An Early Pleistocene interglacial deposit at Pingorsuit, North-West Greenland

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At the Pingorsuit Glacier in North-West Greenland, an organic-rich deposit that had recently emerged from the retreating ice cap was discovered at an elevation of 480 m above sea level. This paper reports on macrofossil analyses of a coarse detritus gyttja and peaty soil, which occurred beneath a thin cover of till and glacifluvial deposits. The sediments contained remains of vascular plants, mosses, beetles, caddisflies, midges, bryozoans, sponges and other invertebrates. The flora includes black spruce, tree birch, boreal shrubs and wetland and aquatic taxa, which shows that mires, lakes and ponds were present in the area. We describe a new extinct waterwort species Elatine odgaardii. The fossils were deposited in a boreal environment with a mean July air temperature that was at least 9 °C higher than at present. The fossil assemblages show strong similarities with others from Greenland that have been assigned an Early Pleistocene age, and we suggest a similar age for the sediments found at the margin of the Pingorsuit Glacier. At the Pingorsuit Glacier in North-West Greenland, an organic-rich deposit was discovered at an elevation of 480 m above sea level. The sediments contained remains of vascular plants, mosses, beetles, caddisflies, midges, bryozoans, sponges and other invertebrates. The fossils were deposited in a boreal environment with a mean July air temperature that was at least 9 °C higher than at present.

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The Thule region in North-West Greenland was repeatedly glaciated during the Quaternary glacial stages, including the Last Glacial Maximum. Nevertheless, Eemian interglacial deposits are fairly common in the region (Kelly et al. 1999), whereas older interglacial deposits have not been reported so far. However, Mörner & Funder (1990) reported on a branch that gave a radiocarbon age of >48 000 ¹⁴C years BP found at an elevation of 400 m a.s.l. This find could indicate that Early Pleistocene deposits occur in the region.

A number of sedimentary successions in Greenland have been referred to the Early Pleistocene, including member B of the Kap København Formation in Peary Land, North Greenland (Fig. 1). Rich and diverse floras and faunas of marine and non-marine environments have been described (e.g. Bennike 1990; Símonarson et al. 1998; Böcher 1995; et al. 2001). The age of member B was suggested to be c. 2 Ma (Repenning et al. 1987; Matthews & Ovenden 1990; Bennike *et al.* 2010) or *c.* 2.4 Ma (Funder et al. 2001). In North-East Greenland, the Île de France Formation and the Store Koldewey

Formation were dated to c. 2 Ma (Bennike et al. 2002, 2010). Farther south, in central East Greenland the glaciomarine Lodin Elv Formation was dated to the Plio-Pleistocene by Feyling-Hanssen et al. (1983). Reworked wood fragments with non-finite radiocarbon ages found on the terrain surface at several sites in northern Greenland have been referred to the Pliocene or Early Pleistocene (Bennike 1998, 2000). The Pátorfik beds in West Greenland may be Early Pleistocene in age (Funder & Símonarson 1984; K.L. Knudsen, pers. comm. 2010).

Plant macrofossils dated to between $<3.2\pm0.4$ and >0.7–1.4 Ma have also been found in subglacial diamicton at the base of the Camp Century ice-core, which was collected 240 km east of Thule Air Base (Christ et al. 2021) and biomolecules have been reported from basal ice from the DYE-3 core (Willerslev et al. 2007). The latter may be of Marine Isotope Stage 11 age. The most famous occurrence in Arctic Canada is the Beaver Pond site on Ellesmere Island; this deposit that is dated to the mid-Pliocene contains remains of mammals such as camel, horse, deerlet, rabbit, bear, badger in addition to beaver (Rybczynski



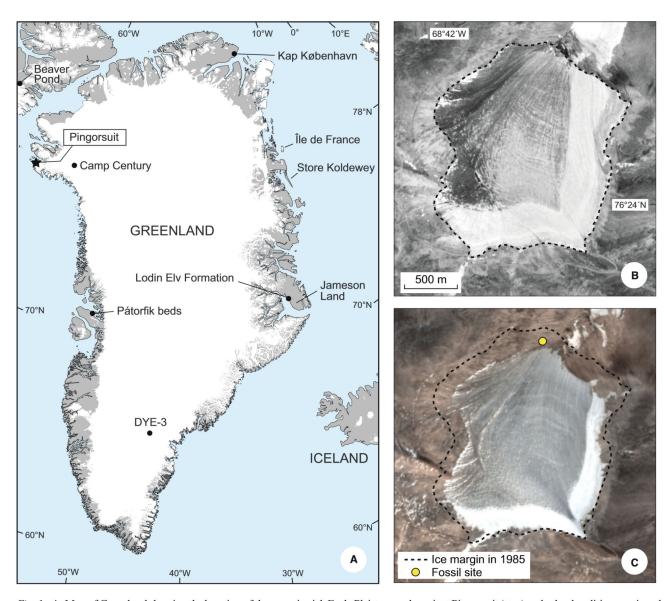


Fig. 1. A. Map of Greenland showing the location of the organic-rich Early Pleistocene deposit at Pingorsuit (star) and other localities mentioned in the text. B. Aerial photograph of the Pingorsuit Glacier in 1985 (Korsgaard et al. 2016). C. Satellite image from 2019 from Planet Scope (Planet Team 2017). The ice margin has retreated about 150 m from 1985 to 2019 at the find site.

et al. 2013). Studies of plant and insect fossils from the Beaver Pond site and other Pliocene, Miocene and Early Pleistocene sites in northern Canada and Alaska have been summarized by for example Matthews et al. (2019), Fletscher et al. (2021) and Barendregt et al. (2021).

The aim of this paper is to describe the interglacial environment and biota near the Pingorsuit Glacier, based on analyses of macrofossil assemblages. The plant and animal remains give unique insights into past warmer-than-present life in the Arctic. The environmental indications of the fossil contents and the chronology of the deposit are discussed in relation to Late Pleistocene, Early Pleistocene and Pliocene deposits in Greenland and northern Canada.

Setting

The Pingorsuit Glacier is located ~ 13 km south of Thule Air Base at $\sim 76.41^{\circ}$ N, 68.66° W. The organic-rich deposit is located at the northern snout of the glacier, at 480 m a.s.l. In this area, Pingorsuit Glacier is the only ice cap situated between the Greenland Ice Sheet and the coast. Perennial snow fields are common, but most of the uplands in the area are snow-free during the summer. The bedrock of the area is characterized by orthogneiss and sedimentary rocks, but the bedrock on the plateau is predominately covered by till and glacifluvial deposits (Dawes 2006).

Meteorological data are not available for the site, but at sea level, at Thule Air Base, the mean July temperature is



4.5 °C and annual precipitation averages 127 mm (Cappelen et al. 2001). If we assume a lapse rate of 5.6 °C per kilometre (Körner 2003), the mean July temperature at 480 m a.s.l. may be estimated as 1–2 °C. The present-day vegetation in the area is dominated by fell fields with herbs, grasses, mosses and lichens. The flora in the region includes the dwarf shrubs Salix arctica, Dryas integrifolia, Cassiope tetragona, Vaccinium uliginosum and Empetrum nigrum. The area is characterized by continuous permafrost, which may reach depths of 500 m (Roethlisberger 1961). During fieldwork in September 2019, the active layer thickness at the site was ~25 cm.

The organic-rich deposit is located in a proglacial terrain that has deglaciated since 1985 (Fig. 1B, C). The deposit consists of five small mounds, with a total area of ~20 m². The mounds have recently emerged from beneath the retreating ice cap margin and appear to have experienced substantial glaciotectonic reworking. No other organic-rich deposits are known from the proglacial area, beyond the 1985 extent of Pingorsuit Glacier, which may suggest that they are thin and eroded relatively quickly after deglaciation. Indeed,

the deposit is being eroded by a proglacial meltwater stream.

The organic-rich deposit was readily identified in the field by its dark colour relative to surrounding till. The organic-rich material is covered by a thin layer of till (Fig. 2), which is composed of boulders, cobbles, pebbles and sand.

Material and methods

A total of 21 bulk samples of organic-rich sediment were collected with a total weight of \sim 25 kg. The samples were shipped to Copenhagen. In the laboratory, samples were wet sieved on a series of sieves, and the residue left on the sieves was analysed for macrofossils using a dissecting microscope. The finest sieve mesh size was 0.1 mm. The results of the macrofossil analyses are presented in Tables 1–5.

To investigate sponges by light microscopy and scanning electron microscopy, samples were treated by (i) dissolving organic sediment in nitric acid to prepare slides and stubs of the siliceous skeleton and (ii) visually sorting entire gemmules (resistant stages).



Fig. 2. Field photographs from the sampling of organic-rich material from the Pingorsuit site in North-West Greenland. A. Looking downvalley from the terminus of Pingorsuit Glacier at hummocky terrain in the proglacial forefield. Person for scale in the ellipse. B. Drone image showing the interglacial deposit covered by till. The samples were collected within an approximately 10-m radius. C. Sample dominated by wood fragments. The ellipse shows a spruce cone. D. Site where organic-rich sediment was sampled. Note the dark colour of the sediment.



Table 1. Remains of plants except bryophytes from Pingorsuit, North-West Greenland. r = rare; c = common.

Taxon	San	nple																	
	26	53	56	103	104	105	107	108	109	110	111	112	114	115	116	117	119	121	122
Terrestrial																			
Cenococcum geophilum	c	-	-	2	r	c	c	c	c	r	c	c	c	4	2	r	_	r	-
Picea mariana	14	4	10	1	27	_	2-	-	_	_	1	_	-	4	20	21	c	90	_
Taxus sp.	_	_	1	-1	-	_	_	-	-	_	-	_	_	-	-	-	_		_
Betula sect. Albae sp.	2	r	2	-	_	c	5	18	13	14	9	r	2	3	6	8	6	7	_
Cornus canadensis	_	_	-	-1	_	c	_	-	_	_	_	_	_	-	_	_	_	-	_
Salix sp.	_	_	-	-	_	2	3	9	_	1	-	3	_		1	_	_	-	-
Rubus idaeaus type	_	_	_	-	_	_	_	-	_	1	_	_	_	_	_	_	_		_
Empetrum nigrum	_	_	1	-	-	4	-	-	-	-	-	2	3	-	-	4	-	-	_
Cerastium sp.	_	_	$1-\epsilon$	-	1	_	-	-	-	-	-	_	_	-	-	_	-	-	-
Swamp																			
Polypodiacaea	r	_	_	_	_	r	_	_	С	_	1	_	_	r	_	r	r	_	_
Andromeda polifolia	_	_	_	1	3	1	_	_	_	_	_	_	_	_	1	_	1	_	_
Myrica sp.	3	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	3	_
Comarum palustre	4	_	_	4	_	c	2	c	c	9	c	c	1	_	1	6	2	2	_
Aracites globosa	18	_	_	3	22	_	_	_	_	_	_	_	1	25	5	2	2	3	_
Carex sp.	r	4	15	r	14	c	12	14	c	3	25	r	-	10	3	c	2	r	_
Juncus sp.	_	1	_	_	_	_	-	_	15	_	2	-	1	_	-	r	_	_	_
Aquatic																			
Nitella or Tolypella	_	4	-	_	2	_	1-1	_	_	_	_	_	_	12	_	_	_	_	_
Nuphar lutea type	5	2	_	_	_	_	_	_	_	_	_	_	_	17	_	_	_	30	_
Menyanthes trifoliata	30	_	1	25	21	_	_	_	_	_	_	_	_	70	30	8	15	40	7
Elatine odgaardii	_	_	_	_	2	-	_	_	_	_	_	_	_	_	_	_	4	_	_
Potamogeton obtusifolius	_	1	_	_	ī	_	_	_	_	-	_	_	_	8	2	_	2	1	24
Stuckenia filiformis	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	_	_	_	_

Results and discussion

Sediments

Some of the samples consisted of peaty soil or decomposed peat, and some of coarse detritus gyttja. The assemblages differ a lot from one sample to another. Even though the distance between the samples was small, sample 105 contained numerous endocarps of *Cornus canadensis*, which was not found in the other samples. On the other hand, sample 105 contained no remains of *Picea mariana*, which were common in samples 56 and 119. We suggest that these differences reflect different local environments. Another aspect of the fossil assemblages is that bryophyte remains were rare in most samples – this is in striking contrast to many other Late Cenozoic sites in the Arctic.

Vascular plants

Macrofossils of 19 taxa of vascular plants were found. The fossils included a cone, spruce needles, fruits, seeds, a catkin scale, sporangia and sclereids (inner hairs) of water lilies (Table 1). Some macrofossils are illustrated in Fig. 3. No leaves of angiosperms were found, which is somewhat unusual because many dwarf shrubs in the Arctic have leathery leaves that often preserve well. The five largest wood fragments of spruce measured 115×20 , 90×25 , 90×20 , 90×13 and 75×9 mm. The growth rings are extremely narrow.

Notes on selected taxa

Picea mariana. – A cone of spruce was found during the fieldwork; it is 12 mm long and 10 mm wide. It is similar to spruce cones from the Kap København Formation that were identified as *Picea mariana* (Mill.) B.S.P. (black spruce). Needles of P. mariana were found in two samples, in addition to twigs and a seed of spruce presumably belonging to the same species. The size and morphology of the needles vary considerably, from short, robust needles with rounded apices to longer, more slender needles with acute or even acuminate apices. The same variation was noted for Picea mariana needles from the Kap København Formation. P. mariana is abundant in the boreal forests of northern North America (Fig. 4) and often forms the Arctic tree line. Trees at the tree line are confined to wind-protected, well-watered areas and the growth form is usually stunted specimens (Laberge et al. 2001; Payette et al. 2001). Picea mariana remains have been reported from the Kap København Formation (Bennike 1990) and from other Late Cenozoic sites from Canada and Alaska (Matthews & Fyles 2000).

Betula sect. Albae sp.. — Remains of Betula sect. Albae sp. (tree birch) are represented by nutlets and a catkin scale. The size and shape of both show that they derive from tree birch and not from dwarf birch. Tree birch is a characteristic element of boreal forests, and it forms the Arctic tree line in Scandinavia. Fossils of arboreal birches are common at many Late Cenozoic sites in Arctic North



Table 2. Remains of bryophytes from Pingorsuit, North-West Greenland, S = shoot; B = branch; L = leaf.

Taxon	Sampl	e									
	26	53	56	103	104	109	112	115	117	119	121
Atrichum sp.	_	_	-	_	1 S	_	1-1	_	_	_	_
Calliergon cordifolium	_	_	_	_	-	2B	_	_	-	_	_
Calliergon cf. richardsonii	_	1 S	_	_	_	_	-	_	_	_	_
Dicranum undulatum	_	_	_	_	-	_	-	_	-	_	1S
Ditrichum sp.	_	_	_	_	_	-	-	2S	_	_	_
Hamatocaulis vernicosus	_	_	1S	1S+2L	-	_	-	_	_	_	_
Paludella squarrosa	_	-	_	49S	_	-	_	_	_	1L	_
Pogonatum dentatum	_	_	_	_	3L	_	-	_	_	_	_
Pogonatum urnigerum	-	_	_	_	_	-	1L	_	_	_	_
Pohlia sp.	_	_	_	_	_	_	_	_	1 S	_	_
Polytrichum juniperinum/strictum ¹	_	-	1S	1—	1S	-	_	_	3B	_	1 B
Polytrichum cf. swartzii	1L	_	10L	_	_	-	_	1L	8L	_	2B
Sanionia uncinata	_	_	_	_	1B	-	_	_	-	_	_
Sarmentypnum exannulatum	15S	31S	19S	_	5S		-	21S	14S	6S	16S
Sarmentypnum tundrae	_	_	1S	_	17S	-	_	_	1B	_	_
Straminergon stramineum	_	-	-	$14S^2$	$8S^2$	-	_	_	-	_	-
Sphagnum teres	_	-	_	12B	_	1 B	9 B	_	_	1 B	_
Sphagnum Sect. Cuspidata	_	-	_	1B	1B	_	-	1B	-	_	_

¹Probably *juniperinum*, largest leaves above, no tomentum observed.

America (e.g. Bennike 1990; Matthews & Fyles 2000; Bennike *et al.* 2010).

Cornus canadensis. – Sample 105 contained numerous endocarps referred to Cornus canadensis L. (dwarf cornel). This plant is found today in southern Greenland and North America. It is a small deciduous shrub that grows in well-drained soils, especially in spruce forests. Cornus canadensis endocarps have also been reported from the Kap København Formation, and endocarps tentatively referred to the species have been reported from Canada (Matthews & Ovenden 1990; Matthews et al. 2019; Barendregt et al. 2021).

Aracites globosa. — A fairly large number of fruits of Aracites globosa (C. & E. Reid) Benn. was found. Aracites globosa is an extinct wetland plant that has been reported from Greenland, Canada, Alaska, Asia and Europe (Bennike 1990; Matthews & Ovenden 1990; Aalto et al. 1992; Field et al. 2017; Fletcher et al. 2021). The stratigraphical range of Aracites extends from the Miocene to the Mid-Pleistocene (Aalto et al. 1992; Fletcher et al. 2021). However, the Mid-Pleistocene occurrences are restricted to Europe. In northern Canada, it is absent from the Worth Point flora that is dated to c. 1.8 Ma (Fletcher et al. 2021).

Myrica sp. – Seven endocarps of Myrica were found. Unfortunately, the lateral lobes were not preserved, but we consider it likely that the fruits belong to the extinct species Myrica arctogale Benn. that was described from the Kap København Formation (Bennike 1990). Myrica endocarps have been reported from many sites in northern North America and Fletcher et al. (2021)

considered the presence of *Myrica* sp. an indication of an Early Pleistocene age or older.

Elatine odgaardii Bennike, sp. nov.

Holotype: MGUH 34065.

Repository: The Natural History Museum of Denmark, Copenhagen.

Type locality: Pingorsuit near Thule Air Base, North-West Greenland.

Age: Early Pleistocene (?).

Etymology: After the Danish palaeoecologist Bent Vad Odgaard.

Remarks: Elatine species are small-sized annuals, characteristic of habitats with fluctuating water levels, where they may grow as aquatic or amphibious plants. They can grow at the shores of lakes or rivers. Their tiny seeds are probably spread by waterfowl. Seeds of *Elatine* spp. (waterwort) are tiny, ~0.5–1 mm long (Brinkkemper et al. 2007; Razifard 2016). The genus Elatine comprises 30 extant species, according to Plants of the World (https://powo.science.kew.org; accessed 30th November 2021). In addition, a few extinct species have been described from Pliocene deposits in eastern Europe: Elatine pseudoalsinastrum and Elatine hydropiperoides (Dorofeev & Velichkevich 1971; Mai & Walther 1988). Seeds of extant *Elatine* species have been reported from Pliocene and Pleistocene deposits in eastern Europe, Early Pleistocene deposits in the Netherlands, from Mid-Pleistocene deposits in Germany, from Late Pleistocene deposits in the Netherlands and from Holocene deposits in the Netherlands, Germany, Britain and Denmark (Watts 1959; Wilson 1975; Velichkevich 1982, 1990; Jensen 1985; Brinkkemper et al. 2007). There is also a fossil record from eastern Russia (Biske et al. 1972, cited by Fletcher et al. 2021).



²Mostly of hoveyi-type.

Table 3. Remains of beetles from Pingorsuit, North-West Greenland.

Bembidion mckinleyi Fall Bembidion dauricum (Motsch.) Pterostichus brevicornis (Kirby) Pterostichus sp. Agonum consimile (Gyll.) Carabidae indet. Hydrophilidae	Samp	ole											
	103	104	105	107	108	110	111	112	114	115	117	119	121
Carabidae													
Bembidion mckinleyi Fall	_	-1	_	-	-	-	-	_	-1	-	-	_	1
Bembidion dauricum (Motsch.)	_	-	1	-	_	1	1	_	-	_	_	-	_
Pterostichus brevicornis (Kirby)	_	2	_	-	_	_	1-	_	-	-	_	_	_
Pterostichus sp.	_	-	1	-	_	_	-	_	_	_	_	-	_
	_	-	_	-	_	1	-	_	-	1	_	_	_
Carabidae indet.	_	-	_	-	1	_	-	_	1	-	_	-	_
Hydrophilidae													
Helophorus sp.	_	_	1	_	_	_	_	_	_	_	_	_	_
Cercyon tristis (Ill.)	_	_	_	_	_	_	_	_	1	_	_	_	_
Staphylinidae													
Philonthus sp.	_	_	_	_	_	_	_	_	-	1	_	_	1
Quedius spp.	_		_	_	_	_	1	1	1	1	_	_	_
Pycnoglypta lurida (Gyll.)	_	1	_	_	_	_	_	_	-	_	_	1-1	_
Omalium cf. rivulare (Payk.)	_	-	_	_	_	_	-	_	1-1	_	_	-	1
Micralymma cf. brevilingue Schiödte	_	-	1	-	_	1	-	_	-	_	_	1-1	_
Olophrum boreale (Payk.)	2	1	_	-	_	_	1	1	_	_	_	_	_
Olophrum rotundicolle (Sahlb.)	1	1	_	_	-	_	-	-	-	-	_	-	_
Eucnecosum cf. brachypterum (Grav.)	1		1	1	-	1	-	1	-	-	_	-	_
Eucnecosum brunnescens (J.Sahlb.)	_	-	1	-	_	_	1	_	_	_	_	-	_
Carpelimus sp.	_	-	1	_	_	_	_	_	_	_	_	-	_
Mycetoporus spp.	_	-	1	-	_	-	-	_	-	-	-	1-	1
Tachinus elongatus Gyll.	_	-	-	-	-	-	-	-	1	-	-	-	_
Stenus spp.	1	-	1	1-	-	_	-	-	-	-	1	-	1
Helodidae													
Cyphon sp.	_	1	_	_	_	_	_	_	_	_	_	_	_
Scarabaeidae													
Aegialia terminalis Brown	_	_	_	_	_	_	1	_	1-1	_	_	_	_
Byrrhidae							•						
Simplocaria cf. metallica (Sturm)								1					
Byrrhus sp.	_	_	1	_	_	_	_	1	-	_	_	_	_
***************************************	_	_	1	_	_	_	_	_	_	_	_	_	_
Melyridae													
Aplocnemus sp.	_	_	_	_	_	_	_	_	_	_	_	_	1
Curculionidae													
Dorytomus cf. imbecillus Faust	-	-	1	-	-	_	_	-	-	_	-	-	-
Litodactylus leucogaster (Marsh.)	_	_	_	_	-	-	1	1	1	_	_	-	_

Diagnosis: The Pingorsuit seeds are cylindrical and gently curved (Fig. 5). The base is rounded and the other end is capped by a lid that is missing. The surface is reticulate to scalariform and the number of cells as seen in the SEM images is five. The seeds are 0.44 to 0.68 mm long and 0.18 to 0.23 mm wide.

Comparison: Based on size, shape and cell pattern, the seeds from Pingorsuit could not be matched with any extant species. The Pingorsuit seeds are somewhat similar to seeds of *Elatine hexandra*, which also have gently curved seeds. However, *E. hexandra* seeds are polygonal in cross-section and they have fewer rows of cells than the seeds from Pingorsuit.

Bryophytes

The samples were poor in bryophyte remains and only 19 taxa were found (Table 2). This is a low number when compared with other Late Cenozoic bryophyte floras

from the region (Hedenäs & Bennike 2009). Most of the fragments are of fen species, whereas the very few other remains represent mosses that are widespread on disturbed ground, such as *Atrichum* sp., *Ditrichum* sp. and *Pogonatum* spp. Another factor is that the bryophyte remains were poorly preserved.

The fossil assemblages are dominated by aquatic species and wetland species. Samples 56 and 103 contained remains of the wetland moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs and sample 103 in addition a few other species, which it often occurs together with, such as *Paludella squarrosa* (Hedw.) Brid. and *Sphagnum teres* (Schimp.) Ångstr. ex Hartm. *Hamatocaulis vernicosus* is rare in arctic areas, and not known from extant localities in Greenland. Remains of *Hamatocaulis vernicosus* were also found in samples from Store Koldewey (Hedenäs & Bennike 2009), but otherwise it has not been reported from Late Cenozoic deposits in northern North America. *Hamatocaulis vernicosus s.l.* consists of two



Table 4. Remains of chironomid larvae from Pingorsuit, North-West Greenland.

Taxon	Sample													
	26	53	56	104	115	117	121							
Orthocladiinae														
Abiskomyia	2	0.5	_	_	_	1	_							
Bryophaenocladius/Gymnometriocnemus	_	_	_	0.5	_	-	_							
Cricotopus/Orthocladius	_	_	1	1	_	-	_							
Cricotopus intersectus/laricomalis-type	2	_	_	_	2.5	1-1	_							
Limnophyes	_	_	_	-	_	0.5	_							
Propsilocerus	1	_	0.5	_	_	-	_							
Psectrocladius (cf. Monopsectrocladius)	1	_	_	_	_	-	_							
Psectrocladius simulans/bisetus-type	5	_	2	1	36	0.5	2							
Psectrocladius sordidellus/barbimanus-type	1.5	_	1	_	10.5	_	8							
Psectrocladius spp. (sordidellus-type sensu lato	9	1.5	1.5	0.5	32.5	_	7.5							
Zalutschia mucronata-type	_	_	_	1	_	_	_							
Zalutschia type B	2	_	1	1.5	5.5		15							
Orthocladiinae indet.	2.5	_	_	1	11.5	_	4.5							
Chironomini														
Chironomus cf. anthracinus-type	_	_	_	_	1	_	_							
Chironomus plumosus-type	_	_	_	1	_	_	_							
Chironomus spp.	1	_	_	_	_	_	_							
Dicrotendipes notatus-type	1	_	_	1	6	_	_							
Dicrotendipes nervosus-type	_	_	_	_	1	_	-							
Phaenopsectra flavipes-type	_	_	_	_	0.5	_	_							
Sergentia coracina-type	_	-	_	0.5	_	1	_							
Chironomini	_	_	_	_	1	_	_							
Tanytarsini					•									
Micropsectra	_	_	_	1	_	1	_							
Paratanytarsus	1	_	_	î	2	_	_							
Tanytarsus mendax-type	î	2	_	_	4	_	_							
Tanytarsini indet.	1	1	_	_	_	_	_							
Tanypodinae														
Pentaneurini	_	_	_	_	_	-	1							
Chaoboridae														
Chaoborus mandible	_	-	_	_	2	-	_							
Chaoborus cf. flavicans-type?	2	_	_	_	_	_	_							

cryptic species, one of which is found in northern Scandinavia at present (Hedenäs 2018). Another remarkable find is *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs. The fossils appear to represent 'var. *hoveyi'* (*Calliergidium pseudostramineum* var. *hoveyi* Grout), which is characterized by more or less acuminate leaves. There are only a few extant finds of this type, all from North America (Hedenäs 2015).

Beetles

A total of 27 beetle taxa (Coleoptera) were identified (Table 3). The majority of the beetle species have a more or less extant northern, circumpolar geographical distribution. An exception is *Aegialia terminalis*, which today is found in boreal environments in North America (Böcher 1995) and *Cercyon tristis*, which presently occurs only in Palaearctic regions (Hansen 1987). Only three of the recorded species, *Micralymma brevilingue*, *Simplocaria metallica* and *Dorytomus imbecillus*, belong to the extant Greenlandic fauna and they are distributed in the southern half of Greenland (Böcher 1988).

The majority of the species are confined to wet environments such as edges of water, e.g. Bembidion mckinleyi, Helophorus spp., Carpelinus spp. and Simplocaria metallica (Harde 1984; Lindroth 1985; Böcher 1988). Rove beetles such as Pycnoglypta lurida, Olophrum boreale, O. rotundicolle, Eucnecosum brachypterum, E. brunnescens and Mycetoporus spp. are mainly found in leaf litter, often in rather wet places (Palm 1948; Harde 1984). In arctic and sub-arctic areas they inhabit leaf litter mainly originating from Salix and Betula. The ground beetle Agonum consimile is confined to moss-rich mires in the birch region (Lindroth 1986). Bembidion dauricum is normally found in the same region, but on sandy surfaces with sparse vegetation (Lindroth 1985). Only two of the recorded species are purely aquatic. Cyphon spp. live in shallow water bodies often within mires, where they often are found on sedges (Carex; Nyholm 1972). The weevil Litodactylus leucogaster lives on Myriophyllum (Rheinheimer & Hassler 2010). Aegalia terminalis feeds on plant roots in sandy areas, such as shores of lakes and rivers (Böcher 1995). The weevil Dorytomus imbecillus mainly feeds on leaves of Salix



Table 5. Remains of animals except beetles and chironomids from Pingorsuit, North-West Greenland. r = rare; c = common.

Taxon	Sar	nple																	
	26	53	56	103	104	105	107	108	109	110	111	112	114	115	116	117	119	121	122
Spongilla lacustris	-	r	r	_	_	_	_	1—	_	_	_	_	_	r	_	r	_	_	-
Ectoprocta (freshwater bryo	zoans	s)																	
Cristatella mucedo	40	c	25	_	2	_	_	_	1	_	3	_	_	8	_	12	4	3	_
Plumatella repens	r	_	_	-	-	_	_	_	-	-	_	-	-	r	-	r	r	_	_
Plumatella fruticosa	_	_	r	-	_	_	_	-	-	-	-	-	-	-	-	-	_	_	_
Fredericella sp.	r	_	r	-	_	-	_	_	_	-	_	-	_	-	_	_	r	r	_
Rhabdocoela	r	r	r	_	-	_	_	-	-	_	_	_	-	r	-	r	r	r	_
Crustacea, Branchiopoda																			
Chydorus cf. sphaericus	c	c	c	_	-	_	_	_	_	-	-	_	-	c	_	_	_	c	_
Eurycercus sp.	r	_	_	_	_	_	-	_	_	-	_	-	_	r	_	r	_	r	_
Acroperus sp.	_	_	_	-	-	_	-	-	_	-1	-	-	-	_	-	r	_	_	_
Alona sp.	-	-	-	-	-	-	-	-	-	-	_		-	c	-	r	-	c	_
Daphnia pulex type	r	r	r	_	_	_	_	_	_	-	_	_	-	r	_	r	r	_	_
Simocephalus sp.	r	r	-	-	-	-	-	-	-	-	-	-	-	r	-	r	r	r	_
Trichoptera																			
Polycentropus sp.	4	1	_	_	_	_	_	_	_	_	_	_	_	3	_	_	_	_	_
Agrypnia (colorata?)	_	_	_	_	_	_	_	_	_	_	-	_	_	_	_	_	_	1	_
Phryganea sp.	_	_	_	_	_	_	-	_	_	_	-	-	-	1	-	-	_	_	_
Apatania sp.	_	_	_	_	1	_	-	_	_	_	_	_	_	_	_	_	_	_	_
Limnephilidae sp. A	1	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_
Limnephilidae sp. B	1	_	_	-	1	_	-	-	-	-	-	-	-	-	-	-	-	-	_
Nemotaulius sp.	_	_	_	-	1	-	-	-	_	_	_	-	-	_	_	-	_	-	_
Psychoglypha sp.	_	_	-	-	-	_	-	-	-	-	_	1?	-	1	-	-	-	-	_
Cyclorrahapha indet. (flies)	_	_	_	2	_	_	_	2	_	1	1	3	1	_	_	_	_	_	_
Chaeoborus sp. (midge)	4	_	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Oribatida indet (mites)	r	r	r	-	r	-	-	1	-	-	-	-	-	r	_	r	-	-	-
Vertebrata (vertebrate) Rodentia indet.					5							15							

(Böcher 1988). Aplocnemus species are found on flowering conifers (Harde 1984). Only Pterostichus brevicornis and Micralymma brevilingue may be regarded as obligate arctic tundra species (Lindroth 1986; Böcher 1988). The other species have a wider range from arctic to boreal environments.

The fossil assemblages indicate a wetland environment with shallow, open water with a relatively sparse water plant vegetation. The terrestrial vegetation was probably a rather open woodland, in accordance with the interpretation based on plant remains. Leaf litter from *Betula*, *Cornus* and *Myrica* would have created suitable habitats for the relatively dominant group of beetles confined to leaf litter. Probably *Salix* was also present according to the find of *Dorytomus imbecillus*. The beetle fauna from the Pingorsuit deposit shows a strong resemblance to the beetle fauna from the Kap København Formation (Böcher 1995). Thus 23 or 85% of the beetle taxa from Pingorsuit have also been recorded from the Kap København Formation.

Quantitative reconstructions of mean July (TMAX) and mean February (TMIN) temperatures were performed based on beetle species in the entire fossil assemblage, and undertaken using the BugStats software, a statistics component of the Bugs Coleopteran Ecology Package (BugsCEP: http://www.bugscep.com;

Buckland 2007, 2014). Eleven species with known adaption to relatively limited climate range were included. The results indicate a TMAX of 9 to 13 °C and a TMIN of -20 to -8 °C. This is similar to the palaeotemperatures reconstructed based on the beetle assemblages from the Kap København Formation (Böcher 1995) and other Late Cenozoic deposits in Arctic North America (Elias & Matthews 2002).

Non-biting midges

Head capsules of chironomid larvae are common in late Quaternary sediments, but rarely reported from Pliocene and early Quaternary sediments. However, a few taxa, including *Corynocera ambigua* Zett., 1838 have been reported from Pliocene deposits in Canada (Matthews *et al.* 2019), and the latter species as well as other taxa were also reported from the Kap København Formation (Böcher 1995).

Several of the samples from Pingorsuit contained fairly frequent remains of chironomid larvae (Table 4). Overall, the larval head capsules appeared well preserved, but were often missing distinctive characteristics for identification such as mandibles or in the case of Tanytarsini, antennal pedestals. However, no evidence of microbial decomposition was observed and the head capsules only showed



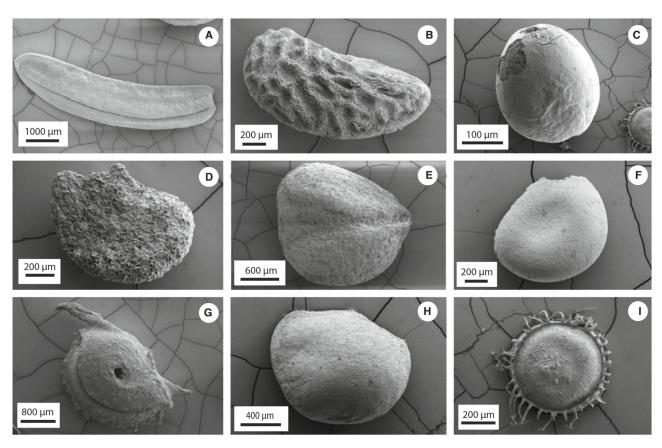


Fig. 3. Scanning electron images of different macrofossils from the Pingorsuit beds. A. Picea mariana needle (MGUH 34056). B. Rubus idaeus type endocarp (MGUH 34057). C. Aracites globose fruit (MGUH 34058). D. Empetrum nigrum endocarp (MGUH 34059). E. Cornus canadensis endocarp (MGUH 34060). F. Andromeda polifolia seed (MGUH 34061). G. Potamogeton obtusifolius endocarp (MGUH 34062). H. Comarum palustre achene (MGUH 34063). I. Cristatella mucedo statoblast (MGUH 34064). MGUH numbers denote specimens in the collection of the Natural History Museum of Denmark.

minor to moderate damage due to compression. The assemblages were dominated by Orthocladiinae, usually split in half and often with strongly worn mentum teeth, which made identification difficult.

The most common head capsules belonged to the widespread genus *Psectrocladius* with at least two separate morphotypes resembling P. simulans/bisetus (Makarchenko & Makarchenko 1999) and Psectrocladius sordidellus/barbimanus-type (Brooks et al. 2007), but with many specimens that could not be clearly separated into these categories due to missing characteristics and worn teeth. Further orthocladiines included Cricotopus intersectus/laricomalis-type, Abiskomyia, Zalutschia type B, Zalutschia mucronata-type and Propsilocerus. Tanytarsini were rare in the samples but included Tanytarsus mendax-type, Micropsectra and Paratanytarsus. Several Chironomini taxa were found, but only as individual specimens including *Chironomus* anthracinus- and plumosus-type, Dicrotendipes notatustype, Sergentia coracina-type and Phaenopsectra flavipes-type. Of Tanypodinae, only a single specimen belonging to the Pentaneurini was found. Overall, the fauna includes many taxa common in arctic to sub-arctic

environments, such as *Psectrocladius*, *Sergentia coracina*-type, *Micropsectra* and *Abiskomyia*. However, many of these are limited to low arctic or even sub-arctic environments (e.g. Walker *et al.* 1997; Brooks & Birks 2001; Heiri *et al.* 2011). For example, Pentaneurini, *Tanytarsus mendax*-type and *Dicrotendipes* usually do not extend much beyond the tree line (e.g. Walker *et al.* 1997; Larocque *et al.* 2006), with a distribution limit to July air temperatures of 8–10 °C or higher (e.g. Brooks & Birks 2001; Heiri *et al.* 2011). In Norway, *Phaenopsectra flavipes*-type is only found regularly at July air temperatures >12 °C and a similar distribution limit has been reported for *Chironomus plumosus*-type in the Swiss Alps (Brooks & Birks 2001; Heiri *et al.* 2011).

Chironomid taxa typical for the coldest arctic environments such as *Paracladius*, *Pseudodiamesa*, *Oliveridia* and *Hydrobaenus* (Walker *et al.* 1997; Brooks & Birks 2004; Francis *et al.* 2006; Gajewski *et al.* 2005; Schmidt *et al.* 2011) are missing from the sediments. The fauna of midges also included a few mandibles of the warmth-demanding 'phantom midge' *Chaoborus*, which does not live in Greenland today. Mandibles of *Chaoborus* have been found in interglacial lake sediments



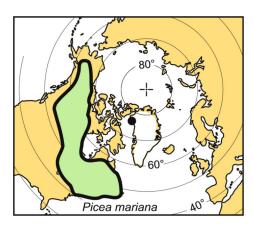


Fig. 4. Modern-day geographical range of *Picea mariana*. Redrawn from Little (1971).

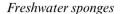
in Wax Lips Lake situated 60 km east of Thule Air Base, at 517 m a.s.l. (McFarlin et al. 2018). Chironomids typical for semiterrestrial or terrestrial environments are absent or rare in the assemblages, with only a half head capsule each of *Bryophaenocladius/Gymnometriocnemus* and *Limnophyes* found (of a total of 215). Similarly, no strictly rheophilous chironomids were detected, indicating that the chironomid assemblages were deposited and representative for standing water environments.

Caddisflies

Remains of eight different taxa of caddisfly larvae were identified (Table 5). Several of them have previously been recorded from Pliocene or Early Pleistocene deposits in northern North America, but the family Polycentropodidae (*Polycentropus*) and the genera *Phryganea* and *Nemotaulius* are new to the fauna of Late Cenozoic deposits in the region (Böcher 1995). According to habitat data in Wiggins (1998) the species composition is consistent with a lake or pond environment.

Freshwater bryozoans

Freshwater bryozoans were represented by statoblasts of three taxa (Table 5). Cristatella mucedo lives in lakes or rivers, often in meso-trophic water (Økland & Økland 2000). The present northern range limit of C. mucedo follows the arctic tree line (Lacourt 1968). Statoblasts of it have been reported from Neogene and Early Pleistocene sites in Canada and Greenland (Bennike et al. 2004). In contrast, statoblasts of Plumatella have only been reported from the Kap København Formation (Bennike 1990) and from the Beaufort Formation on Meighen Island (Matthews et al. 2019). Fredericella appears to be new to Late Cenozoic deposits in northern North America; its statoblasts are indistinctive and perhaps overlooked.



Gemmules of sponges were noted in four samples, two of which were analysed for sponge remains. Freshwater sponges were represented by siliceous skeletal spicules and gemmules (Fig. 6). The single recorded species is *Spongilla lacustris* (Linnaeus, 1759), characterized by smooth oxeas (megascleres), spiny oxeas (microscleres) and gemmular spicules (spiny strongyloxeas). In some cases, specimens from the Arctic are reported as *Spongilla arctica* described by Annandale (1915) from Siberia. Morpho-traits of *Spongilla lacustris* and *S. arctica* are very similar (Holmquist 1973), and some authors have suggested the second as a junior synonym.

Living populations of *S. lacustris* are commonly recorded inhabiting plant substrata (e.g. *Potamogeton*) or rocks of circumpolar areas of the present Nearctic and Palaearctic regions. *S. lacustris* is sometime found together with a few other Spongillidae species, i.e. *Anheteromeyenia ryderi*, *Ephydatia fluviatilis*, *Ephydatia muelleri* and *Eunapius fragilis* from 60°N up to 71°03′N (Annandale 1915; Rezvoj 1928, 1929; Arndt 1931; Bagge 1968; Holmquist 1973; Røen 1975; Tendal 1976; Økland & Økland 1996; Pronzato & Manconi 2001; Sharapova *et al.* 2021). The only previous Greenland record of freshwater sponges is *Spongilla arcticus* and *Spongilla* sp. from southern Greenland (Røen 1975, 1987).

The fossil record from Pingorsuit is far north of the present-day range of *S. lacustris* or any other sponge species. The presence of body skeleton spicules (active phase) and cryptobiotic gemmules (hibernant dormant phase) indicates the population persistence by a seasonally controlled pluri-annual life cycle by regeneration of the active sponge from totipotent cells contained in the gemmular theca. This life style is in agreement with a climate warmer than at present in the Pingorsuit region.

Other animal remains

A few puparia fragments of Calliphoridae were found. The larvae live in vertebrate carcasses. Diapriidae (Hymenoptera) was represented by a head. Two of the samples contained droppings of a small rodent. The droppings are similar to lemming droppings, which are fairly common in fossil assemblages from North and North-East Greenland (Bennike & Wagner 2021).

Palaeoecology, palaeoclimate and biogeography

The fossil assemblages indicate that the Pingorsuit deposit includes plant and animal remains from a local environment with a variety of habitats. Open boreal woodland with *Picea mariana* and *Betula* were probably found at sheltered sites. Only one beetle species living on



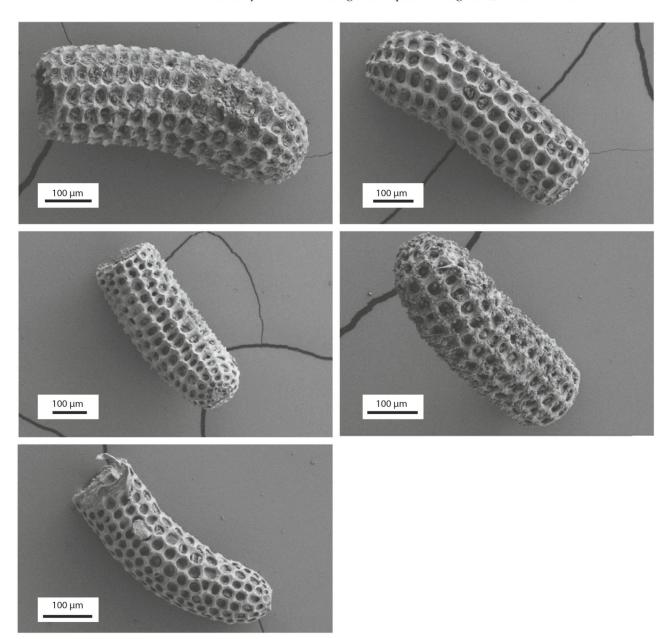


Fig. 5. Scanning electron images of five different seeds of Elatine odgaardii Bennike, sp. nov. from the Pingorsuit beds (MGUH 34065–34 069).

conifers is recorded, which may suggest that *Picea mariana* was not abundant. The absence of saproxylic species living on dead wood indicates an environment with a sparseness of trees. Heaths with *Empetrum* and *Salix* may have been found at more exposed sites. Fens with *Myrica* and *Aracites* were found in poorly drained areas and lakes or ponds with *Menyanthes, Potamogeton, Elatine* and many different species of invertebrates also occurred. The plant taxa indicate that the mean July temperature was at least 10 °C, or at least 9 °C higher than at present, in accordance with temperature estimates from beetle and chironomid data. Several of the species, notably *Empetrum*, indicate a continuous snow

cover during the winter. Many of the taxa from the Pingorsuit beds are of circumpolar distribution today, but *Picea mariana* and *Cornus canadensis* are confined to North America. Their presence indicates that the fossil flora was more closely allied with North America than Eurasia.

Comparisons with other fossil assemblages

The fossil assemblages from Pingorsuit can be compared with last interglacial assemblages from Greenland, which are well-dated. One last interglacial assemblage with non-marine fossils comes from a coastal cliff section at



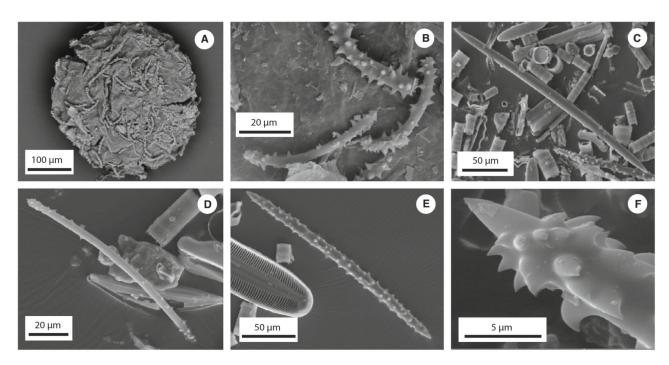


Fig. 6. Scanning electron images of Spongilla lacustris remains from Pingorsuit, North-West Greenland. A. Gemmular theca armed with tangential, straight to curved gemmuloscleres bearing large spines. B. Siliceous gemmuloscleres with acute to blunt tips and spines more dense towards tips. C. Skeletal siliceous oxea (megasclere) with smooth surface and acute tips, surrounded by diatom frustules; a densely spiny microsclere is also present. D–F. Skeletal microscleres as slim, short oxeas with scattered spines (D) to densely spiny; spines mostly simple but sometimes ornamented by microspines (E). Microxea tips from acute and smooth to blunt with spines (F).

Narsaarsuk near Pingorsuit. The flora and fauna were documented by Bennike & Böcher (1992), Hedenäs & Bennike (2003) and Brodersen & Bennike (2003). The presence of several southern extralimital taxa indicates that the mean July air temperature was about 4 °C higher than today. However, the flora is distinctly Arctic, similar to that found in North-West or West Greenland today and very different from the Pingorsuit flora. In southern and western Jameson Land, in central East Greenland, last interglacial sites are quite common (Bennike & Böcher 1994; Hedenäs 1994). The fossil assemblages from Jameson Land also comprise a number of southern extralimital taxa, indicating that the mean July air temperature was at least 5 °C higher than today. Again, the flora is Arctic, similar to the current flora found in East or South Greenland.

Comparisons with assemblages of vascular plants from the Kap København Formation (member B) in eastern North Greenland (Bennike 1990), the Île de France Formation (Bennike et al. 2002) and the Store Koldewey Formation (Bennike et al. 2010) in North-East Greenland show a number of similarities. For example, Aracites globosa, Picea mariana, Myrica, Rubus and Nuphar are present in both the Pingorsuit beds and the Kap København Formation. As mentioned above, spruce seeds from the Île de France Formation were referred to Picea cf. mariana, but the flora of vascular plants from this succession is sparse. The flora from the Store Koldewey Formation is also sparse; it includes for

example Larix, Betula sect. Albae, Alnus and Andromeda. The Kap København Formation is rich in remains of Arctic species and a forest-tundra environment is indicated. The Store Koldewey Formation is rich in remains of dwarf shrubs, but truly Arctic species are only represented by Saxifraga oppositifolia. Nevertheless, a forest-tundra was also suggested for the environment of the Store Koldewey Formation. The age of these three Greenland formations is c. 2 Ma (Bennike et al. 2010).

The flora of the Pliocene Beaufort Formation in Arctic Canada includes three *Pinus* (pine) species, *Larix* (larch), *Abies* (fir), *Thuja* (cedar) and *Tsuga* (hemlock), which shows that the forest was much more diverse than the forest at Pingorsuit (Fletcher *et al.* 2021).

On Ellesmere Island, high terrace Pliocene sediments not belonging to the Beaufort Formation have been found at many sites, the most famous of which is the Beaver Pond site that has yielded mammal fossils. The floras from high terrace sediments on Ellesmere Island include *Pinus*, *Larix*, *Picea*, *Physocarpus*, *Comptonia*, *Epipremnum* and *Aracites*. We suggest that the Pingorsuit flora is younger than the floras from the Beaufort Formation and the high terrace floras from Ellesmere Island, because of the lower diversity of the flora from the Pingorsuit than the floras from Canada.

The Pingorsuit flora is somewhat similar to the Kap København flora. However, it is strange that there is no sign of *Larix*, which is the dominant conifer in the Kap København flora. It is also noteworthy that there are no



remains of Arctic taxa, such as *Dryas*, *Saxifraga oppositifolia* and *Oxyria digyna* in the Pingorsuit flora. Despite these differences, which may be due to taphonomical factors, we suggest that the species assemblage of the Pingorsuit deposit is most consistent with an Early Pleistocene age.

Conclusions

The macrofossil assemblages represent an open boreal woodland ecosystem with intermittent standing water as indicated by the lacustrine invertebrate remains including benthic (chironomids, Bryozoa) and planktonic taxa (Chaoborus). This is confirmed by the occurrence of macrofossils from trees (*Picea mariana* and *Betula* sect. Albae sp.), shrubs (Empetrum nigrum, Cornus canadensis and Salix sp.) and the beetles Aegialia terminalis and Aplocnemus sp. The occurrence of wetland taxa such as Sphagnum, Paludella, Carex and Comarum palustre and several beetle species shows that mires were also common. The presence of the vascular plants Nuphar, Potamogeton, Menyanthes trifoliata, the freshwater bryozoan Cristatella mucedo and the freshwater sponge Spongilla lacustris together with other aquatic invertebrates indicates that lakes or ponds were also found in the area. Analogous contemporary sub-Arctic or boreal forest ecosystems exist in settings where the mean July temperatures are somewhat above 10 °C (D'Odorico et al. 2013). This implies that local mean July temperatures at Pingorsuit Glacier were at least 9 °C higher than at present when the organic-rich material was deposited.

The fossil flora from the Pingorsuit beds shows similarities with the fossil flora from the Kap København Formation, which is dated to c. 2 Ma (Bennike 1990; Bennike et al. 2010). The majority of the fossil remains are referred to extant species, but the flora includes the extinct plant Aracites globosa, an extinct Elatine species and probably the extinct Myrica arctogale. We describe the extinct species Elatine odgaardii sp. nov. The Kap København flora is characterized by a mixture of boreal and arctic plants, whereas no arctic species were discovered in the samples from Pingorsuit. These differences, which may reflect different climates or different taphonomical processes, could also reflect different ages. The Pingorsuit flora also shows similarities with the flora from the Mid-Pliocene (>3.4 Ma) Beaver Pond site on Ellesmere Island, but the flora from this site is generally much richer than the Pingorsuit flora (Matthews & Ovenden 1990; Fletcher et al. 2021).

The discovery of Early Pleistocene organic-rich sediments described here adds to a growing body of Late Cenozoic deposits discovered in the High Arctic since the 1960s. The Pingorsuit deposit, however, is unique for at least two practical reasons. Firstly, the Pingorsuit deposit appears rather ephemeral, as it only exists in terrain deglaciated within the past two decades. This immedi-

ately proglacial location means the organic-rich material starts being preferentially eroded, relative to the boulders and cobbles in surrounding till, by hydrological processes immediately after emergence. Secondly, the Pingorsuit deposit is logistically very accessible. Its location within 1 km of a primitive road offers possibilities for sophisticated sampling approaches and further analyses, which have not been possible at the more logistically difficult Late Cenozoic deposits discovered to date.

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Author contributions. — Samples were collected by AAB and WC and analysed by OB, LH, OH, GL, PWL, RP and RM. OB compiled the manuscript with help from all authors.

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