Polar Research

ISSN: (Print) 1751-8369 (Online) Journal homepage: http://www.tandfonline.com/loi/zpor20

Holocene insect remains from south-western Greenland

Jens Böcher, Ole Bennike & Bernd Wagner

To cite this article: Jens Böcher, Ole Bennike & Bernd Wagner (2012) Holocene insect remains from south-western Greenland, Polar Research, 31:1, 18367, DOI: 10.3402/polar.v31i0.18367

To link to this article: http://dx.doi.org/10.3402/polar.v31i0.18367

RESEARCH/REVIEW ARTICLE

Holocene insect remains from south-western Greenland

Jens Böcher[1], Ole Bennike[2] & Bernd Wagner[3]

[1] Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
[2] Geological Survey of Denmark and Greenland, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
[3] Institute for Geology and Mineralogy, University of Cologne, Zülpicher Str. 49a, DE-50674 Cologne, Germany

Keywords
Greenland; Arctic; Holocene; insects; beetles; palaeoenvironments.

Correspondence
Jens Böcher, Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.
E-mail: jjbocher@snm.ku.dk

Abstract

Remains of plants and invertebrates from Holocene deposits in south-western Greenland include a number of insect fragments from Heteroptera and Coleoptera. Some of the finds extend the known temporal range of the species considerably back in time, and one of the taxa has not previously been found in Greenland either fossil or extant. The fossil fauna includes the weevil *Rutidosoma globulus* which is at present extremely rare in Greenland. Its rarity might indicate that it is a recent immigrant, but the fossil finds provide a minimum date for its arrival at around 5840 cal. years B.P. Other remains of terrestrial insects complement the scarce fossil Greenland record of the species concerned.

The history of the Greenland flora and fauna has been much debated, especially regarding survival in ice-free areas during the last ice age versus immigration after the last partial deglaciation of Greenland. In his review, Bennike (1999) concluded that most species immigrated after the last deglaciation. This was mainly based on two arguments: (1) According to temperature reconstructions, the mean annual air temperature in Greenland was around 23°C lower than at present during the last glacial maximum ca. 25 000 years before present (Dahl-Jensen et al. 1998). It was argued that only few hardy species of vascular plants or animals would be able to cope with such harsh conditions. (2) The Greenland Ice Sheet was much larger during the last glacial maximum than at present, and the margin reached the edge of the continental shelf (Vinther et al. 2009), leaving only comparatively small ice-free areas on mountains and in certain lowland areas (Funder 1979; Funder et al. 2011). It is noteworthy that the ground beetle *Amara alpina* that is well adapted to Arctic conditions and was widespread in Greenland during the last interglacial stage (Böcher 1989; Bennike & Böcher 1994; Bennike 2002) apparently did not survive the last ice age. Nevertheless, it must still be emphasized that the microclimate, especially on south-facing slopes, must have created fairly favourable conditions, regardless of the low mean-temperature. The fact that the sun stays permanently above the horizon during summer in large parts of Greenland also helps to maintain fairly high temperatures locally.

During the past decades, insect remains have been studied from Late Pliocene/early Pleistocene and last interglacial deposits in Greenland (Bennike & Böcher 1994; Böcher 1995; Brodersen & Bennike 2003). Deposits of Holocene age have also been analysed (e.g., Böcher & Fredskild 1993; Böcher & Bennike 1996; Bennike et al. 2000), but Holocene lake, mire and river deposits offer a large potential for further work on insect remains. Such work can help unravel environmental and climatic changes, but also shed light on the history of the insects and providing data on their temporal range in Greenland. The present fauna of Greenland Coleoptera has been treated by Böcher (1988). Here we report on some insect remains that were found in Holocene sediment samples from the Sisimiut region in south-western Greenland (Figs. 1, 2).

Setting

The samples were collected near the outer coast in south-western Greenland (Figs. 1, 2). This region belongs to the low-arctic bioclimatic zone. The mean July temperature was 6.3°C and the mean annual precipitation 383 mm during the period from 1961 to 1990 (Cappelen et al. 2001). Permafrost is discontinuous. The local bedrock is

Citation: *Polar Research* 2012, *31*, 18367, http://dx.doi.org/10.3402/polar.v31i0.18367

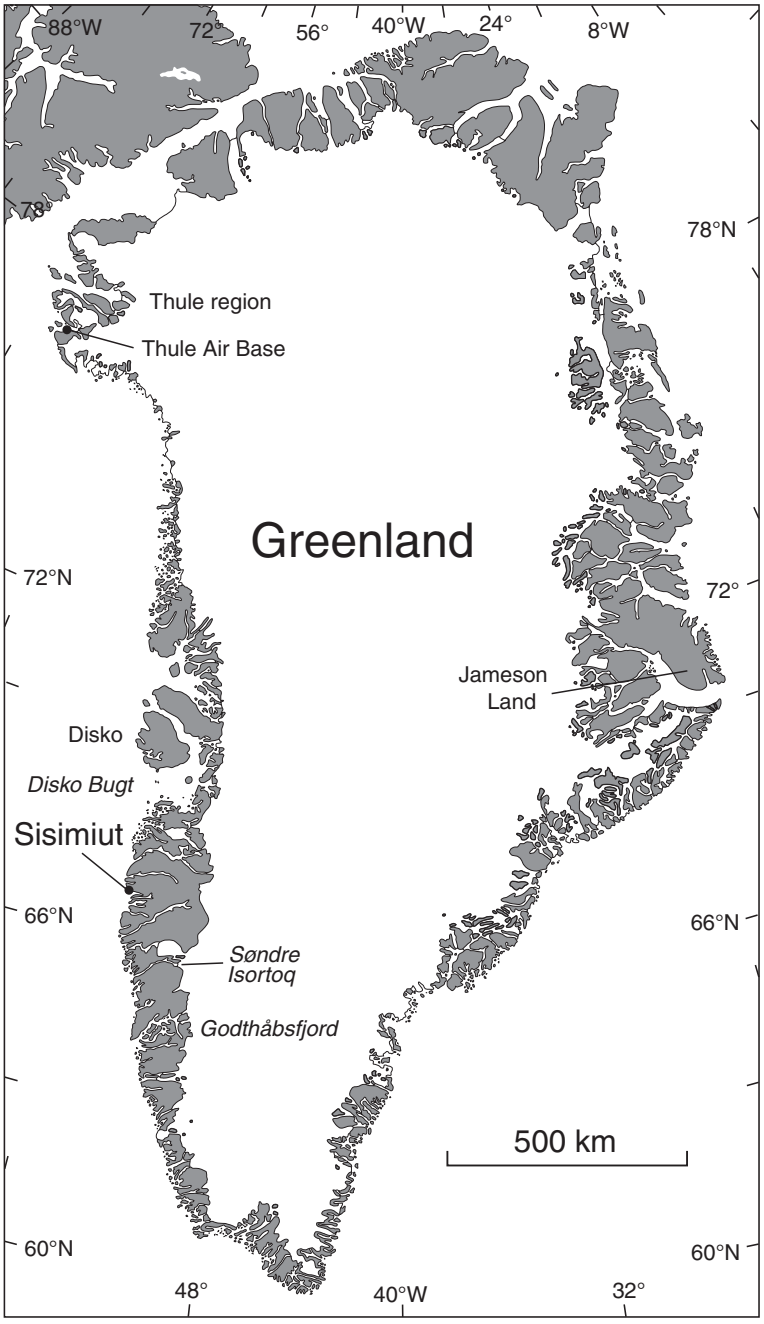

Fig. 1 Map of Greenland showing the location of Sisimiut and other places mentioned in the text.

dominated by glacially scoured Precambrian crystalline basement gneiss. Thin Quaternary till and gravel deposits are widespread. The topography is rugged with abundant lakes, and the highest mountain in the area is 554 m a.s.l. The vegetation is dominated by moss-rich scrubs and heaths with *Salix glauca*, *Betula nana* and ericaceous dwarf shrubs such as *Empetrum nigrum* and *Ledum palustre*. Fens, bogs and snow-bed vegetation are widespread on poorly drained sites and the uplands are characterized by fell-field vegetation. The terrestrial insect fauna includes around ten species of beetles (Böcher 1988).

The samples come from lake sediment cores collected from unnamed lakes, here referred to as Sisi 12, Sisi 14 and Sisi 15, located north north-west of Sisimiut (Holsteinsborg). Sisi 12 is located at ca. 200 m a.s.l., and the 341-cm long sequence was collected at 66°58.925′N, 53°43.090′W,

Citation: *Polar Research* 2012, *31*, 18367, http://dx.doi.org/10.3402/polar.v31i0.18367

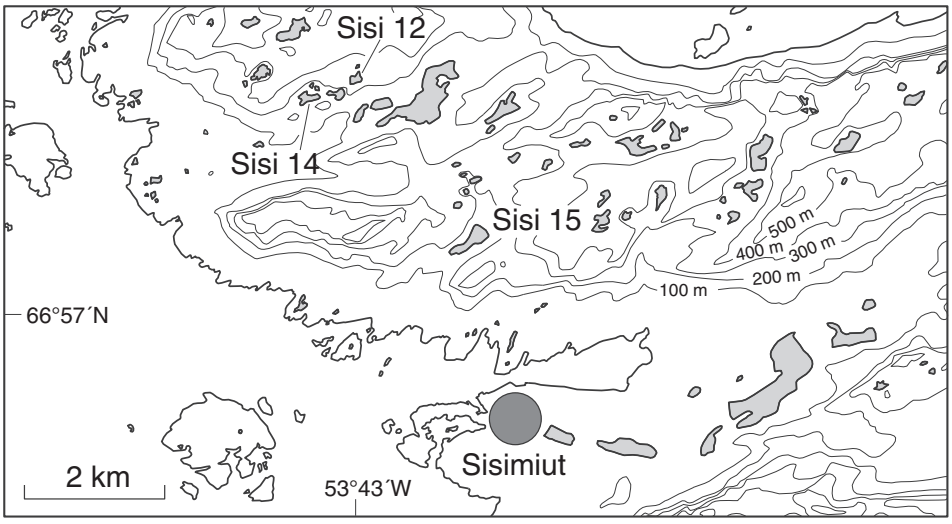

Fig. 2 Detailed map of the Sisimiut area showing the position of the sampled lakes.

at a water depth of 7.7 m. Sisi 14 is located at ca. 185 m above sea level, and the 440 cm long sequence was collected at 66°58.786′N, 53°44.005′W, at a water depth of 7.3 m. Sisi 15 is situated 129.9 m a.s.l. The core from this lake was collected at 66°57.72′N, 53°40.55′W, at a water depth of 5.6 m. The core was 356 cm long, but the insect remains discussed here come from the upper part of the core, which was relatively rich in macroscopic remains of terrestrial plants. This is probably because a small delta to the north of the lake prograded towards the core site during the Holocene. A small section ca. 0.5 m high that was eroded in the onshore delta sediments revealed fine-grained sand and silt with a thin organic-rich layer, from which a sample was also collected. The latter sample consisted of fine-grained sand, whereas the other samples consisted of gyttja (lake mud).

Methods

Sediment cores were collected with a Russian corer and sub-sampled in the laboratory. Small sub-samples around 15 ml were wet-sieved, and the residue left on the sieves was studied using a dissecting microscope. For insect analyses such samples are small, but this was balanced by a large number of analysed samples (830). A 2-kg sample was collected from an open section in the delta at Sisi 15 and also wet-sieved and analysed.

Samples of terrestrial plant macrofossils were dated using accelerator mass spectrometry radiocarbon age determination. The dates have been calibrated to calendar years according to the INTCAL09 data set. The sequence from Sisi 12 was dated on the basis of five age determinations, the sequence from Sisi 14 on the basis of six age determinations and the sequence from Sisi 15 on the basis of five age determinations. All gave well constrained age-depths curves that have enabled us to put ages on the recovered insect remains (Fig. 3). The remains from the delta at Sisi 15 were dated on the basis of an age of 3725 ± 50 ^{14}C years B.P. (LuS-8463; date based on *Salix herbacea* leaves). This corresponds to a calibrated age of 4236–3959 cal. years B.P., or ca. 4100 cal. years B.P.

Results

A number of fragments of Heteroptera (true bugs) and Coleoptera (beetles) were found in the samples (Fig. 4). This is not by itself sensational, but the evidence provided about their former presence in south-western Greenland is highly interesting. Here we present some notes on the species recorded.

Nysius groenlandicus (Zetterstedt, 1838) (Heteroptera: Lygaeidae)

One head and seven prothoraces, with ages between 9140 and 3515 cal. years B.P., were collected. The Greenland seed bug is common and found almost throughout the ice-free parts of Greenland, with increasing abundance from the coast inland, reflecting the extreme thermophily and xerophily of the species. It is a polyphagous seed-feeder with a single yearly generation and overwintering in the egg-stage (Böcher 1972, 1975, 1976; Böcher & Nachman 2001, 2010). The distribution is palaearctic and Arctic–alpine, at least covering Iceland and Scandinavia, Arctic Russia and (apparently) Asian mountains. An occurrence in sub-Arctic North America has still to be confirmed (Danks 1981).

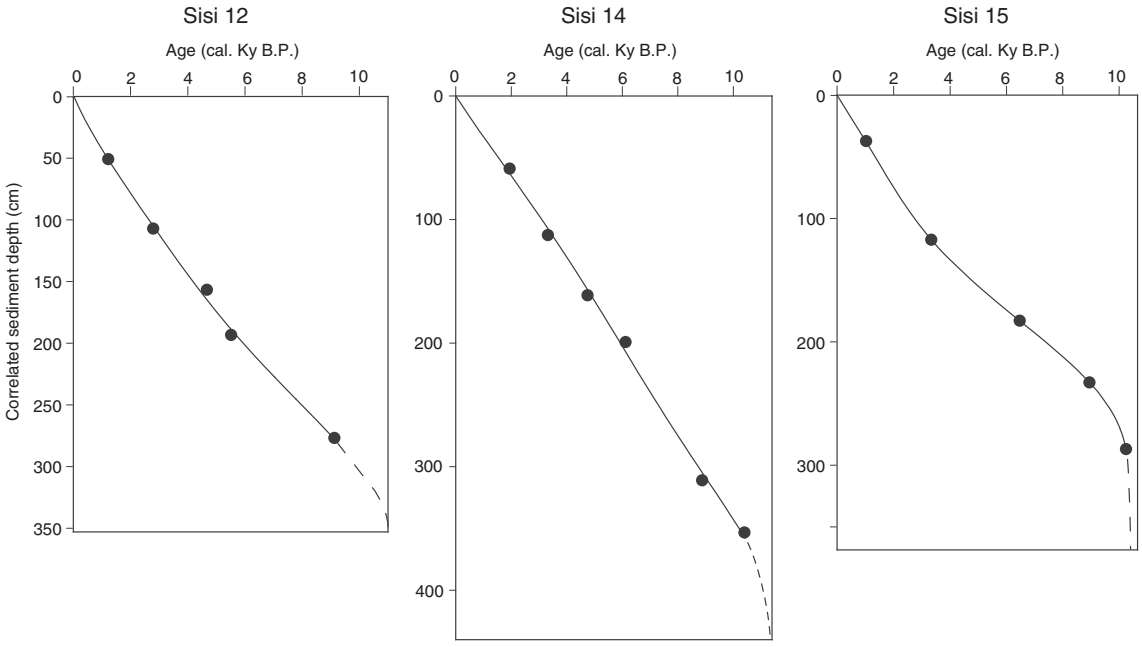

Fig. 3 Age–depth curves for Sisi 12, Sisi 14 and Sisi 15.

Nysius groenlandicus was present in Jameson Land, east Greenland and the Thule region, north-west Greenland, during the last interglacial stage (Bennike & Böcher 1992, 1994) and recorded from early Holocene deposits in north-eastern Greenland (Böcher & Bennike 1996; Christiansen et al. 2002). The earliest Holocene records are dated to ca. 9800 cal. years B.P. (west Greenland) and 8700 cal. years B.P. (east Greenland). The finds from the Sisimiut region confirm that *N. groenlandicus* was an early member of the Holocene fauna of Greenland. Remains of the species have been recorded from a large number of mid- and late Holocene deposits in Greenland (Buckland et al. 1983; McGovern et al. 1983; Böcher & Fredskild 1993; Böcher 1998; Bennike 2000; Bennike et al. 2000; Wagner et al. 2008; Buckland et al. 2009; Bennike, Knudsen et al. 2010).

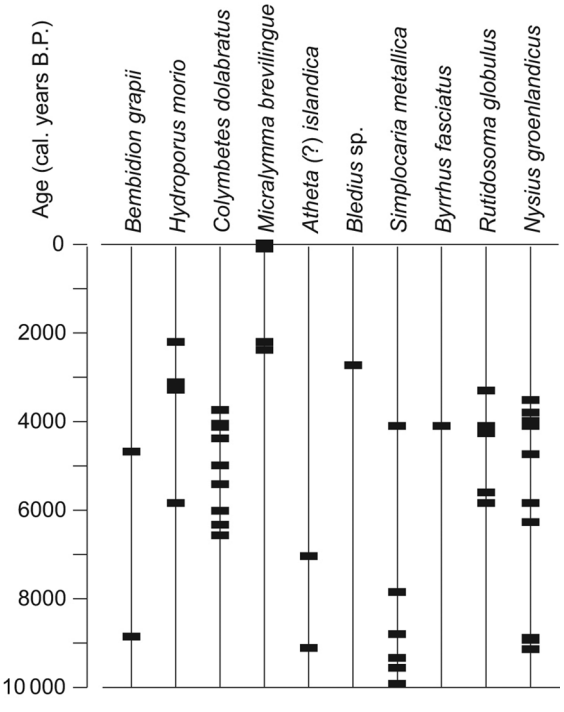

Fig. 4 Temporal ranges of insect taxa from the Sisimiut region discussed in this paper.

Bembidion grapii (Gyllenhal, 1827) (Coleoptera: Carabidae)

Two front halves of right elytra of this ground beetle were found, with ages around 8855 and 4680 cal. years B.P. The species is fairly common in west Greenland, has been found northwards to 72°20′N and is therefore the only Greenland carabid extending almost to the High Arctic. In east Greenland its occurrence seems to be much more scattered northwards to ca. 69°N. The general distribution is circumpolar, low Arctic and sub-Arctic, mostly in alpine regions. *B. grapii* preferably lives in fairly warm and dry situations, e.g., among low vegetation or in birch coppices on south-facing slopes.

As a fossil in Greenland *B. grapii* has been recorded from central east Greenland (early Holocene; Böcher & Bennike 1996), south-east Greenland (late Holocene; Hasholt 2000), west Greenland (mid-Holocene; Böcher &

Citation: *Polar Research* 2012, *31*, 18367, http://dx.doi.org/10.3402/polar.v31i0.18367

Fredskild 1993; Bennike et al. 2000) and south Greenland (Buckland et al. 2009).

Hydroporus morio (Aubé, 1823) (Coleoptera: Dytiscidae)

One right elytron, two left elytra and two meso+metasterna were found in sediments from Sisi 14, with ages between 5840 and 2205 cal. years B.P. The small of the two Greenland predacious water beetles is very common and widely distributed along the western coast, at least north to Thule Air Base at 76°30′N. The species is also common in south-east Greenland, recorded north to 65°N. *H. morio* inhabits any kind of small ponds and pools, frequently temporary pools, and also marshes, but shallow ponds with a muddy bottom are preferred. The species is circumpolar, Arctic to northern temperate.

In Greenland, remains of *H. morio* have been found in last interglacial deposits (Bennike & Böcher 1994) and in Holocene deposits (Fredskild et al. 1975; Fredskild 1983, 1985; Buckland et al. 1983; Böcher & Fredskild 1993; Bennike 1995, 2000; Eisner et al. 1995). The oldest Holocene finds of the species are dated to around 9500 years old (Fredskild et al. 1975; Fredskild 1983).

Colymbetes dolabratus (Paykull, 1789) (Coleoptera: Dytiscidae)

Many fragments of elytra were found in the sediments from Sisi 12 and Sisi 14, with ages between 6570 and 3740 cal. years B.P. *C. dolabratus* is the largest beetle in Greenland and abundant in the southern half of the country, with a northern limit in the southern High Arctic at ca. 74°N in both west and east Greenland. This is a circumpolar species with an Arctic to northern temperate range.

The species typically lives in ponds with rich vegetation, but it is highly eurytopic and may be present in almost any kind of stagnant water where larvae and adults are found together during the summer. In late summer the imagines migrate to hibernate in lakes that do not freeze to the bottom. During winter the species depends on diffusion of oxygen into the air bubble under the elytra. The air bubble decreases in size if not replenished, and if the lake is ice covered for extended time the imagines may suffer from lack of oxygen. The northern limit in Greenland is probably determined by the length of the period of ice cover.

Remains of *C. dolabratus* have been reported from many Holocene sites in Greenland (Fredskild et al. 1975; Fredskild 1985; Böcher & Fredskild 1993; Björck et al. 1994; Bennike 1995, 2000; Eisner et al. 1995; Bennike & Funder 1997; Bennike et al. 1999; Bennike, Anderson et al. 2010). The oldest remains are dated to ca. 10 800 cal. years B.P. (east Greenland; Björck et al. 1994) and ca. 9500 cal. years B.P. (north-west Greenland; Fredskild 1985). Both species of predaceous diving beetles were among the first insects to appear in Greenland following the last partial deglaciation.

Micralymma brevilingue (Schiödte, 1845) (Coleoptera: Staphylinidae)

One pronotum, two left elytra and one set of paired elytra were found in sediments from Sisi 14, and dated to ca. 2205–200 cal. years B.P. *M. brevilingue* is the most widespread rove-beetle in Greenland, found even in the southern part of the High Arctic and very commonly along the western coast. In most cases the species lives close to the beach. It can also be found elsewhere, for example, in snow-beds and luxuriant herbslopes. The species is circumpolar and Arctic. According to Makarova et al. (2007) the species is widespread in the High Arctic archipelago of Severnaya Zemlya, Siberia, and is thus the northernmost occurring beetle-species in Eurasia.

Fossil *M. brevilingue* have been reported from south-west Greenland (Bennike 1992; Böcher & Fredskild 1993; Böcher 1998). The finds are middle to late Holocene in age.

Atheta cf. *islandica* (Kraatz, 1856) (Coleoptera: Staphylinidae)

One left and one right elytron, dated to 9110 and 7040 cal. years B.P. were found. The genus *Atheta* comprises four Greenland species of which *A. (Boreophilia) islandica* seems to be most common and to have the greatest geographical range in Greenland (north to 68°40′N in west Greenland and 63°N in east Greenland). The species is palaearctic and Arctic–alpine.

Remains of another species, *Atheta (Boreophilia) hyperborea* Brundin, 1940 were found fairly frequently in palaeo-Eskimo sediments from Disko Bugt (Böcher & Fredskild 1993), but it is highly surprising to find the genus as early as 9110 cal. years B.P.

Bledius sp. (Coleoptera: Staphylinidae)

One right elytron was found in the sediment sequence from Sisi 12, dated to around 2730 cal. years B.P. The large genus *Bledius* primarily comprises small species living in burrows on mud-flats. The find is important because the genus has never before been reported from Holocene Greenland deposits and is unknown from the modern-day fauna of Greenland. It was, however, recorded from the early Quaternary Kap København

and Store Koldewey Formations in north and north-east Greenland, both dated to around 2 Mya (Böcher 1995; Funder et al. 2001; Bennike, Knudsen et al. 2010).

Simplocaria metallica (Sturm, 1807) (Coleoptera: Byrrhidae)

Two heads, five left elytra (four fragments) and four right elytra (two fragments) of this pill beetle were found, dated to between 9920 and 4100 cal. years B.P. The species is fairly common in western Greenland south of Disko, although occurring scattered; also found locally in south-eastern Greenland. *S. metallica* is undoubtedly a moss-feeder, always found in the vicinity of water. It is of circumpolar distribution, Low Arctic to northern temperate, alpine in southern Europe.

Simplocaria metallica has hitherto been recorded from mid- and late Holocene deposits in southern and western Greenland (Buckland et al. 1983; Böcher & Fredskild 1993; Böcher 1998; Bennike et al. 2000; Buckland et al. 2009) and also from the last interglacial stage in central east Greenland (Bennike & Böcher 1994). Previously the oldest (Holocene) find was dated to ca. 5800 cal. years B.P. Hence the present records extend the known temporal Holocene range far back in time, and the find dated to 9920 cal. years B.P. is the oldest record of a terrestrial beetle species from Holocene deposits in Greenland.

Byrrhus fasciatus (Forster, 1771) (Coleoptera: Byrrhidae)

One pronotum was recorded from the delta deposit dated to ca. 4100 cal. years B.P. *B. fasciatus* is common and widespread in Greenland, reaching the High Arctic in both west and east Greenland. The species is circumpolar and like *S. metallica* a moss-feeder found in highly different, both humid and dry situations. Both larva and adult feed on mosses. The distribution is circumpolar, Low-Arctic to temperate.

Fragments of *B. fasciatus* have been found in last interglacial deposits (Bennike & Böcher 1994) and in mid- and late Holocene sediments in south-western Greenland (Buckland et al. 1983; Böcher & Fredskild 1993). The earliest Holocene record (from Disko Bugt) is about 4400 cal. years old.

Rutidosoma globulus (Herbst, 1795) (Coleoptera: Curculionidae)

One prothorax, two left elytra and two right elytra were found (Fig. 5), dated to between 5840 and 3300 cal. years B.P. The sculpture of the fossil specimens seems to be a little less pronounced than that of recent specimens, but the identification has been confirmed by Robert Anderson (pers. comm. 2008). The present distribution of *Rutidosoma globulus* comprises most of northern and central Europe, but it is absent from the Faroe Islands and Iceland. In Denmark *Rutidosoma globulus* is a rare species (Hansen 1964). In Europe it is monophagous on *Populus tremula* (Hoffman 1958; Bullock 1992).

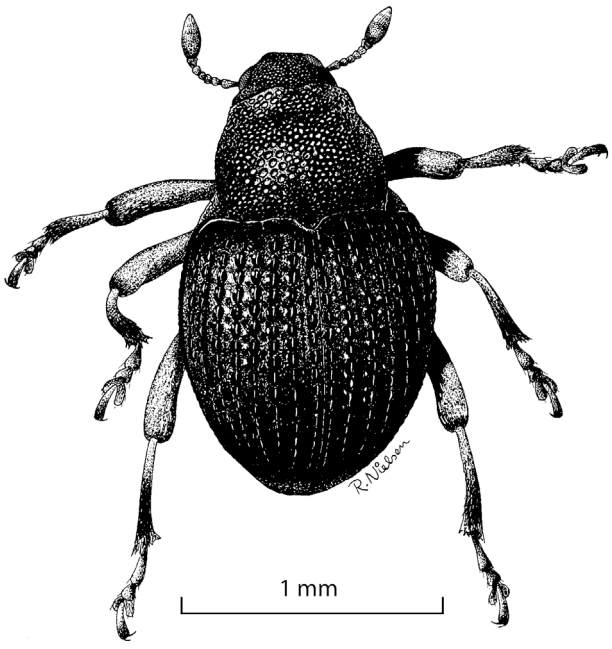

Fig. 5 *Rutidosoma globulus* (Herbst, 1795), a modern Greenland specimen drawn by Robert Nielsen.

In Greenland *R. globulus* appears to be extremely rare, and only three extant specimens are known. In addition to an old find from an unknown locality, one specimen was collected in the fjord Søndre Isortoq in 1885. During fieldwork in 2003 another specimen was found in the same fjord by sweeping in a small valley with snow patch vegetation comprised of *Salix herbacea*, *S. arctophila*, *S. glauca*, *Polygonum viviparum* and *Carex* spp. *Populus* does not grow in Greenland, and the food plant here is probably one or more species of *Salix*.

The only previous fossil record of *R. globulus* in Greenland is of late Holocene age and comes from a Norse ruin in Nuup Kangerlua (Godthåbsfjord; McGovern et al. 1983). It is indeed surprising to find an apparently rare species to be fairly numerous in the fossil material.

Discussion and conclusion

The colonization of Greenland by insects, especially beetles (Coleoptera) following the last ice age has been the object of a long-lasting debate which is by no means

Citation: *Polar Research* 2012, *31*, 18367, http://dx.doi.org/10.3402/polar.v31i0.18367

finished. However, these new finds add some facts to the discussion.

The rare Greenland occurrence of the weevil *Rutidosoma globulus* might suggest that the species is a fairly recent immigrant which has not yet had time to spread over large areas. If it feeds on willow (*Salix* spp.) one would assume that it has plenty of opportunities in Greenland, as willows are common and widespread. The fossil finds reported here provide a minimum date for its arrival in Greenland at around 5840 years B.P. ago, and it is surprising that it is so rare. It is a possibility that *Salix* spp do not constitute an optimal diet for the species.

Most of Greenland's terrestrial beetle species arrived from north-west Europe, in many cases using the Faroe Islands and Iceland as stepping stones. It is clear from its modern geographical range that *Rutidosoma globulus* also arrived from Europe, but the species does not occur in the Faeroe Islands or Iceland, so in some way it must have dispersed directly across the North Atlantic Ocean.

In general, the data from the Sisimiut region combined with other data from Greenland imply that many insect species were present in the early Holocene. This could be used as an argument in favour of survival in Greenland during the last glacial stage. However, large areas were deglaciated during the late Weichselian, from around 15 000–12 000 cal. years B.P. (e.g., Björck et al. 2002; Kelly et al. 2008). During this time period many plant and animal species may have immigrated to Greenland. We conclude that fossil finds to date do not tell us whether some insect species survived in Greenland during the last glacial stage.

Acknowledgements

OB is grateful to the Carlsberg Foundation for funding. Robert S. Anderson, Canadian Museum of Nature, Ottawa, kindly scrutinized the *Rutidosoma* elytra. Alexey Solodovnikov, at the Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, is thanked for identifying a pronotum of *Micralymma brevilingue*.

References

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. 1999. Colonisation of Greenland after the last ice age: a review. *Polar Record 35*, 323–336.

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

Bennike O. 2002. Late quaternary history of Washington Land, north Greenland. *Boreas 31*, 260–272.

Bennike O., Anderson N.J. & McGowan S. 2010. Holocene palaeoecology of south-west Greenland inferred from macrofossils in sediments of an oligosaline lake. *Journal of Paleolimnology 43*, 787–798.

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.

Bennike O., Björck S., Böcher J. & Walker I. 2000. The quaternary arthropod fauna of Greenland: a review with new data. *Bulletin of the Geological Society of Denmark 47*, 111–134.

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., Knudsen K.L., Abrahamsen N., Böcher J., Cremer H. & Wagner B. 2010. Early Pleistocene sediments on Store Koldewey, northeast Greenland. *Boreas 39*, 603–619.

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

Björck S., Bennike O., Rosén P., Andresen C.S., Bohncke S.J.P., Kaas E. & Conley D.J. 2002. Anomalously mild Younger Dryas summer conditions in south Greenland. *Geology 30*, 427–430.

Böcher J. 1972. *Feeding biology of Nysius groenlandicus (Zett.) (Heteroptera: Lygaeidae) in Greenland. With a note on oviposition in relation to food-source and dispersal of the species. Meddelelser om Grønland 191(4)*. Copenhagen: C.A. Reitzel.

Böcher J. 1975. Notes on the reproductive biology and egg-diapause in *Nysius groenlandicus* (Heteroptera: Lygaeidae). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 138*, 21–38.

Böcher J. 1976. Population studies on *Nysius groenlandicus* (Zett.) (Heteroptera: Lygaeidae) in Greenland, with particular reference to climatic factors, especially the snow cover. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 139*, 61–89.

Böcher J. 1988. *The Coleoptera of Greenland. Meddelelser om Grønland, Bioscience 26*. Copenhagen: Commission for Scientific Research in Greenland.

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*. Copenhagen: Commission for Scientific Research in Greenland.

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

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 Qeqertasussuk, west Greenland. Meddelelser om Grønland, Geoscience 30*. Copenhagen: Commission for Scientific Research in Greenland.

Böcher J. & Nachman G. 2001. Temperature and humidity responses of the Arctic–alpine seed bug *Nysius groenlandicus*. *Entomologica Experimentalis et Applicata 99*, 319–330.

Böcher J. & Nachman G. 2010. Are environmental factors responsible for geographic variation in the sex ratio of the Greenlandic seed-bug *Nysius groenlandicus*? *Entomologia Experimentalis et Applicata 134*, 122–130.

Brodersen K. & Bennike O. 2003. Interglacial Chironomidae (Diptera) from Thule, northwest Greenland: matching modern analogues to fossil assemblages. *Boreas 32*, 560–565.

Buckland P.C., Edwards K.J., Panagiotakopulu E. & Schofield J.E. 2009. Palaeoecological and historical evidence for manuring and irrigation at Gardar (Igaliku), Norse Eastern Settlement, Greenland. *The Holocene 19*, 105–116.

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.

Bullock J.A. 1992. *Host plants of British beetles: a list of recorded associations. Amateur Entomologist Pamphlets*. Feltham, UK: Amateur Entomologists' Society.

Cappelen J., Jørgensen B.V., Laursen E.V., Stannius L.S. & Thomsen R.S. 2001. *The observed climate of Greenland, 1958-99—with climatological standard normals, 1961–90. Technical Report 00–18*. Copenhagen: Danish Meteorological Institute.

Christiansen H.H., Bennike O., Böcher J., Elberling B., Humlum H. & Jakobsen B.H. 2002. Holocene environmental reconstruction from deltaic deposits in northeast Greenland. *Journal of Quaternary Science 17*, 145–160.

Dahl-Jensen D., Mosegaard K., Gundestrup N., Clow G.D., Johnsen S.J., Hansen A.W. & Balling N. 1998. Past temperatures directly from the Greenland Ice Sheet. *Science 282*, 268–271.

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

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

Fredskild B. 1983. *The Holocene vegetational development of the Godthåbsfjord area, west Greenland. Meddelelser om Grønland, Geoscience 10*. Copenhagen: Commission for Scientific Research in Greenland.

Fredskild B. 1985. *The Holocene vegetational development of Tugtuligssuaq and Qeqertat, northwest Greenland. Meddelelser om Grønland, Geoscience 14*. Copenhagen: Commission for Scientific Research in Greenland.

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)*. Copenhagen: C.A. Reitzel.

Funder S. 1979. Ice-age plant refugia in east Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology 28*, 279–295.

Funder S., Bennike O., Böcher J., Israelson C., Petersen K.S. & Símonarson L.A. 2001. Late Pliocene Greenland—the Kap København Formation in north Greenland. *Bulletin of the Geological Society of Denmark 48*, 117–134.

Funder S., Kjellerup K.K., Kjær K.H. & Ó Cofaigh C. 2011. The Greenland Ice Sheet during the past 300,000 years: a review. In J. Ehlers et al. (eds.): *Quaternary glaciations—extent and chronology. A closer look*. Pp. 699–714. Amsterdam: Elsevier.

Hansen V. 1964. *Fortegnelse over Danmarks biller (Coleoptera). (Survey of Danish beetles [Coleoptera].) Entomologiske Meddelelser 33*. Copenhagen: Entomological Society of Copenhagen.

Hasholt B. 2000. Evidence of a warmer climate around AD 600, Mittivakkat Glacier, south east Greenland. *Danish Journal of Geography 100*, 88–90.

Hofman A. 1958. *Coléopteres curculionides. Faune de France 62. (Coleoptera: curculionides. Fauna of France 62.)* Paris: Lechevalier.

Kelly M.A., Lowell T.V., Hall B.L., Schaefer J.M., Goehring B.M., Alley R.B. & Denton G.H. 2008. A ^{10}Be chronology of late-glacial and Holocene mountain glaciation during late-glacial time. *Quaternary Science Reviews 27*, 2273–2282.

Makarova O.L., Bienkowski A.O., Bulavintsev V.I. & Sokolov A.V. 2007. Beetles (Coleoptera) in polar deserts of the Severnaya Zemlya Archipelago. *Entomological Review 87*, 1142–1154.

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 farms in the Western Settlement, Greenland. *Arctic Anthropology 20*, 93–120.

Vinther B.M., Buchardt S.L., Clausen H.B., Dahl-Jensen D., Johnsen S.J., Fisher D.A., Koerner R.M., Raynaud D., Lipenkov V., Andersen K.K., Blunier T., Rasmussen S.O., Steffensen J.P. & Svensson A.M. 2009. Holocene thinning of the Greenland Ice Sheet. *Nature 461*, 385–388.

Wagner B., Bennike O., Bos J.A.A., Cremer H., Lotter A.F. & Melles M. 2008. A multidisciplinary study of Holocene sediment records from Hjort Sø on Store Koldewey, north-east Greenland. *Journal of Paleolimnology 39*, 381–398.