike, O., Hjort, C. & Persson, T. 1994b: Revision of the early Holocene lake sediment based chronology and event stratigraphy on Hochstetter Forland, NE Greenland. Boreas 23, 513–523.

Björck, S., Walker, M. J. C., Cwynar, L. C., Johnsen, S., Knudsen, K.-L., Lowe, J. J., Wohlfarth, B. & INTIMATE members 1998: An event stratigraphy for the last termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. Journal of Quaternary Science 13, 283–292.

Blake, W., Jr. 1975: Glacial geological investigations in northwestern Greenland. Geological Survey of Canada Paper 75-1A, 435–439.

Blake, W., Jr. 1977: Radiocarbon age determinations from the Carey Islands, northwest Greenland. Geological Survey of Canada Paper 77-1A, 445–454.

Blake, W., Jr. 1987: Geological Survey of Canada radiocarbon dates XXVI. Geological Survey of Canada Paper 86-7, 60 pp.

Blake, W., Jr., Boucherle, M. M., Fredskild, B., Janssens, J. A. & Smol, J. P. 1992: The geomorphological setting, glacial history and Holocene development of "Kap Inglefield Sø", Inglefield Land, North-west Greenland. Meddelelser om Grønland, Geoscience 27, 42 pp.

Böcher, J. 1988: The Coleoptera of Greenland. Meddelelser om Grønland, Bioscience 26, 100 pp.

Böcher, J. 1989: First record of an interstadial insect from Greenland: *Amara alpina* (Paykull, 1790) (Coleoptera: Carabidae). Boreas 18, 1–4.

Böcher, J. 1995: Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland. Meddelelser om Grønland, Geoscience 33, 82 pp.

Böcher, J. 1997: Insektrester fra Asummiut. Grønland 1997, 260–262.

Böcher, J. 1998: Insect remains from Asummiut. In Arneborg, J. & Gulløv, H.C. (eds.) Man, culture and environment in ancient Greenland. 133–134. Copenhagen: Danish Polar Center.

Böcher, J. 1999: Mystisk opdukken af biller i Grønland. Dyr i natur og museum 1999, 22–24.

Böcher, J. & Bennike, O. 1996: Early Holocene insect and plant remains from Jameson Land, East Greenland. Boreas 25, 187–193.

Böcher, J. & Fredskild, B. 1993: Plant and arthropod remains from the palaeo-Eskimo site on Qeqertasusuk, West Greenland. Meddelelser om Grønland, Geoscience 30, 35 pp.

Brady, G. S. 1878: Notes on the ostracoda. In Nares, G. S. Narrative of a voyage to the Polar Sea during the years 1875–76 in H.M. ships "*Alert*" and "*Discovery*" 2, 253-256. London: Sampson Low, Marston, Searle and Rivington.

Brodersen, K. P. & Anderson, N. J. 2000: Subfossil insect remains (Chironomidae) and lake-water temperature inference in the Sisimiut–Kangerlussuaq region, southern West Greenland. Geology of Greenland Survey Bulletin 186, 78–82.

Brouwers, E. M., Jørgensen, N. O. & Cronin, T. M. 1991: Climatic significance of the ostracode fauna from the Pliocene Kap København Formation, north Greenland. Micropaleontology 37, 245–267.

Buckland, P. C. 1988: North Atlantic faunal connections - introductions or endemics? Entomologica Scandinavica Supplement 32, 7–29.

Buckland, P. C., Sveinbjarnardóttir, G., Savory, D., McGovern, T. H., Skidmore, P. & Andreasen, C. 1983: Norsemen at Nipáitsoq, Greenland: a palaeoecological investigation. Norwegian Archaeological Review 16, 86–98.

Buckland, P. C., Buckland, P. I. & Skidmore, P. 1998: Insect remains from GUS, an interim report. In Arneborg, J. & Gulløv, H.C. (eds.) Man, culture and environment in ancient Greenland. 47–79. Copenhagen: Danish Polar Center.

Coope, G. R. 1986: The invasion and colonisation of the North Atlantic islands: a palaeoecological solution to a biogeographic problem. Philisophical Transactions of the Royal Society of London B314, 619–635.

Danks, H. V. 1981: Arctic Arthropods: A review of systematics and ecology with particular reference to the North American fauna. 608 pp. Ottawa: Entomological Society of Canada.

Delorme, L. D. 1970a: Freshwater ostracodes of Canada. Part II. Subfamily Cypridopsinae and Herpetocypridinae, and family Cyclocyprididae. Canadian Journal of Zoology 48, 253–266.

Delorme, L. D. 1970b: Freshwater ostracodes of Canada. Part III. Family Candonidae. Canadian Journal of Zoology 48, 1099–1127.

Duigan, C. A. & Birks, H. H. 2000: The late-glacial and early Holocene palaeoecology of cladoceran microfossil assemblages at Kråkenes, western Norway, with a quantitative reconstruction of temperature changes. Journal of Paleolimnology 23, 67–76.

Dyke, A. S., Dale, J. E. & McNeely, R. N. 1996: Marine molluscs as indicators of environmental change in glaciated North America and Greenland during the last 18 000 years. Géographie physique et Quaternaire 50¸125–184.

Eisner, W. R.., Törnqvist, T. E., Koster, E. A., Bennike, O. & van Leeuwen, J. F. N. 1995: Paleoecological studies of a Holocene lacustrine record from the Kangerlussuaq (Søndre Strømfjord) region of West Greenland. Quaternary Research 43, 55–66.

Elias, S. A. 1994: Quaternary insects and their environment. 284 pp. Washington: Smithsonian Institution Press.

Enckell, P. H. 1998: Kräftdjur. 685 pp. Odense: Gr@phic Publishing.

Fredskild, B. 1967: Palaeobotanical investigations at Sermermiut, Jakobshavn, West Greenland. Meddelelser om Grønland 178, 4, 54 pp.

Fredskild, B. 1978: Palaeobotanical investigations of some peat deposits of Norse age at Qagssiarssuk, South Greenland. Meddelelser om Grønland 204, 5, 41 pp.

Fredskild, B. 1983: The Holocene vegetational development of the Godthåbsfjord area, West Greenland. Meddelelser om Grønland, Geoscience 10, 28 pp.

Fredskild, B. 1985: The Holocene vegetational development of Tugtuligssuaq and Qeqertat, Northwest Greenland. Meddelelser om Grønland, Geoscience 14, 20 pp.

Fredskild, B. 1992: The Greenland limnophytes – their present distribution and Holocene history. Acta Botanica Fennica 144, 93–113.

Fredskild, B. 1995: Palynology and sediment slumping in a high arctic Greenland lake. Boreas 24, 345–354.

Fredskild, B. & Humle, L. 1991: Plant remains from the Norse farm Sandnes in the western Settlement, Greenland. Acta Borealia 1, 69–81.

Fredskild, B. & Røen, U. 1982: Macrofossils in an interglacial peat deposit at Kap København, North Greenland. Boreas 11, 181–185.

Fredskild, B., Jacobsen, N. & Røen, U. 1975: Remains of mosses and freshwater animals in some Holocene lake and bog sediments from Greenland. Meddelelser om Grønland 198, 5, 44 pp.

Frey, D. G. 1958: The late-glacial cladoceran fauna of a small lake. Archiv für Hydrobiologie 54, 209–275.

Frey, D. G. 1962: Cladocera from the Eemian interglacial of Denmark. Journal of Paleontology 36, 1133–1155.

Frey, D. G. 1964: Remains of animals in Quaternary lake and bog sediments and their interpretation. Archiv für Hydrobiologie Beihefte Ergebnisse Limnologie 2, 1–114.

Frey, D. G. 1991: First fossil records of *Daphnia* headshields and shells (Anomopoda, Daphnidae) about 10 000 years old from northernmost Greenland, plus *Alona guttata* (Chydoridae). Journal of Paleolimnology 6, 193–197.

Frich, P. & Ingólfsson, O. 1990: Det holocæne sedimentationsmiljø ved Igpik samt en model for den relative landhævning i Disko Bugt området, Vestgrønland. Årsskrift for Dansk Geologisk Forening 1987-89, 1–10.

Funder, S. 1978: Holocene stratigraphy and vegetation history in the Scoresby Sund area, East Greenland. Bulletin Grønlands Geologiske Undersøgelse 129, 66 pp.

Funder, S. 1979: The Quaternary geology of the Narssaq area, South Greenland. Rapport Grønlands Geologiske Undersøgelse 86, 24 pp.

Funder, S. (co-ordinator) 1989: Quaternary geology of the ice-free areas and adjacent shelves of Greenland. In Fulton, R.J. (ed.) Quaternary geology of Canada and Greenland, 743–792. The geology of Canada, Vol. 1. Ottawa: Geological Survey of Canada.

Funder, S. (ed.) 1990: Late Quaternary stratigraphy and glaciology in the Thule area, Northwest Greenland. Meddelelser om Grønland, Geoscience 22, 63 pp.

Funder, S. & Simonarson, L. A. 1984: Bio- and aminostratigraphy of some Quaternary marine deposits in West Greenland. Canadian Journal of Earth Sciences 21, 843–852.

Funder, S. & Weidick, A. 1991: Holocene boreal molluscs in

Greenland: palaeoceanographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 85, 123–135.
Funder, S., Hjort, C., Landvik, J. Y., Nam, S.-I., Reeh, N. & Stein, R. 1998: History of a stable ice margin – East Greenland during the Middle and Upper Pleistocene. Quaternary Science Reviews 17, 77–123.
Graversen, C. B. 1931: Notizen über Grönlandische Oribatiden. Meddelelser om Grønland 91, 2, 18 pp.
Griffiths, H. I., Pietrzeniuk, E., Fuhrmann, R., Lennon, J. J., Martens, K. & Evans, J. G. 1998: *Tonnacypris glacialis* (Ostracoda, Cyprididae): taxonomic position, (palaeo-)ecology, and zoogeography. Journal of Biogeography 25, 515–526.
Haarløv, N. 1967: Arthropoda (Acarina, Diptera) from subfossil layers in West Greenland. Meddelelser om Grønland 184, 3, 17 pp.
Hald, M. & Aspeli, R. 1997: Rapid climatic shifts of the northern Norwegian Sea during the last deglaciation and the Holocene. Boreas 26, 15–28.
Hammer, M. 1944: Studies on the Oribatids and Collemboles of Greenland. Meddelelser om Grønland 141, 3, 210 pp.
Hammer, R. R. J. 1889: Undersøgelse af Grønlands Vestkyst fra 68°20' til 70°N.B. Meddelelser om Grønland 8, 1–32.
Harder, P., Jensen, A. S. & Laursen, D. 1949: The marine Quaternary sediments in Disko Bugt. Meddelelser om Grønland 149, 1, 85 pp.
Heide-Jørgensen, H. S. & Johnsen, I. 1997: Ecosystem vulnerability to climate change in Greenland and the Faroe Islands. Danish Environmental Protection Agency, Working Report 97, 266 pp.
Helland, A. 1876: Om de isfyldte Fjorde og de glaciale Dannelser i Nordgrönland. Archiv for Mathematik og Naturvidenskab 1, 58–125.
Hjort, C. 1987: The Ymer-Formation - an interglacial sequence in northeasternmost Greenland. Polar Research 5, 347–350.
Holst, N. O. 1886: Berättelse om en år 1880 i geologisk syfte företagen resa till Grönland. Sveriges Geologiska Undersökning C81, 68 pp.
Iversen, J. 1934: Moorgeologische Untersuchungen auf Grönland. Meddelelser fra Dansk Geologisk Forening 8, 341–358.
Jensen, A. S. 1917: Quaternary fossils collected by the Danmark Expedition. Meddelelser om Grønland 43, 619–632.
Jensen, A. S. 1942: Two new West Greenland localities for deposits from the ice age and the post-glacial warm period. Det Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser 17, 4, 35 pp.
Jensen, A. S. & Harder, P. 1910: Post-glacial changes of climate in arctic regions as revealed by investigations of marine deposits. Postglaziale Klimaveränderungen, 399–407. Stockholm.
Jensen, J. A. D. 1889: Undersøgelse af Grønlands Vestkyst fra 64° til 67° N.B. Meddelelser om Grønland 8, 33–121.
Kelly, M. 1973: Radiocarbon dated shell samples from Nordre Strømfjord, West Greenland. Rapport Grønlands Geologiske Undersøgelse 59, 20 pp.
Kelly, M. 1975: A note on the implications of two radiocarbon dated samples from Qaleragdlit ima, South Greenland. Bulletin of the Geological Society of Denmark 24, 21–26.
Kelly, M. 1979: Comments on the implications of new radiocarbon dates from the Holsteinsborg region, central West Greenland. Rapport Grønlands Geologiske Undersøgelse 95, 35–42.
Kelly, M. 1980: Preliminary investigations of the Quaternary of Melville Bugt and Dundas, North-West Greenland. Rapport Grønlands Geologiske Undersøgelse 100, 33–38.
Kelly, M. 1986: Quaternary, pre-Holocene marine events of western Greenland. Rapport Grønlands Geologiske Undersøgelse 131, 23 pp.
Kelly, M. & Bennike, O. 1992: Quaternary geology of western and central North Greenland. Rapport Grønlands Geologiske Undersøgelse 153, 34 pp.
Kelly, M., Funder, S., Houmark-Nielsen, M., Knudsen, K. L., Kronborg, C., Landvik, J. & Sorby, L. 1999: Quaternary glacial and marine environmental history of northwest Greenland: a review and reappraisal. Quaternary Science Reviews 18, 373–392.
Kornerup, A. 1879: Geologiske Iagttagelser fra Vestkysten af Grønland (62°15' - 64°15'N.B.). Meddelelser om Grønland 1, 77–139.
Kusakin, O. G. 1982: Morskie i colonovatovodnye ravnonogie rakoobraznye (Isopoda) kholnykh i umerennykh vod severnogo polushariya. Opredeliteli po fauna SSSR 131, 461 pp.
Laursen, D. 1944: Contributions to the Quaternary geology of northern West Greenland, especially the raised marine deposits. Meddelelser om Grønland 135, 8, 125 pp.
Laursen, D. 1950: The stratigraphy of the marine Quaternary deposits in West Greenland. Meddelelser om Grønland 151, 1, 142 pp.
Lütken, C. F. 1875: List of Crustacea, known from Greenland. In T. R. Jones (ed.) Manual and instructions for the Arctic Expedition 1875, vol. 2, 146–165. London
Madsen, H. 1940: A study of the littoral fauna of Northwest Greenland. Meddelelser om Grønland 124, 3, 24 pp.
Mangerud, J. & Funder, S. 1994: The interglacial–glacial record at the mouth of Scoresby Sund, East Greenland. Boreas 23, 349–358.
McGovern, T. H., Buckland, P. C., Savory, D., Sveinbjarnardóttir, G., Andreasen, C. & Skidmore, P. 1983: A study of the faunal and floral remains from two Norse frams in the Western Settlement, Greenland. Arctic Anthropology 20, 93–120.
Meldgaard, M. & Bennike, O. 1989: Interglacial remains of caribou (*Rangifer tarandus*) and lemming (*Dicrostonyx torquatus* (?)) from North Greenland. Boreas 18, 359–366.
Miers, E. J. 1877: Report on the Crustacea collected by the Naturalists of the Arctic Expedition 1875-76. Annals and Magazine of Natural History 20, 52–66 & 96–110.
Miers, E. J. 1881: On a small collection of Crustacea made by Edward Whymper, Esq., chiefly in the N. Greenland Seas; with an Appendix on additional species collected by the late British Arctic Expedition. Journal of the Linnaean Society, Zoology 15, 59–73.
Nordenskiöld, A. E. 1871: Redogörelse för 1870 års expedition til Grönland. Öfversigt af det Kungliga Vetenskabs Akademiens Förhandlingar 1870, 973–1082.
Oliver, D.R. & Roussel, M.E. 1983: The insects and arachnids of Canada. Part 11. The genera of larval midges of Canada; Diptera: Chironomidae. Agriculture Canada Publication No. 1746, 263 pp.
Penney, D. N. 1993: Late Pliocene to Early Pleistocene ostracod stratigraphy and palaeoclimate of the Lodin Elv and Kap København formations, East Greenland. Palaeogeography, Palaeoclimatology, Palaeoecology 101, 49–66.

Pjetursson, H. 1898: Geologiske Optegnelser. Meddelelser om Grønland 14, 288–347.
Quervain, A. d. & Mercanton, P.-L. 1925: Résultats scientifiques de l'Expédition Suisse au Groenland 1912-1913. Meddelelser om Grønland 59, 55–271.
Reinhardt, J. 1857: Fortegnelse over Grønlands krebsdyr, Annelider og Indvoldsorme. In H. Rink (Ed), Grønland geographisk og statistisk beskrevet vol. 2, 28–29. Copenhagen: Universitetsboghandler Andr. Fred. Høst.
Røen, U. I. 1957: Contributions to the biology of some Danish free living freshwater copepods. Biologiske Skrifter fra det Kongelige Danske Videnskabernes Selskab 9, 2, 101 pp.
Røen, U. I. 1962: Studies on freshwater Entomostraca in Greenland II. Meddelelser om Grønland 170, 2, 249 pp.
Røen, U. I. 1968: Studies on freshwater Entomostraca in Greenland III. Entomostraca from Peary Land with notes on their biology. Meddelelser om Grønland 184, 4, 59 pp.
Røen, U. I. 1975: On a southern faunal element in Greenlandic freshwaters past and present. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 19, 2874–2878.
Røen, U. I. 1981: Studies on freshwater Entomostraca in Greenland V. The fauna of the Hazen Camp study area, Ellesmere Island, N.W.T., Canada, compared to that of the Thule area, Greenland. Steenstrupia 7, 321–335.
Røen, U. I. 1987: *Chydorus arcticus* n.sp., a new cladoceran crustacean (Chydoridae: Chydorinae) from the North Atlantic Arctic and Subarctic areas. Hydrobiologia 145, 125–130.
Røen, U. I. 1988: Remains of early glacial Cladocera from North Greenland. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 32, 845–847.
Røen, U. I. 1992: Review of Greenlandic species of *Alona* Baird, 1850, with descriptions of three new species (Cladocera: Chydoridea: Aloninae). Steenstrupia 18, 101–109.
Røen, U. I. 1994: Studies on freshwater Entomostraca in Greenland VI. The Entomostraca of the Kap Farvel area, southernmost Greenland. Meddelelser om Grønland, Bioscience 41, 21 pp.
Sadler, J. P. 1998: "Is Greenland a zoogeographic unit?" A response to Bergersen. Journal of Biogeography 25, 399–403.
Schmidt, P. P. 1976: Recent and subfossil finds of a new species of ostracod, *Potamocypris parva*, in Greenland (Crustacea, Ostracoda, Cyprididae). Astarte 9, 13–17.
Símonarson, L. A. 1981: Upper Pleistocene and Holocene marine deposits and faunas on the north coast of Nûgssuaq, West Greenland. Bulletin Grønlands Geologiske Undersøgelse 140, 107 pp.
Símonarson, L., Petersen, K. S. & Funder, S. 1998: Molluscan palaeontology of the Pliocene-Pleistocene Kap København Formation, North Greenland. Meddelelser om Grønland, Geoscience 36, 103 pp.
Spengler, L. 1790: Beskrivelse og Oplysning over den hidindtil lidet udarbejdede Slægt af mangeskallede Konchylier, som Linnæus har kaldet Lepas, med tilføjede nye og ubeskrevne Arter. Skrivter af Naturhistorie Selskabet 1, 158–212.
Steenstrup, K. J. V. 1881: Bemærkninger til et geognostisk Oversigtskaart over en del af Julianehaabs Distrikt. Meddelelser om Grønland 2, 27–41.
Steenstrup, K. J. V. 1883: Bidrag til Kjendskab til de geognostiske og geographiske Forhold i en Del af Nord-Grønland. Meddelelser om Grønland 4, 173–242.
Stephensen, K. 1913: Grønlands Krebsdyr og Pycnogoider (Conspectus Crustaceorum et Pycnogonidorum Groenlandiæ). Meddelelser om Grønland 22, 1, 479 pp.
Stephensen, K. 1914: Account of the Crustacea and Pycnogonida collected by Dr. V. Nordmann in the summer of 1911 from Northern Strømfjord and Giesecke Lake in West Greenland. Meddelelser om Grønland 51, 2, 57–77.
Stephensen, K. 1933: Havedderkopper og rankefødder. Danmarks Fauna, 38, 158 pp. Copenhagen: Gads Forlag.
Stephensen, K. 1936: Crustacea varia. The Godthaab Expedition 1928. Meddelelser om Grønland 80, 2, 38 pp.
Stephensen, K. 1943: The zoology of East Greenland. Marine ostracoda, parasitic and semi-parasitic copepoda and cirrioedia. Meddelelser om Grønland 121, 9, 24 pp.
Stoltze, M. 1981: Grønlandske vårfluers udbredelse og indvandringshistorie. 16 pp. Unpublished report. Copenhagen: Zoological Museum.
Stuiver, M., Reimer, P. J., Bard, E., Beck, J. W., Burr, G. S., Hughen, K. A., Kromer, B., McCormac, F. G., Plicht, J. v. d. & Spurk, M. 1998: INTCAL radiocarbon age calibration, 24,000–0 cal BP. Radiocarbon 40, 1041–1083.
Sugden, D. 1972: Deglaciation and isostasy in the Sukkertoppen ice cap area, West Greenland. Arctic and Alpine Research 4, 97–117.
Tauber, H. 1960: Copenhagen radiocarbon dates IV. American Journal of Science, Radiocarbon supplement 2, 12–25.
van Tatenhove, F. G. M., Van der Meer, J. J. M. & Koster, E. A. 1996: Implications for deglaciation chronology from new AMS age determinations in central West Greenland. Quaternary Research 45, 245–253.
Vibe, C. 1950: The marine mammals and the marine fauna in the Thule District (Northwest Greenland). Meddelelser om Grønland 150, 6, 115 pp.
Vosgerau, H., Funder, S., Kelly, M., Knudsen, K. L., Kronborg, C., Madsen, H. B. & Sejrup, H.-P. 1994: Palaeoenvironments and changes in relative sea level during the last interglaciation at Langelandselv, Jameson Land, East Greenland. Boreas 23, 398–411.
Walker, I. R. & MacDonald, G. M. 1995: Distributions of Chironomidae (Insecta: Diptera) and other freshwater midges with respect to treeline, Northwest Territories, Canada. Arctic and Alpine Research 27, 258–263.
Walker, I. R., Levesque, A. J., Cwynar, L. C. & Lotter, A. F. 1997: An expanded surface-water palaeotemperature inference model for use with fossil midges from eastern Canada. Journal of Paleolimnology 18, 165–178.
Weidick, A. 1968: Observations on some Holocene glacier fluctuations in West Greenland. Meddelelser om Grønland 165, 6, 202 pp.
Weidick, A. 1972a: C^{14} dating of Survey material performed in 1971. Rapport Grønlands Geologiske Undersøgelse 45, 58–67.
Weidick, A. 1972b: Holocene shore-lines and glacial stages in Greenland - an attempt at correlation. Rapport Grønlands Geologiske Undersøgelse 41, 39 pp.
Weidick, A. 1972c: Notes on Holocene glacial events in Greenland. Acta Universitatis Ouluensis. Series A, Scientiae Rerum Naturalium 3, 1, 177–204.
Weidick, A. 1973: C^{14} dating of survey material performed in 1972. Rapport Grønlands Geologiske Undersøgelse 55, 66–75.
Weidick, A. 1974: C^{14} dating of survey material performed in 1974. Rapport Grønlands Geologiske Undersøgelse 75, 19–20.

Weidick, A. 1975: C^{14} dating of survey material performed in 1974. Rapport Grønlands Geologiske Undersøgelse 75, 19–20.
Weidick, A. 1976: Glaciation and the Quaternary of Greenland. In A. Escher, W. S. Watt, Geology of Greenland (pp. 431–458). Copenhagen: Geological Survey of Greenland.
Wesenberg-Lund, C. 1901: Studier over Søkalk, Bønnemalm og Søgytje i danske indsøer. Meddelelser fra Dansk Geologisk Forening 2, 1–144.
Williams, N. E., Westgate, J. A., Williams, D. D., Morgan, A. & Morgan, A. V. 1981: Invertebrate fossils (Insecta: Trichoptera, Diptera, Coleoptera) from the Pleistocene Scarborough Formation at Toronto, Ontario, and their paleoenvironmental significance. Quaternary Research 16, 146–166.