Lateglacial and Holocene floras and faunas from the Salpetermosen area, north-east Sjælland, Denmark

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The Salpetermosen area in north-east Sjælland, Denmark, was deglaciated about 18 000 to 17 000 years ago. Melting of bodies of stagnant glacier ice led to the formation of kettle holes, which contain Lateglacial and Holocene sediments with remains of plants and animals that provide information on the past flora and fauna of the area. During the Allerød period, open forests with *Betula pubescens* (downy birch) characterised the area, the flora included light-demanding species such as *Arctostaphylos uva-ursi* (bearberry), *Empetrum nigrum* (crowberry) and rare *Populus tremula* (aspen), *Betula nana* (dwarf birch) and *Rubus saxatilis* (stone bramble), as well as the thermophilous swamp plant *Oenanthe aquatica* (fine-leaved water dropwort). During the Younger Dryas, the vegetation was characterised by dwarf-shrub heaths dominated by *Betula nana*, but including *Dryas octopetala* (mountain avens), *Salix herbacea* (least willow), *Arctostaphylos alpina* (alpine bearberry,) and rare *Betula pubescens*, as well as the thermophilous plants *Urtica dioeca* (stinging nettle) and *Lychnis flos-cuculi* (ragged robin). The Early Holocene forests were dominated by *Betula pubescens*, *Populus tremula* and *Pinus sylvestris* (scots pine), but included rare *Betula nana*. *Alnus glutinosa* (alder) arrived at c. 10 000 cal. years BP. The calciphilous sedge *Cladium mariscus* (fen-sedge) and the macrolimnophyte *Najas marina* (spiny naiad) were common. The Late Holocene flora included the acidophilous plant *Scheuchzeria palustris* (rannoch-rush).

Keywords: Lateglacial, Holocene, Quaternary, vegetation history, fauna history, immigration history, Denmark, macrofossils.

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In September 2012, the plans for a new state-of-the art hospital south of Hillerød became a reality. The hospital was to be situated in the Salpetermosen area in north-east Sjælland (*c.* 55.910°N, 12.30°E; Fig. 1). Shortly after archaeological excavations were initiated following the Danish Museum's Act of developer-funded excavations. A crucial part of the archaeological surveys was to visualise the prehistoric landscape and to understand the development of this rather boggy terrain, thus the Geological Survey of Denmark and Greenland was asked to assist in this part of the project. This paper presents some of the results of the geological surveys.

According to the deglaciation chronology of north-east Sjælland, Denmark, the last active glacier ice disappeared about 18 000 to 17 000 years ago (Houmark-Nielsen *et al.* 2012). The oldest animal remains from the region is a thorasic vertebra of a *Pusa hispida* (ringed seal) from Nivå. The bone was dated to *c.* 17 100 cal. years BP (Lagerlund & Houmark-Nielsen 1993). However, the oldest dated plant remains from the region gave an age of only 13 660 cal. years BP (Bennike & Mortensen 2018). Studies of plant and animal remains from lake and bog deposits from Denmark have a long tradition, but many details of environmental changes are still unknown. The chronology of events is poorly constrained, but the introduction of radiocarbon dating by accelerator mass spectrometry (AMS) means that it is now possible to improve on the chronology. High-resolution studies of continuous records are crucial for understanding the late Quaternary history of southern Scandinavia. We studied macroscopical remains of plants and animals to assess the environmental changes of the area.

The studied area is located 8 km from the classic Allerød clay pit that was studied by Hartz & Milthers (1901) and Hartz (1902). Hartz and Milthers found evidence of a warm Lateglacial period in the Allerød clay pit. The age of the Allerød period was originally determined by conventional radiocarbon dating of bulk sediment samples and wood from western Sjælland and Jylland (Iversen 1953).

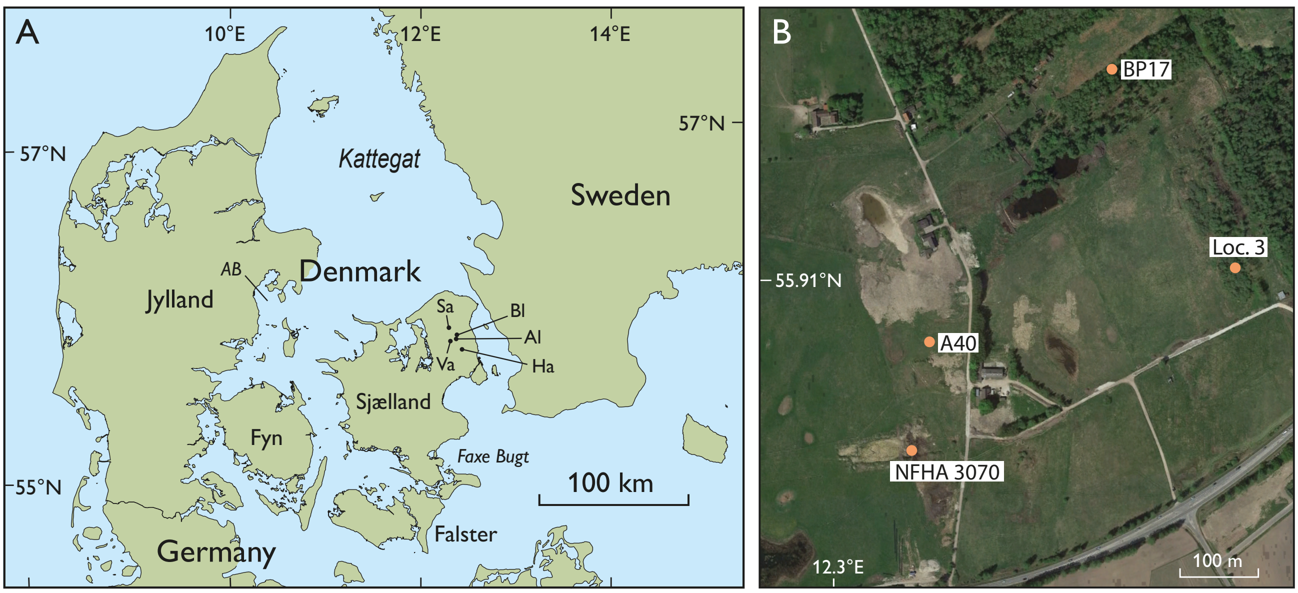

Fig. 1. A: Map of Denmark showing the location of the study area. Sa: Salpetermosen, Bl: Blovstrød, Al: Allerød clay pit, Ha: Hareskovene, Va: Vassingerød, AB: Aarhus Bugt. **B**: Map of the Salpetermosen area showing the core sites discussed in this paper.

Table 1. Radiocarbon ages from Salpetermosen, Vassingerød and Blovstrød, north-east Sjælland, Denmark

Locality	N. lat. °	E. long. °	Depth (cm)	Laboratory number	Material	Age (^{14}C years BP)[1]	Cal. age (years BP)[2]
BP 17	55.913	12.306	36	Poz-114722	*Carex paniculata*	2295 ± 30	2182–2354
BP 17	55.913	12.306	63	Poz-114679	*Scheuchzeria palustris*	2690 ± 30	2753–2848
BP 17	55.913	12.306	83	Poz-114461	*Betula* wood	2835 ± 35	2858–3058
BP 17	55.913	12.306	92	Poz-114382	*Menyanthes trifoliata*	2870 ± 30	2879–3136
A40	55.910	12.302	130–132	Poz-114383	*Arctostaphylos uva-ursi*	11510 ± 60	13234–13469
NF HA 3070	55.908	12.301	40–44	Poz-114729	*Menyanthes trifoliata*	8860 ± 50	9744–10172
NF HA 3070	55.908	12.301	108–112	Poz-114385	*Pinus sylvestris*	9460 ± 50	10567–11068
NF HA 3070	55.908	12.301	148–152	Poz-114728	*Betula, Pinus*	9650 ± 50	10785–11198
NF HA 3070	55.908	12.301	204–208	Poz-114384	*Menyanthes trifoliata*	9690 ± 50	10795–11225
NF HA 3070	55.908	12.301	268–272	Poz-114462	Bark	10950 ± 60	12712–12978
Loc. 3	55.910	12.309	30	Poz-114726	*Menyanthes trifoliata*	4405 ± 35	4861–5262
Loc. 3	55.910	12.309	70	Poz-114725	*Nuphar, Alnus*	4810 ± 35	5471–5604
Loc. 3	55.910	12.309	114	Poz-114724	*Alnus, Betula*	7370 ± 50	8044–8324
Loc. 3	55.910	12.309	178	Poz-114723	*Nymphaea, Pinus, Betula*	8110 ± 50	8794–9256
Vassingerød	55.834	12.319		LuS-8464	*Rangifer tarandus* antler	10130 ± 70	11401–12032
Blovstrød	55.868	12.385		Poz-109697	*Rangifer tarandus* antler	10340 ± 60	11953–12418

[1] Radiocarbon ages are reported in conventional radiocarbon years BP (before present = 1950; Stuiver & Polach (1977)).
[2] Calibration to calendar years BP (2 sigma) is according to the INTCAL13 data (Reimer *et al.* 2013).

Numerous remains of mammals have been recovered from Lateglacial and Holocene deposits in north-east Sjælland. From the Allerød clay pit Hartz (1902) reported on a cast antler of *Rangifer tarandus* (reindeer), a cast antler of *Alces alces* (elk) and a mandible of *Canis lupus* (wolf). The latter has been radiocarbon dated to the Younger Dryas (Aaris-Sørensen 2009). The reindeer was assigned to the Allerød period and the elk antler to pre-Allerød time by Hartz (1902). However, we consider these age estimates uncertain because the antlers were found by local workers and later purchased by Hartz. Degerbøl & Krog (1959) ascribed the majority of the reindeer remains from Denmark that were dated by pollen analysis to the Younger Dryas period, but it has later been demonstrated that the species also lived in Denmark during the Allerød period (Aaris-Sørensen *et al.* 2007).

No remains of reindeer were found in Salpetermosen, but two other recent finds of cast antlers from north-east Sjælland have been dated (Table 1). The finds gave median probability ages of 11 760 and 12 190 cal. years BP corresponding to late Younger Dryas ages; they represent the first radiocarbon dated reindeer remains from north-east Sjælland. Radiocarbon dated Lateglacial and Early Holocene finds from other parts of Denmark gave ages between *c.* 10 300 and 14 500 cal. years BP (Aaris-Sørensen *et al.* 2007).

The work by Hartz (1902) was based on macrofossils, but later work on the vegetation and flora history of Denmark concentrated on pollen analysis. In recent years, the importance of macrofossils has been recognised again, not least in connection with dating of plant remains (e.g. Bennike *et al.* 2004a; Mortensen *et al.* 2011; Bennike & Mortensen 2018). Macrofossils have several advantages compared to pollen. Macrofossils usually do not spread as far as pollen and may therefore provide more accurate information on the local vegetation. Furthermore, macrofossils can often be determined to species, whereas pollen grains can generally be determined to genus or family. In addition, it is possible to use samples of macroscopic plant remains for radiocarbon dating by AMS. In this way it is possible to date remains of key species directly and provide minimum age for the time of their immigration to the find spot. The geological and archaeological chronological terms used in this paper are shown in Fig. 2.

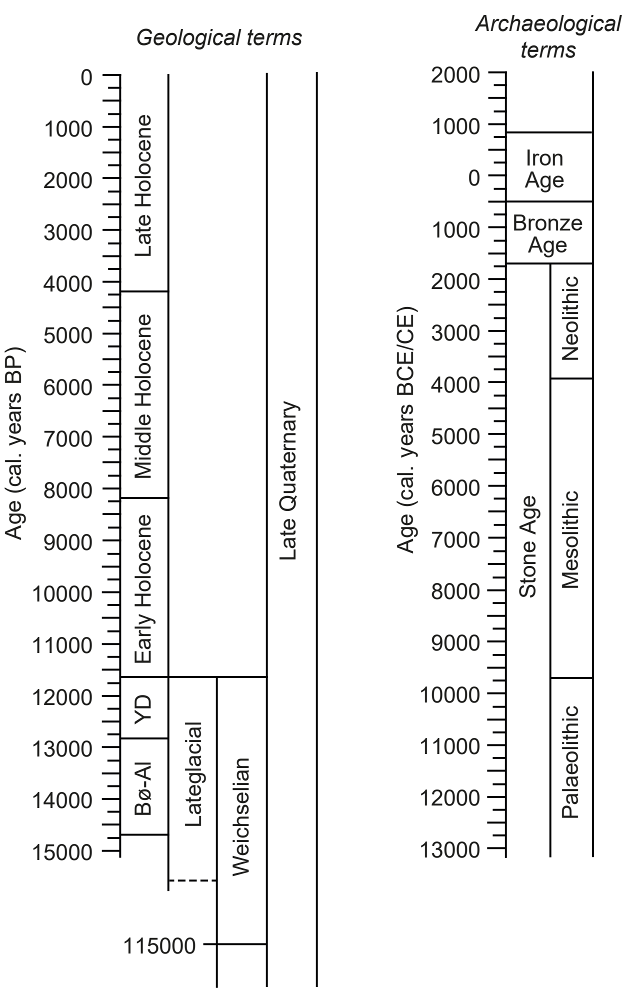

Fig. 2. Late Quaternary geological and archaeological terms used in this paper. YD: Younger Dryas stadial, Bø-Al: Bølling-Allerød interstadial. The term Lateglacial is used in this paper for the time period from the last deglaciation to the transition to the Holocene. The division of the Holocene is according to Walker *et al.* (2019) and the chronology of the archaeological time periods is according to Skousen (2008). BP (before present) refers to 1950 CE. CE: Common Era, BCE: Before Common Era.

The Salpetermosen area

Until fairly recently, the Salpetermosen area (Fig. 1) was an area with agricultural land, meadows and peat bogs that represent overgrown lakes. Peat extraction started in the Iron Age but was intensified during the 1800s and 1900s. Archaeological excavations from 2012 and onwards revealed that in Prehistoric Times the cultivated area was characterised by several small basins with lake and bog sediments. The elevation of the area is 20–25 m above sea level. In its original shape, the landscape was hilly, but the topography has been leveled due to many years of agriculture. The surficial geology of the area is dominated by peat and clayey till, but glaciofluvial deposits are also widespread in the region (Rørdam 1893; Milthers 1922).

Archaeological surveys and excavations have uncovered human settlements and activities from a greater part of the Danish prehistory in and around the Salpetermosen area. The recent excavations have

Table 2. Vertebrate remains from Salpetermosen, north-east Sjælland, Denmark, based on excavations from 1957 to 1961 and identified by Ulrik Møhl

Fish
Abramis brama (bream)
Rutilus rutilus (roach)
Scardinius erytrophthalmus (rudd)
Tinca tinca (tench)
Cyprinidae (cyprinids)
Anguilla anguilla (eal)
Belone belone (garfish)
Perca fluviatilis (perch)
Pleuronectidae (flat fish)
Amphibian
Bufo bufo (common toad)
Reptile
Emys orbicularis (pond turtle)
Birds
Podiceps cristatus (Great crested grebe)
Botaurus stellaris (bittern)
Cygnus cygnus? (whooper swan?)
Anser (*anser*) (greylag goose?)
Anas platyrhynchos (mallard)
Anas (*penelope*) (wigeon?)
Anas acuta (pintail)
Aythya nyroca (ferruginous duck)
Aythya fuligula (tufted duck)
Bucephala clangula (golden-eye)
Mergus albellus (smew)
Haliaeetus albicilla (white-tailed eagle)
Milvus sp. (kite)
Pandion haliaetus (osprey)
Tetrao urogallus (capercaillie)
Grus grus (crane)
Fulica atra (coot)
Sterna hirundo (common tern)
Columba palumbus (wood pigeon)
Strix aluco (tawny owl)
Asio otus (eagle owl)
Corvus corone (crow)
Turdus merula (blackbird)
Turdus sp. (thrush)
Sturnus vulgaris (starling)
Passer? (sparrow?)
Mammals
Cervus elaphus (red deer)
Capreolus capreolus (roe deer)
Alces alces (elk)
Sus scrofa (wild boar)
Erinaceus europaeus (hedgehog)
Apodemus sp. (field mouse)
Arvicola terrestris (water vole)
Castor fiber (beaver)
Lutra lutra (otter)
Sciurus vulgaris (squirrel)
Martes martes (pine marten)
Felis silvestris (wild cat)
Halichoerus grypus (grey seal)
Canis familiaris (dog)
Bos taurus (domestic cattle)

revealed substantial Neolithic and Iron Age remains, whereas the earlier excavations mainly uncovered remains from the Mesolithic (Becker 1947; Kramer 2001; Aarsleff 2013; Casati 2013; Pantmann 2014; Jørgensen & Hagedorn 2015; Pantmann 2017, 2019). The finds include stray finds from the Maglemose culture, 11 000–8400 cal. years BP, amongst others an adze made of an antler from a *Cervus elaphus* (red deer); this find is dated to 9585–9360 cal. years BP. Four examples of *Alces alces* bones have been found as secondary placed, in Iron Age or Neolithic contexts, in the Salpetermosen area. None of these have been dated but we presume that they are Early Holocene.

During the following Kongemose and Ertebølle Cultures, 8400–5900 years BP, a season-based hunting station at the shore of the Salpetermosen lake was used repeatedly, which has resulted in a great amount of bones that were collected during excavations between 1943 and 1997. In 1957 to 1961 Ulrik Møhl from the Zoological Museum in Copenhagen took part in the excavations and he identified the vertebrate remains collected during these years (Table 2; unpublished data in the archives of the Zoological Museum). Møhl also submitted four samples of charcoal for radiocarbon dating; the samples gave late Ertebølle ages and we suggest that the majority of the bones belongs to the Ertebølle Culture (Sørensen 2014; laboratory numbers K-1232 to K-1235). The presence of *Bos taurus* (domestic cattle) indicates that some Neolithic material is included. *Aythya nyroca* (ferruginous duck) is new to the fossil fauna of Denmark. At the present, *Aythya nyroca* is a rare straggler in Denmark (Olsen 1992). Its geographical range is similar to that of *Emys orbicularis* (pond turtle), which was common in north-east Sjælland during the Early to Mid-Holocene thermal maximum and it is possible that *Aythya nyroca* was also breeding in Denmark during this time. The presence of marine species shows contact with people living at the sea.

In the Neolithic, 5900–3700 years BP, there was a lot of different activities around the Salpetermosen lake. From the earliest part of the period, 5900–5500 years BP, a fishing trap system with three deposited goat skulls and an intact skeleton of an *Emys orbicularis* with six eggs inside have been found. Several fragments of carapaces from other *E. orbicularis* specimens have also been uncovered. *Emys orbicularis* is a thermophilous species that requires high summer temperatures for the eggs to develop. A large number of remains of the species have been found in north-east Sjælland, most of them of Mid-Holocene age (Degerbøl & Krog 1951; Sommer *et al.* 2007). Other finds from the earliest part of the Neolithic comprise a possible offering platform with finds of pottery and axes, a bog body and a settlement with poorly preserved bones, mainly from domestic mammals.

In the following centuries, from 5500 to 5000 cal. years BP, there is an increase in the number of settlements, but due to poor preservation only a few contain animal bones. At one site, named Salpetermosen I, the excavation uncovered a varied bone material mainly of domesticated animals, but including bones of *Cervus elaphus*, *Sciurus vulgaris* (squirrel) and *Tetrao urogallus* (capercaillie). *Tetrao urogallus* is a forest bird, bones of it may indicate that areas with open vegetation were fairly widespread in the forests. Bones of the species have mainly been reported from the Maglemose and Ertebølle Cultures, but there is also a former record from the Neolithic of eastern Jylland (Degerbøl 1942).

From 5000 to 2500 cal. years BP the activities in the Salpetermosen area are scarce, but with the onset of the pre- Roman Iron Age, people are once again inhabiting the areas around Salpetermosen, though not closely related to the lake, which in the meantime had developed into a fen.

Material and methods

Coring was carried out with a Russian peat corer (Jowsey 1966). The chamber was 1 m long and had a diameter of 5 or 7.5 cm. The corer was hammered down into the often compact sediments. At some places we used an excavator to dig trenches.

Whole cores were brought back to the laboratory, where they were cleaned and subsampled. Contiguous 2 or 4 cm thick samples were taken for macrofossil analyses. Sediment samples were wet sieved on 0.4, 0.2 and 0.1 mm sieves, and the residue left on the sieves was transferred to a petri dish. Some of the samples were treated with 10% NaOH at room temperature before they could be sieved. Macroscopic remains of plants and animals were identified and counted using a dissecting microscope. Plant and animal remains were identified using reference material as well as published keys and illustrations. The numbers in the macrofossil diagrams refer to the number of fossils per sample. In general, preservation was good to excellent. A total of 463 samples from 20 localities within the survey area were analysed for macrofossils. Most of the samples came from small basins that are interpreted as kettle holes formed by melting of bodies of stagnant ice. The holes have been filled up with sediments and overgrown. Here we present four macrofossil diagrams.

Selected remains of terrestrial plants were dried and submitted for radiocarbon dating using AMS (Table 1). Dating was carried out at the Poznań Radiocarbon Laboratory in Poland and at the Radiocarbon Dating Laboratory in Lund, Sweden. The samples were treated with HCl to remove carbonates and with NaOH to remove humic acids. The widespread occurrence of carbonate-rich glacial deposits in Denmark may result in large hard-water effects, and thus it is important to use remains of terrestrial plants for dating. Two samples of reindeer antlers from north-east Sjælland were also dated, using the collagen fraction. The radiocarbon ages were calibrated to calendar years before present (BP) using the CALIB program (Stuiver *et al.* 2017), which calibrates to calendar years according to the INTCAL13 calibration curve (Reimer *et al.* 2013).

Macrofossils

Here we present the results from four of the analysed localities. The results from the other localities are incorporated in the discussion below.

BP 17

This locality is situated in the northern part of the investigated area. The site was chosen because preliminary reconnaissance work indicated that the thickest succession of Lateglacial and Holocene sediments could be found here. Prehistoric peat excavations were discovered in this area, but the cores showed no evidence of disturbance. We collected a 380 cm thick succession consisting of gyttja and peat, separated by a sharp boundary at 120 cm depth.

We did not find sufficient remains of terrestrial plants in the lower part of the succession for dating, but the fossil assemblage indicates a Holocene age. The upper part of the succession, from 92 cm to 36 cm is dated to between *c.* 3000 and 2300 cal. years BP (Table 1).

The lower part of the succession only contained few macrofossils, dominated by bones, scales and a few pharyngeal teeth from fish (Fig. 3). At 300 to 260 cm calcareous gyttja is found, it contains abundant oospores of *Chara* sp., opercula of the gastropod *Bithynia tentaculata* and seeds of the macrolimnophyte *Najas marina*. In a sample from 255 cm, leaf-margin spines of *Stratiotes aloides* were common. *Stratiotes aloides* is currently fairly rare in Denmark, but it had immigrated to the region in the Early Holocene (Bennike & Hoek 1999). Remains of it has not been found at other sites in the Salpetermosen area.

From 240 to 140 cm many remains of macrolimnophytes were present. *Potamogeton* is represented by six species: *Potamogeton perfoliatus*, *P. praelongus*, *P. crispus*, *P. compressus*, *P. obtusifolius* and *P. friesii*. Other aquatic plants are represented by *Ceratophyllum demersum*, *Ceratophyllum submersum*, *Najas marina* and *Nymphaea alba*. Egg cocoons of the leach *Erpobdella* sp. and statoblasts of bryozoans are found at the same depth, these invertebrates are often associated with limnophytes. The succession of aquatic plants shows that the water depth at the core site was decreasing, probably as a consequence of sedimentation. Fishes are represented by scales of *Perca fluviatilis*, spines of *Gasterosteus aculeatus*, pharyngeal teeth of *Scardinus erythrophtalmus* and other un-identified carp fishes.

At around 120 cm the lake turned into a bog and the upper part of the succession is characterised by rootlets and remains of bryophytes. The bryophytes are dominated by *Sphagnum* sp. but include *Climacium dendroides*, *Tomentypnum nitens*, *Paludella squarrosa*, *Dicranum bonjeanii*, *Calliergon* sp. and *Brachythecium* sp. (not shown in the diagram). The lower part of the peat contains seeds of *Menyanthes trifoliata*, then follows remains of *Carex paniculata*, a few *Carex riparia*, *Betula* sect. *Albae*, *Alnus glutinosa*, *Scheuchzeria palustris* and *Pinus sylvestris*. The presence of tree remains indicate that trees now grew close to the core site. A few remains of *Erica tetralix* and especially *Calluna vulgaris* indicate fairly dry conditions; these plants may have been growing on hummocks in the bog. The upper part of the peat contained no seeds or fruits. The site probably became too dry for such remains to be preserved.

A40

This locality is situated in the western part of the area, it is a small basin with detritus gyttja overlain by peat. The lower part of the macrofossil diagram is dominated by *Betula pubescens* but there are also fruit stones of the dwarf shrubs *Arctostaphylos uva-ursi* and *Empetrum nigrum* and a single nutlet of *Betula nana* (Fig. 4). There are abundant remains of cladocerans, chironomid larvae, an egg cocoon of *Erpobdella* sp. and rare statoblasts of *Cristatella mucedo* and *Plumatella* sp. Swamp plants are represented by numerous remains

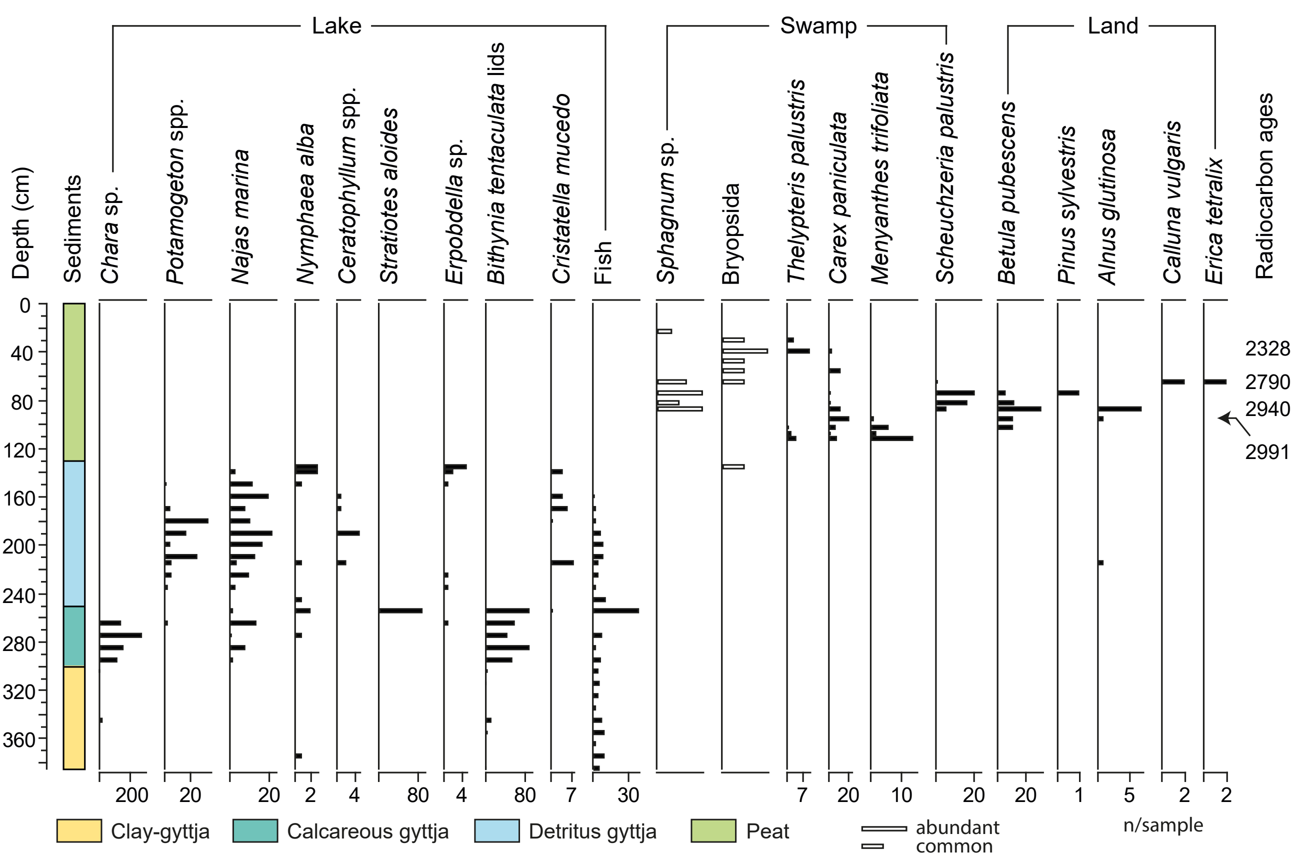

Fig. 3. Simplified macrofossil diagram for core site BP 17 from Salpetermosen. The radiocarbon ages show median probability.

of *Carex rostrata*, *Menyanthes trifoliata*, *Comarum palustris* and a single fruit of *Oenanthe aquatica*. The moss flora incudes the peat forming species *Tomentypnum nitens*, *Calliergon* sp., *Drepanocladus* s.l. sp., *Scorpidium scorpioides*, *Hylocomium splendens* and *Aulacomnium palustre* as well as a stem of *Plagiomnium affine*. Dating of *Arctostaphylos uva-ursi* stones yielded an age of *c.* 13 300 cal. years BP (Table 1), corresponding to a mid-Allerød age.

The middle part of the diagram shows a dominance of *Betula nana*, whereas *B. pubescens* is missing. A single well-preserved leaf of *Dryas octopetala* was found. The moss flora is dominated by *Drepanocladus* s.l. sp. This part of the diagram is referred to the Younger Dryas cold period (Fig. 4).

The upper part of the diagram is characterised by remains of *Carex rostrata* and *Populus tremula*. *Betula pubescens*, *Betula nana*, *Arctostaphylos uva-ursi*, *Empetrum nigrum* and *Menyanthes trifoliata* are rare. This part of the diagram is referred to the Early Holocene (Fig. 4). A single fruit of *Hydrocotyle vulgaris* was found, this plant is rare in Early Holocene deposits in Denmark. According to pollen data, it arrived at *c.* 10 000 cal. years BP at Skånsø in western Jylland (Odgaard 1994). The uppermost part of the succession is dominated by rootlets and bryophyte remains (*Drepanocladus* s.l. sp, *Calliergon* sp., *Hylocomium splendens* and *Tomentypnum nitens*).

NFHA 3070

This locality is situated in the south-western part of

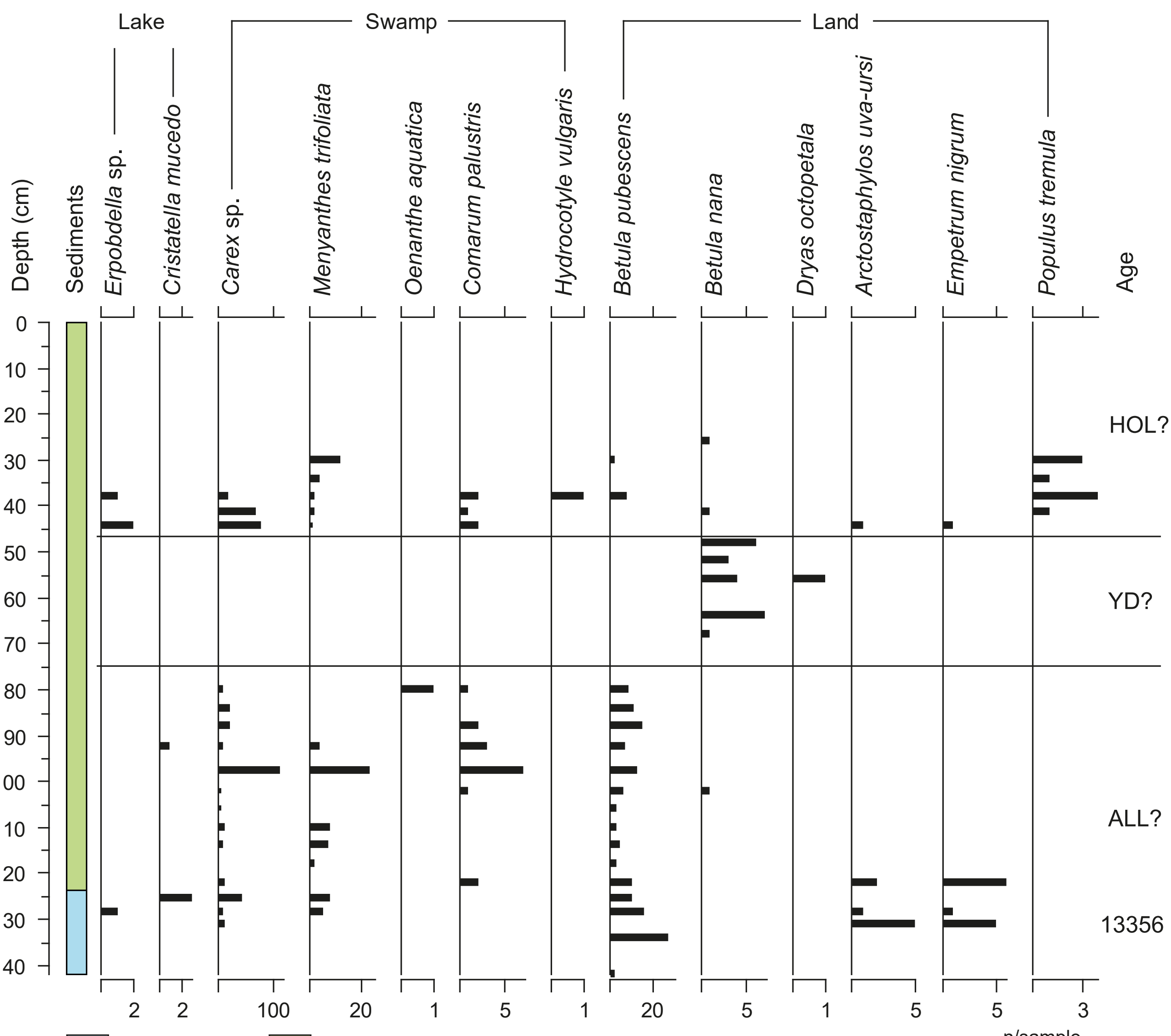

Fig. 4. Simplified macrofossil diagram for core site A40 from Salpetermosen. The radiocarbon age shows the median probability. All: Allerød, YD: Younger Dryas, HOL: Holocene.

the area, where we found a 290 cm thick succession (Fig. 5). The sediments consist of calcareous gyttja and detritus gyttja overlain by peat. In the lower part of the macrofossil diagram *Betula pubescens* remains were found, this part of the diagram may perhaps belong to the Allerød period. In addition to *B. pubescens* remains we note remains of *Distichium* sp. and *Comarum palustre*.

This interval is followed by an assemblage characterised by *Betula nana* remains, other terrestrial fossils comprise *Dryas octopetala*, *Selaginella selaginoides*, *Distichium* sp. and rare *Betula pubescens*. Aquatic plants are represented by *Hippuris vulgaris* and *Ranunculus* sect. *Batrachium* sp., and aquatic invertebrates by for example *Valvata piscinalis*, *Valvata cristata*, *Pisidium* sp., *Candona* sp., *Limnocythere* sp. and *Daphnia* sp. A sample of bark from a depth of 268–272 cm was dated to *c.* 12 800 cal. years BP, corresponding to an early Younger Dryas age.

Deposits dated to the Early Holocene contain macrofossils of trees such as *Betula pubescens*, *Betula pendula*, *Populus tremula* and *Pinus sylvestris*. There are also a few finds of *Betula nana* and *Empetrum nigrum*. Wetland plants are dominated by *Carex* spp. (*Carex paniculata*, *C. riparia* and *C. rostrata*) but include for example *Schoenoplectus lacustris*, *Menyanthes trifoliata*, *Solanum dulchamara* and *Thelypteris palustris*. Aquatic plants comprise *Nymphaea alba*, *Ranunculus* sect. *Batrachium* sp., *Potamogeton natans* and *P. gramineus* and and aquatic invertebrates comprise *Valvata piscinalis*, *Valvata cristata*, *Pisidium* sp., *Candona* sp., *Limnocythere* sp., *Cypria ophthalmica*, *Daphnia* sp., *Sialis* sp. and *Cristatella mucedo*. Fishes are represented by *Gasterosteus aculeata*. The sediments also contained a single vertebra of a mouse, either from *Apodemus flavicollis* or *Apodemus sylvaticus*. The peat is dominated by rootlets and remains of the bryophytes *Tomentypnum nitens*, *Paludella squarrosa*, *Calliergon* sp. and some *Philonotis* sp.

Loc. 3

This locality is situated in the eastern part of the area, in an area with peat pits. The sediments consist of clayey gyttja, calcareous gyttja, detritus gyttja, peat and decomposed peat. The lower part of the macro-

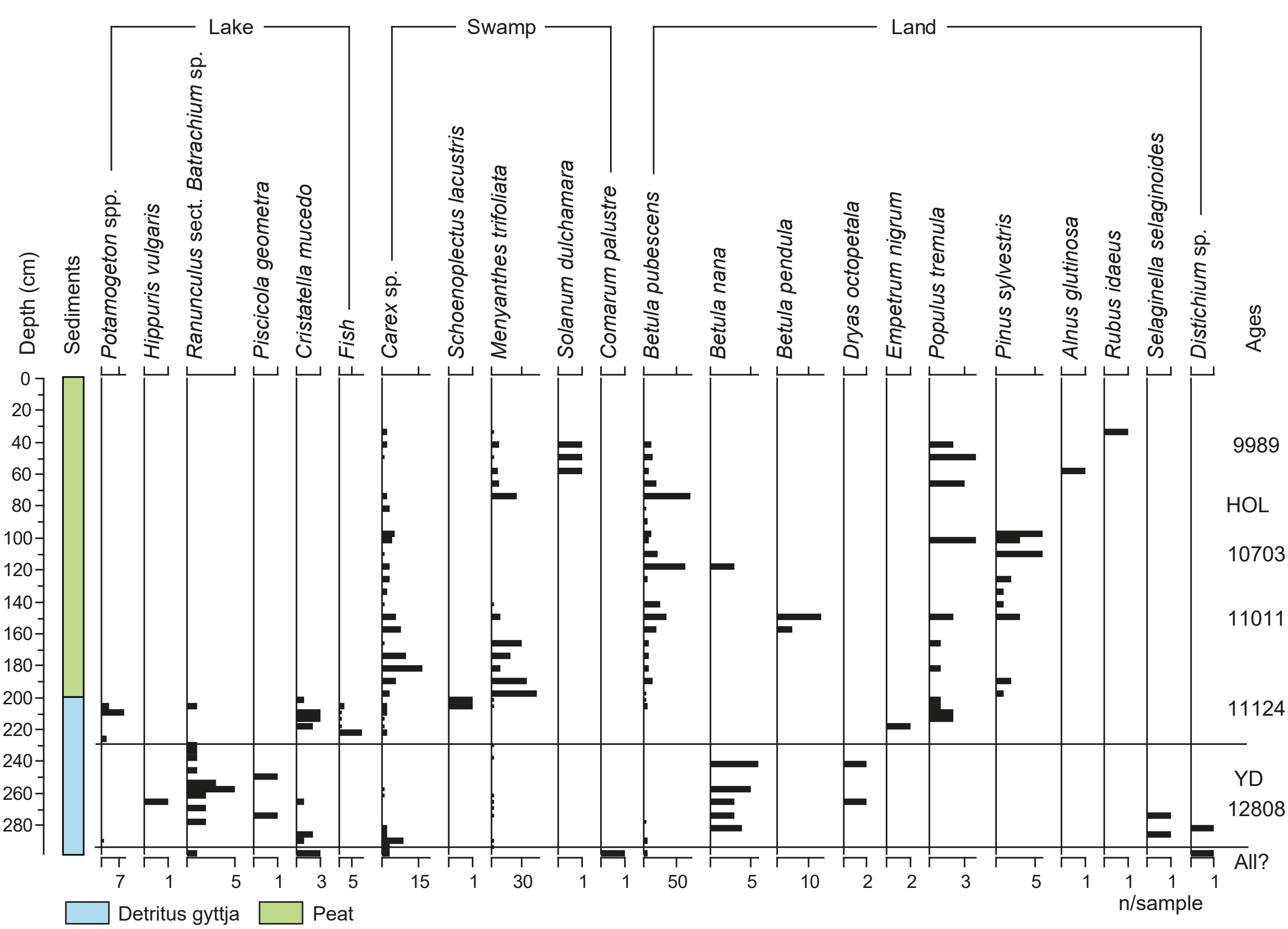

Fig. 5. Simplified macrofossil diagram for core site NFHA 3070 from Salpetermosen. The radiocarbon ages show median probability. All: Allerød, YD: Younger Dryas, HOL: Holocene.

fossil diagram is dominated by stems of *Fontinalis antipyretica* (Fig. 6). The stems were leafless, long, straight black stems with a characteristic look (Hartz 1902; Dickson 1973). *Myriophyllum* sp., was represented by a single small leaf fragment; it was the only other macrolimnophyte recorded. Aquatic invertebrates include *Candona* sp., *Limnocythere* sp., *Cytherissa lacustris* and *Cristatella mucedo*. The presence of egg cocoons of the fish leach *Piscicola geometra* shows that the lake housed fishes. The rare occurrence of remains of terrestrial and swamp plants indicates that the core site was located far from the lake shore. The deposits are with hesitation referred to the Younger Dryas.

The Early Holocene deposits contain remains of *Betula pubescens* and rare remains of *Pinus sylvestris*. Two nutlets of *Betula nana* were also found. Swamp plants include *Cladium mariscus* and *Schoenoplectus lacustris*. Aquatic plants comprise *Najas marina* and *Nymphaea alba* and aquatic animals comprise *Piscicola geometra*, *Valvata cristata*, *Valvata piscinalis*, *Bithynia tentaculata*, *Candona* sp., *Limnocythere* sp., *Darwinula stevensonii*, *Sialis* sp., *Cristatella mucedo* and the fish *Perca fluviatilis*. Two ^{14}C samples from 178 and 114 cm gave ages of *c.* 9000 and 8200 cal. years BP.

The upper part of the diagram is of Mid-Holocene age. Two samples from 70 and 30 cm gave ages of *c.* 5500 and 5000 cal. years BP. The ages from Loc. 3 indicate either a major hiatus or a period with very low sedimentation rate below 70 cm. The lake was overgrown in the Mid-Holocene and turned into a bog. At the transition to lake to bog *Menyanthes trifoliata* occurred at the core site.

Discussion

According to the deglaciation chronology of the region, active glacier ice disappeared from the area at about 18 000 to 17 000 years ago (Houmark-Nielsen *et al.* 2012). However, the oldest dated remains of terrestrial plants found so far in the Salpetermosen area are only *c.* 13 300 years old. This means that about 4000 years elapsed from the disappearance of active ice until we

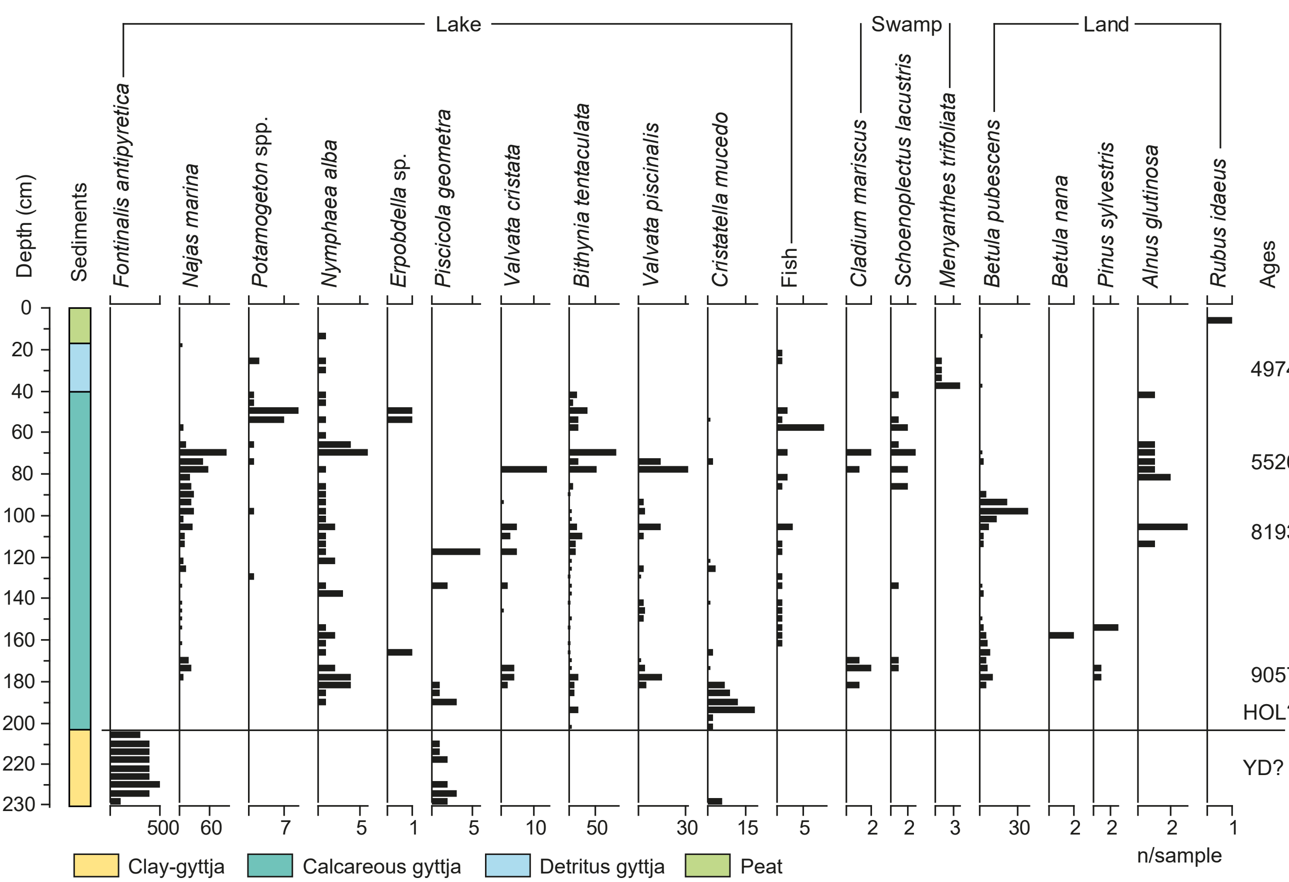

Fig. 6. Simplified macrofossil diagram for core site loc. 3 from Salpetermosen. The radiocarbon ages show median probability. HOL: Holocene, YD: Younger Dryas.

find the oldest traces of plant life. The lack of older dated plant remains may be due to extensive occurrences of bodies of stagnant ice, which could lead to unstable soil conditions. Meltwater from bodies of stagnant ice may have been turbid and oligotrophic – conditions that would inhibit algal colonization and limnic succession. However, it is also important to note that the time period from 18 000 to 14 700 years BP was characterised by low $\delta^{18}O$ values and therefore low temperatures according to studies of ice cores from Greenland (Rasmussen *et al.* 2014). Low temperatures would obviously also lead to slow development of vegetation. Another potential factor could be that the adjacent areas lacked plants that could colonize the region. However, the oldest dated plant remains from southern Jylland gave an age of *c.* 16 700 years BP (Mortensen *et al.* 2011), so this explanation appears unlikely.

The oldest organic deposits found in the Salpetermosen area are of Allerød age. The most important land plant was *Betula pubescens*, which formed open forests. *Populus tremula* also immigrated during the Allerød, but only two bud scales of the species were found in a layer referred to the Allerød, so it must have been rare in the area. Remains of the species were also very rare in Allerød layers from Søndre Kobberdam in north-east Sjælland (Bennike & Mortensen 2018).

Pollen grains of *Pinus sylvestris* (scots pine) occur abundantly in Lateglacial deposits in Denmark, but so far, no macrofossils of *Pinus sylvestris* have been found in Denmark, hence the pollen grains were probably transported to Denmark from the south. We suggest that *Pinus sylvestris* immigrated to Denmark in the Early Holocene, probably around 11 000 cal. years BP (Bennike & Lemke 2001; Bennike & Mortensen 2018). However, *in situ* Lateglacial pine stumps dated to the Younger Dryas and Allerød periods have been recorded from northern Germany, as summarised by Kaiser *et al.* (2018).

Shrubs or bushes included *Salix* sp., *Arctostaphylos uva-ursi* and *Empetrum nigrum*. *Arctostaphylos uva-ursi* fruit stones are fairly common in Lateglacial deposits from Denmark (Jensen 1985; Bennike & Jensen 1995; Jensen *et al.* 1997; Bennike *et al.* 2004b; Mortensen *et al.* 2014a; Bennike & Mortensen 2018). To our knowledge five finds of *A. uva-ursi* stones from eastern Denmark have been directly dated, they gave ages between *c.* 13 100 and 13 700 cal. years BP, corresponding to mid-Allerød ages. Based on this we suggest that the species was an important component of the mid-Allerød vegetation in eastern Denmark.

A few remains of *Betula nana* and a few fruit stones of *Rubus saxatilis* were also found in layers referred to the Allerød period. *Rubus saxatilis* is rare in Lateglacial deposits from Denmark, but it has been reported from Allerød deposits from north-east Sjælland before (Hartz 1902; Jessen 1920) and from Falster in south-eastern Denmark (Mortensen *et al.* 2014a). The terrestrial flora also included *Salix* sp., *Potentilla* sp., *Selaginella selaginoides* and *Plagiomnium affine*.

Among swamp plants *Carex rostrata* was one of the dominating species, wheras *Menyanthes trifoliata* and *Comarum palustre* were rarer. A few fruits of *Cicuta virosa* were found at one of the investigated sites, this warmth-demanding swamp plant was probably rare. A single fruit of *Oenanthe aquatica* was found at A40, in a layer referred to the Allerød period. The species is rare in Lateglacial deposits, but it has previously been recorded from Allerød deposits on southern Fyn (Hartz 1902). *Oenanthe aquatica* is one of the most warmth-demanding plants from Lateglacial deposits in Denmark, the northern geographical limit of the species is found in south-central Sweden (Hultén 1950). The fossil occurrence of *O. aquatica* in Denmark supports the conclusion by Schenk *et al.* (2020) that summer temperatures during the Allerød period in southern Scandinavia were higher than previously believed by for example Iversen (1954). Nutlets of *Urtica dioeca* were found to be common at one site; this plant is characteristic of nutrient-rich soils, which could be caused by dung from herbivores.

The lakes housed a rich flora of macrolimnophytes with *Potamogeton praelongus*, *P. perfoliatus*, *P. pusillus*, *P. alpinus*, *Stuckenia filiformis*, *Ranunculus* sect. *Batrachium* sp., *Myriophyllum alterniflorum*, and *Hippuris vulgaris*. The fauna of the lakes included *Erpobdella* sp., *Piscicola geometra*, *Cypria* sp., *Diaptomus* cf. *castor*, *Sialis* sp., *Valvata piscinalis*, *V. cristata*, *Radix balthica* (syn. *Lymnaea peregra*), *Pisidium* sp., *Cristatella mucedo* and the fish fauna included *Esox lucius*.

During the Younger Dryas *Betula nana* and *Dryas octopetala* were the main woody plants and the landscape was a tundra-like and dominated by dwarf-shrub heaths. *Betula nana* appears to have been the dominating woody plant in the region during the Younger Dryas. This is in accordance with the results of Hartz (1902) from the Allerød clay pit and in accordance with results from Søndre Kobberdam (Bennike & Mortensen 2018). *Betula pubecens* probably did not disappear, but it became rare. A stem of tree birch from Birkerød has been ^{14}C dated to the Younger Dryas (Mortensen *et al.* 2014b). Other shrubs are represented by *Salix herbacea*, which is a tiny willow species that grows in late snow beds. *Arctostaphylos alpina*, *Luzula* sp. and *Selaginella selaginoides* are only represented by few finds. Among swamp plants taxa such as *Carex* spp., *Menyanthes trifoliata*, *Urtica dioeca*, *Aulacomnium palustre*, *Scorpidium scorpioides* and *Paludella squarrosa* may be mentioned. *Lychnis flos-cuculi* is represented by a single seed; seeds of this warmth demanding plant were found in Allerød sediments at Søndre Kobberdam (Bennike & Mortensen 2018), but it is surprising to find seeds of it in Younger Dryas sediments.

The macrolimnophyte vegetation varied from site to site. The large basin (loc. 3) was dominated by *Fontinalis antipyretica*. The smaller basins housed a more species-rich flora with *Potamogeton praelongus*, *P. perfoliatus*, *P. friesii*, *P. alpinus*, *P. obtusifolius*, *Stuckenia filiformis*, *Hippuris vulgaris*, *Callitriche hermaphroditica*, *Nuphar lutea* and *Ranunculus* sect. *Batrachium* sp. The invertebrate lake fauna included for example *Piscicola geometra*, *Cytherissa lacustris*, *Cyclocypris* sp., *Sialis* sp., *Valvata cristata*, *Pisidium* sp., *Cristatella mucedo*, *Plumatella* sp. and *Fredericella* sp. and the fish fauna included *Perca fluviatilis* and *Pungitius pungitius*.

Egg cocoons of the fish leech *Piscicola geometra* are rare in Younger Dryas deposits in Denmark, but they have also been reported from Younger Dryas deposits from Faxe Bugt in south-eastern Denmark (Bennike & Jensen 1995). The species is warmth demanding, but with rare occurrences in northern Sweden (https://artfakta.se/artbestamning/taxon/piscicola-geometra-225478). A few bones and spines of the small fish *Pungitius pungitius* were found in late Younger Dryas and early Holocene sediments; the species is new to the fossil fauna of Denmark (Rosenlund 1976).

At the beginning of the Holocene, *Betula pubescens* spread rapidly. *Populus tremula* arrived shortly after and became an important component of the forests. It was followed by *Pinus sylvestris*, then by *Betula pendula* and later *Alnus glutinosa*. The area became covered by open forests and *Betula nana* survived for some time. There are a several other records of Early Holocene *B. nana* remains from Denmark (Jessen 1920; Jensen 1985; Bennike & Jensen 2011). Other land plants in the Salpetermosen area are represented by *Salix* sp., *Empetrum nigrum*, *Arctostaphylos uva-ursi*, *Vaccinium oxycoccus* and *Rhizomnium punctatum*. The timing of the immigration of *Betula pendula* to Denmark is poorly constrained due to problems of separating remains of it from *Betula pubescens*. At NFHA 3007 some remains of *B. pendula* were found, they are dated to *c.* 10 800 cal. years BP. *Betula pendula* is a fairly warmth-demanding tree, it is for example more warmth demanding than *Pinus sylvestris* (Hultén 1950). Therefore we consider it likely that it arrived later than pine. It has been discussed whether *Betula pendula* was already present during the Allerød period (Hartz 1902; Jessen 1920) but we follow Iversen (1954) who did not include the species in his list of Danish Lateglacial plants.

During this study we obtained a direct age of macrofossils of *Alnus glutinosa* (alder), the sample was dated to *c.* 8200 cal. years BP (Table 1). However, a single find of *Alnus glutinosa* from NFHA 3070 has an interpolated age of *c.* 10 000 cal. years (Fig. 4). In Aarhus Bugt the oldest *A. glutinosa* remains were dated to *c.* 9800 cal. years BP (Rasmussen *et al.* 2019), and in the Great Belt direct ^{14}C dating of *A. glutinosa* nutlets gave an age of *c.* 9500 cal. years BP (Bennike *et al.* 2004b). The find from NFHA 3070 indicates that the species immigrated to north-east Sjælland about 10 000 cal. years BP.

The flora of swamp plants included *Carex paniculata*, *C. riparia*, *Schoenoplectus lacustris*, *Cladium mariscus*, *Stachys palustris*, *Lycopus europaeus*, *Comarum palustre*, *Eupatorium cannabinum*, *Alisma plantago-aquatica*, *Climacium dendroides*, *Tomentypnum nitens* and *Paludella squarrosa*.

Schoenoplectus lacustris (syn. *Scirpus lacustris*; bulrush) immigrated to Denmark during the Allerød period, but it was rare, with only a single record from the Great Belt (Bennike *et al.* 2019). It probably died out during the cold Younger Dryas period and re-immigrated in the Early Holocene and soon became common and widespread. *Cladium mariscus* (fen-sedge) also immigrated to Denmark during the Allerød period, but it was also rare, with a single record from south-eastern Denmark (Bennike & Jensen 2013). It probably also re-immigrated in the Early Holocene and soon became much more common and widespread than today. *Cladium mariscus* is a calciphilous and thermophilous sedge and its decreasing occurrence is probably due to leaching of carbonate and decreasing temperatures after the Holocene thermal maximum.

The lakes housed a rich vegetation with many species of aquatic plants including *Nuphar lutea*, *Nymphaea alba*, *Ceratophyllum submersum*, *C. demersum*, *Ranunculus* sect. *Batrachium* sp., *Myriophyllum alterniflorum*, *Hippuris vulgaris*, *Potamogeton natans*, *P. praelongus*, *P. perfoliatus*, *P. friesii*, *P. gramineus*, *P. obtusifolius*, *P. crispus*, *P. pusillus*, *P. compressus*, *Stuckenia filiformis* and *Najas marina*. The invertebrate fauna included many species of bivalves and gastropods, one of the most common being *Bithynia tentaculata*. The ostracode fauna included *Darwinula stevensonii* and *Cypria ophtalmica* and the fish fauna included *Perca fluviatilis*, *Esox lucius*, *Pungitius pungitius* and Cyprinidae indet.

Najas marina (spiny naiad) is a small, submerged limnophyte that was common in Denmark during the Early to Mid-Holocene (Jessen 1920; Bennike *et al.* 2001). The oldest records of it in Salpetermosen are dated to *c.* 9000 cal. years BP, but the oldest find from Denmark is at least 10 300 cal. years old. Today it is very rare in Denmark, partly because of cooling after the Holocene thermal maximum and partly due to changes in lake water chemistry and trophic stage. Competition with other water plants may also be an important factor.

Late Holocene deposits were only found at one site, where we found peat with *Sphagnum* sp. and *Scheuchzeria palustris*, indicating acidic soil conditions. *Pinus sylvestris* was still growing in the area in the Late Holocene.

Scheuchzeria palustris (Rannoch-rush) is rarely recorded as a subfossil from Danish deposits, but there are some finds, mainly from Jylland and north-east Sjælland and mainly of Late Holocene age (Jessen 1920; Tallis & Birks 1965; Jensen 1985). At the present day, the species is rare in Denmark; it is known from *c.* 10 localities, most of them in north-east Sjælland and eastern Jylland (Hartvig 2015). The find from Salpetermosen is the first directly dated fossil find from Denmark; the age of *c.* 2800 cal. years BP corresponds with most other finds from Denmark. The species grows in areas of permament standing water, as a constituent of wet *Sphagnum*-carpet, often on a floating raft of vegetation. The species has become rare due to peat cutting, drainage of bogs, eutrophication and overgrowth of bogs by shrubs and trees.

Summary

This macrofossil studies of Lateglacial and Holocene lake and bog deposits from the Salpetermosen area, north-east Sjælland show that the vegetation and animal life have undergone a dynamic development. Active glacier ice disappeared from the region 18 000 to 17 000 years ago, but the oldest dated remains of terrestrial plants found so far are only *c.* 13 300 years old. The delayed establishment of plants may be due to extensive occurrences of bodies of stagnant ice.

During the Allerød period open forests with *Betula pubescens* and rare *Populus tremula* dominated the area. The terrestrial flora included *Arctostaphylos uva-ursi*, *Empetrum nigrum* and *Rubus saxatilis*. The lakes housed rich floras and faunas, including *Esox lucius*.

During the Younger Dryas, a tundra-like landscape with dwarf-shrub heaths dominated by *Betula nana*, but including *Dryas octopetala*, *Salix herbacea*, *Arctostaphylos alpina* and rare *Betula pubecens* was found. Finds of the thermophilous plants *Urtica dioeca* and *Lychnis flos-cuculi* indicate fairly high summer temperatures. The fish fauna included *Perca fluviatilis* and *Pungitius pungitius*. Radiocarbon dating of cast antlers of *Rangifer tarandus* (reindeer) from other parts of north-east Sjælland shows that this large herbivore occurred in the region during this period.

The Early Holocene forests were open and dominated by *Betula pubescens*, *Populus tremula* and *Pinus sylvestris*, with rare *Betula nana*. The sedge *Cladium mariscus* and the macrolimnophyte *Najas marina* were common in the area. The Late Holocene flora included the acidophilous plant *Scheuchzeria palustris*, which is very rare in Denmark today.

The lakes of the area housed rich and diverse floras and faunas. Several of the recorded species have decreased markedly in Denmark, partly due to pollution and eutrophication of water bodies.

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