A multi-disciplinary macrofossil study of late glacial to early Holocene sediments from Søndre Kobberdam, Hareskovene, Denmark

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During the early part of the Allerød period, from *c.* 13 600 to 13 330 years BP, unstable soils with a tundra-like open, treeless vegetation with *Betula nana* and *Dryas octopetala* were found around Søndre Kobberdam in Hareskovene. Open *Betula pubescens* woodland was not established until the middle Allerød about 13 330 years BP. During the Younger Dryas, *Betula nana* and *Dryas octopetala* spread again, and *Betula pubescens* almost disappeared. From the onset of the Holocene warming an open tundra landscape characterised the area. About 11 300 years BP *Betula pubescens* started to recolonise the region and *Populus tremula* and *Pinus sylvetris* arrived at *c.* 11 000 years BP, replacing the open landscape by woodland. Along the margin of the lake *Carex paniculata*, *Carex riparia* and *Cladium mariscus* were growing. The lake fauna included a rich and diverse fauna of molluscs that thrived in the carbonate-rich waters. We did not find any evidence for the local presence of *Pinus sylvestris* during the late glacial.

Keywords: Late glacial, vegetation history, fauna history, immigration history, Denmark.

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The study of macrofossils has a long history in Denmark, which is due to the former exploitation of peat and interest in how peat formed. In the beginning of the 1800s there was a great demand for peat in Denmark, particularly in Copenhagen, and huge amounts of peat were cut in bogs north of the city. As much as 70 000 wagonloads of peat were transported by horses to the capital each year (Garboe 1961). This exploitation led to interest in understanding how peat was formed, and in 1816 the Danish Agricultural Society (Landhusholdningsselskabet) offered a prize for a paper on this subject. No one responded, so the price was offered again in 1819, and this time a paper was submitted by Heinrich Dau. Sadly, the high quality of Dau's pioneering work was not recognised, and he did not win the prize, but he published his work as a book (Dau 1823). Dau continued to study peat and published a new book on the results, where he mentioned that he had found remains of *Pinus*, *Betula*, *Quercus* and *Alnus* in bogs on Sjælland, and that these remains showed that the vegetation had changed over time (Dau 1829). However, soon after he committed suicide (Rørdam 1914; Garboe 1961).

In 1835 the Royal Danish Academy of Sciences offered a new prize for a study of peat formation, and a manuscript was submitted by Japetus Steenstrup who won high honours for the work. Steenstrup established a zonation for Holocene vegetation development in north-eastern Sjælland, with four zones, successively *Populus*, *Pinus*, *Quercus* and *Alnus* (Steenstrup 1842). In 1871 A.G. Nathorst from Sweden found remains of arctic plants in late glacial sediments in north-eastern Sjælland (Nathorst 1892, 1914). Steenstrup's work on plant macrofossils in Danish deposits was continued by Nicolaj Hartz who concentrated on late glacial and interglacial deposits (Hartz & Milthers 1901; Hartz 1902, 1909). Hartz and Milthers found evidence of a warm late glacial period in the Allerød clay pit. Numerous later works on the vegetation history of Denmark have been conducted, mainly based on pollen analysis alone. In recent years, however, the importance of macrofossils has been recognised again (e.g. Birks 1993; Mortensen *et al.* 2011). Macrofossils have a number of advantages compared with pollen. For example, macrofossils do not spread as far and wide as pollen and may therefore provide a better picture of the local vegetation. The local presence of prolific pollen producers, such as *Betula* and *Pinus*, is particularly difficult to establish from pollen analysis. Another advantage is that macrofossils commonly can be determined to species, whereas pollen grains commonly can be determined to genus or family only. Moreover, it is possible to use samples of macroscopic plant remains for radiocarbon age determinations by accelerator mass spectrometry (AMS). In this way it is possible to directly date remains of key species and provide minimum ages for the timing of their immigration to the study site.

Even though studies of the vegetation history of Denmark go back almost 200 years, and even though many studies have been conducted in past decades, many details of late glacial and Holocene vegetation and environmental changes are still poorly known. The aim of this paper is to describe and interpret the results of macrofossil studies of Søndre Kobberdam, a small lake basin in Hareskovene, north-eastern Sjælland, not far from the classical sites investigated by Steenstrup and Hartz. The study is the first radiocarbon dated macrofossil study of late glacial deposits from north-eastern Sjælland. Data from the site were used in the analysis by Mortensen *et al.* (2014a, supplementary material), but no details were provided. The results are compared with other recent detailed works on late glacial and early Holocene deposits in Denmark (Bennike *et al.* 2004; Mortensen *et al.* 2011, 2014a, b; Fischer *et al.* 2013).

Study area

The studied lake, Søndre Kobberdam, is located in north-eastern Sjælland, approximately 13 km from the centre of Copenhagen and 9.4 km south-south-west of the classical Allerød clay pit locality (Fig. 1; Hartz & Milthers 1901). Søndre Kobberdam is located in the eastern part of Hareskovene. There are three small lakes east of a hill named Højnæsbjerg, which reaches a height of 48 m above sea level. The lakes are named Kobberdammene and Søndre Kobberdam is the southernmost of them (Gladsaxe 2017). Because of its small size it was considered suitable for plant macrofossil analyses. The lake is oval in shape and measures 60 × 40 m; it is located 21 m above sea level and was presumably formed as a kettle hole by melting of a body of stagnant ice. The geographical coordinates of the coring site are 55°46.33´N, 12°26.29´E and the water depth was 450 cm.

The region was glaciated during the last glacial maximum and was deglaciated between 17 000 and 18 000 years BP, according to cosmogenic surface exposure dating of large erratic boulders (Houmark-Nielsen *et al.* 2012). The pre-Quaternary bedrock of the region consists of Lower Tertiary (Danian) limestone, and the area is a moraine landscape that formed during the Weichselian. It is dominated by glaciofluvial sand and gravel and sandy clayey till (Milthers 1922). The glacial and glaciofluvial deposits are carbonate-rich except near the soil surface where they have been leached during the Holocene. The landscape is hilly with numerous kettle holes and the area is unsuitable for agriculture due to its poor nutrient status and because it is hilly. Hence parts of the area have probably been covered by forests during most of the Holocene. The present

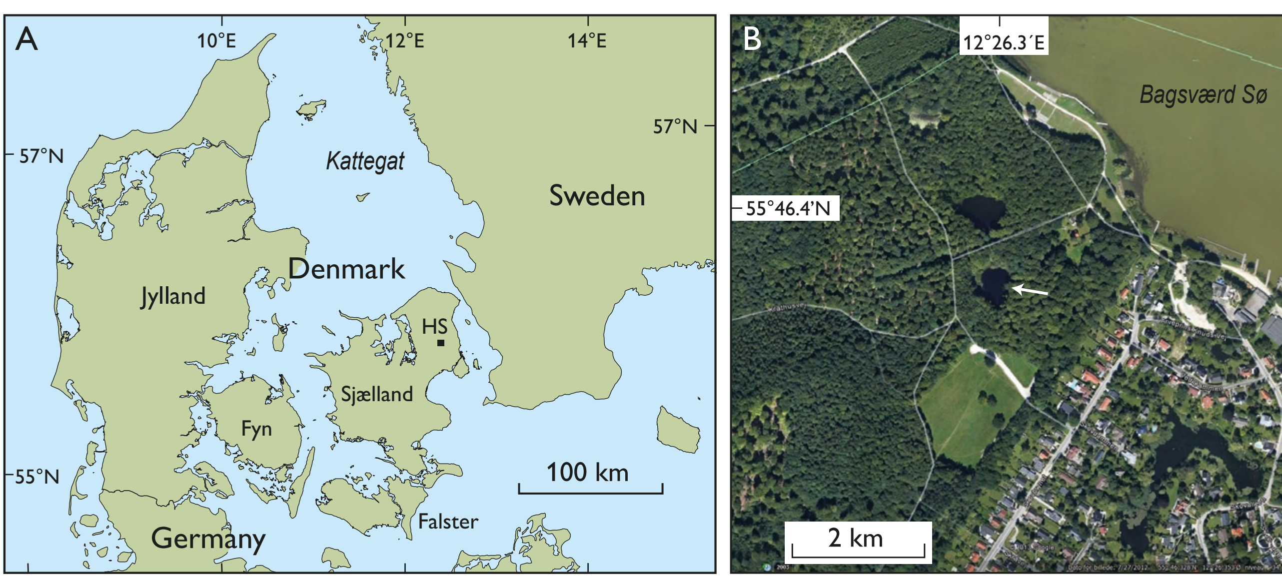

Fig. 1. A. Map of Denmark showing the location of Hareskovene (HS). **B.** Google Earth satellite image of the study area. The arrow shows Søndre Kobberdam.

day forests in Hareskovene are dominated by *Fagus sylvestris*, with some *Quercus robur* and *Tilia cordata* on well-drained soils. Moist and wet soils are dominated by *Ulmus glabra*, *Fraxinus excelsior*, *Alnus glutinosa*, *Betula pubescens* and *Betula pendula*. *Acer pseudoplatanus* is currently spreading rapidly. The climate is temperate; the mean July temperature was 17.1°C and the mean annual precipitation was 620 mm during the period from 1982 to 2012, according to https://da.climate-data.org/.

Methods

Coring was carried out in the central and deepest part of the lake, in winter during a short cold period when the lake was ice-covered. The coring equipment was a Russian peat corer with a chamber length of 100 cm and a diameter of 7.5 cm (Jowsey 1966). We took overlapping cores to ensure that the nose of the corer did not disturb the sediments below. The cores were transferred from the corer to plastic liners, and whole cores were brought to the laboratory where the cores were opened and correlated visually. The cores were carefully cleaned to avoid down-core contamination, and 64 contiguous samples of 2 cm length were taken for macrofossil analysis. The samples were wet sieved on 0.4 and 0.2 mm sieves and the residues left on the sieves were transferred to petri dishes and investigated using a dissecting microscope. Plant and animal remains were identified using reference material as well as keys and illustrations in books and papers.

Selected identified macrofossils of terrestrial plants from four levels were dried and submitted for accelerator mass spectrometry (AMS) radiocarbon dating. Dating was carried out at the Universities of Cologne (COL) and Lund (LuS). 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 data. In this paper we only discuss calibrated ages. The widespread occurrence of carbonate-rich glacial deposits in Denmark results in large hard-water effects, and hence it is important to use remains of terrestrial plants for dating.

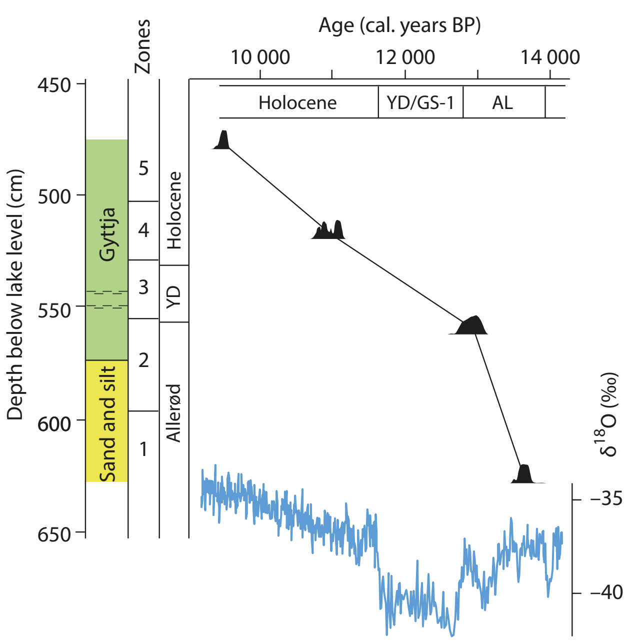

Fig. 2. Age–depth model for the succession in Søndre Kobberdam. Thin clay layers are found at 550–551 cm and 543–544.5 cm. YD = Younger Dryas, AL = Allerød, GS-1: Greenland stadial 1. The lower part of the figure shows oxygen isotope ratios from the GRIP deep ice core from Greenland from Johnsen *et al.* (1992). The ice core chronology is from Rasmussen *et al.* (2014).

Results

Sediments, dating and sedimentation rates

The analysed core was 155 cm long (Fig. 2). The lower part of the succession from 630 to 573 cm below lake level consists of layered fine-grained sand and silt, and the upper part from 573 to 475 cm consists of gyttja. Thin clay layers are found at 550–551 cm and at 543–544.5 cm. The gyttja is homogenous up to 507 cm and laminated in the upper part. Above 475 cm a thin layer of greenish, fresh-looking *Fagus sylvatica* leaves was found. This indicates that a major part of the Holocene sediments is missing. As mentioned above, large amounts of peat have been cut in bogs north of Copenhagen, and it is likely that peat digging transformed a former bog into a lake during the 1800s and is the reason for the lack of Holocene sediments.

The late glacial and early Holocene stratigraphy in Søndre Kobberdam differs from other sites in the area. The sediments in the Allerød clay pit consisted of clay, Allerød gyttja, Younger Dryas clay and Holocene peat, and similar successions have been found in other clay pits on Sjælland (Hartz & Milthers 1901; Hartz 1902; Krog 1954). Iversen (1947) listed a number of different late glacial sedimentary successions, but none of them is similar to the succession from Søndre Kobberdam. Hence it may represent a local, rather unusual lithostratigraphy.

Results of the radiocarbon dating of four samples are shown in Table 1. Based on these ages, a tentative age-depth curve can be drawn (Fig. 2). There are too few ages to construct a well constrained age-depth curve, but according to the tentative curve the sedimentation rate was *c.* 0.94 mm/year in the lower part of the succession and *c.* 0.24 mm/year in the upper part. The mineral-rich sediments in the lower part indicate that there was a marked in-wash into the lake, which is confirmed by the age-depth model.

Macrofossils

The results of the macrofossil analyses are presented in two macrofossil diagrams (Figs 3, 4). The diagrams were divided by visual inspection into four local macrofossil assemblage zones that are described in the following.

Zone 1 (13 600–13 330 years BP, 628–596 cm)
Zone 1 is dominated by *Dryas octopetala* and *Betula nana*. Other woody plants are represented by a few leaves of *Salix polaris*, a few endocarps of *Arctostaphylos uva-ursi*. Herbaceous plants are dominated by *Carex* sp., a few of which could be identified as *Carex rostrata*; all may

Table 1. AMS radiocarbon ages from Søndre Kobberdam, Hareskovene, 55°46.33´N, 12°26.29´E

Laboratory number	Depth (cm)	Material	Age (^{14}C years BP)[1]	Calibrated age (years BP)[2]	Calibrated age (years BP)[3]
COL-1059	475–477	*Salix* sp.	8483 ± 41	9447–9537	9499
LuS-9172	515–517	*Pinus sylvestris*	9650 ± 65	10 775–11 200	10 992
COL-1060	557–561	*Betula pubescens*	11 077 ± 45	12 808–13 063	12 944
LuS-9173	624–628	Twigs	11 840 ± 70	13 482–13 780	13 657

[1] Radiocarbon ages are reported in conventional radiocarbon years BP (before present = 1950; Stuiver & Polach 1977). The ^{14}C ages have been corrected for isotopic fractionation by normalising to a $\delta^{13}C$ value of –25 ‰. [2] Calibration to calendar years BP is according to the INTCAL13 data (Reimer *et al.* 2013). [3] Mean probability ages.

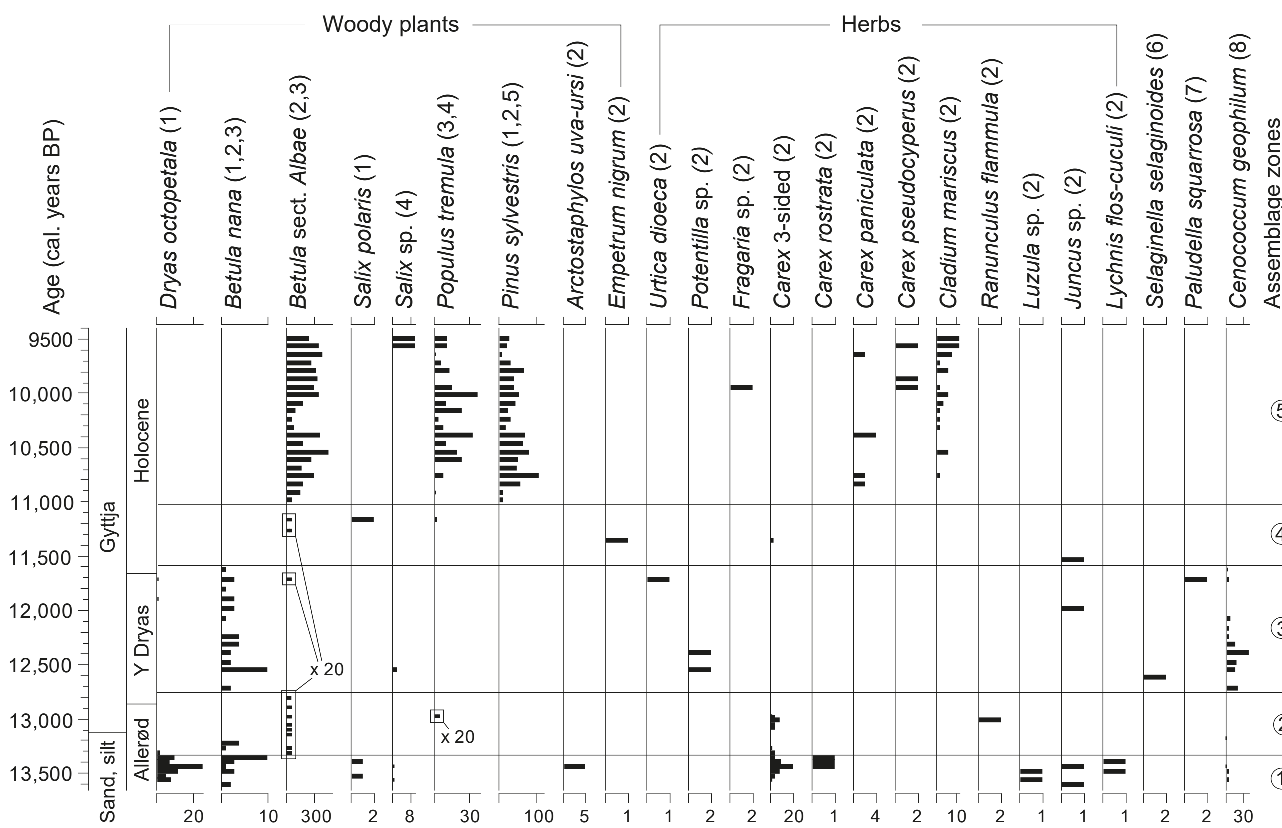

Fig. 3. Simplified macrofossil concentration diagram for Søndre Kobberdam (terrestrial and telmatic species). × 20: the columns are exaggerated 20 times. 1: leaves and leaf fragments, 2: seeds and fruits, 3: female catkin scales, 4: bud scales, 5: bark fragments, 6: megaspores, 7: leafy shoots, 8: sclerotia.

belong to this species which is common in late glacial assemblages from Denmark. *Juncus* sp., *Luzula* sp. and *Lychnis flos-cululi* are represented by few seeds. Only few remains of limnic plants (*Chara* sp. and *Potamogeton filiformis*) and invertebrates were found, including a few *Daphnia* cf. *pulex* type, chironomids (not shown in the diagram), the alder fly *Sialis* sp., trichopterans (not shown) and the bryozoans *Cristatella mucedo* and *Plumatella* sp.

Zone 2 (13 330–12 780 years BP, 596–555 cm)
Zone 2 is characterised by the occurrence of tree birch (*Betula* sect. *Albae*) remains. Remains that could be identified to species came from *Betula pubescens*. In the lower part of Zone 2 *Dryas octopetala* and *Betula nana* also occur. Woody plants are also represented by a single bud scale of *Populus tremula*. *Carex* sp. and two achenes of *Ranunculus flammula* are the only herbaceous telmatic plants in this zone.

At the beginning of zone 2 there are marked peaks of *Chara* sp. and *Potamogeton perfoliatus*; other water plants include *Ranunculus* sect. *Batrachium*, *Hippuris vulgaris*, *Myriophyllum alterniflorum, Ceratophyllum demersum* and *Potamogeton filiformis*. Limnic invertebrates include the fish leach *Piscicola geometra*, the tad-pole shrimp *Lepidurus* sp., *Daphnia* cf. *pulex*, chironomids, trichopterans, *Sialis* sp. and *Cristatella mucedo*. In the middle of the zone ostracodes are abundant; they include *Cytherissa lacustris*, *Limnocythere* spp. and *Candona* spp. Scales of the fish *Perca fluviatilis* are also found in part of zone 2.

Zone 3 (12 780–11 600 years BP, 555–529 cm)
Zone 3 is characterised by *Betula nana* remains; in addition there are a few *Dryas octopetala*, *Betula* sect. *Albae* and *Salix* sp. remains. Herbaceous plants include *Urtica dioeca* and *Potentilla* sp.. Sclerotia of *Cenococcum geophilum* are common; in addition two spores of *Selaginella selaginoides* and two shoots with leaves of the bryophyte *Paludella squarrosa* were also found.

Remains of macrolimnophytes are rare in zone 3, only *Ranunculus* sect. *Batrachium*, *Hippuris vulgaris* and *Myriophyllum alterniflorum* were noted. *Ranunculus* sect. *Batrachium* is common in the upper part of the zone. Remains of limnic invertebrates are rare and include *Daphnia* cf. *pulex*, ostracodes, chironomids,

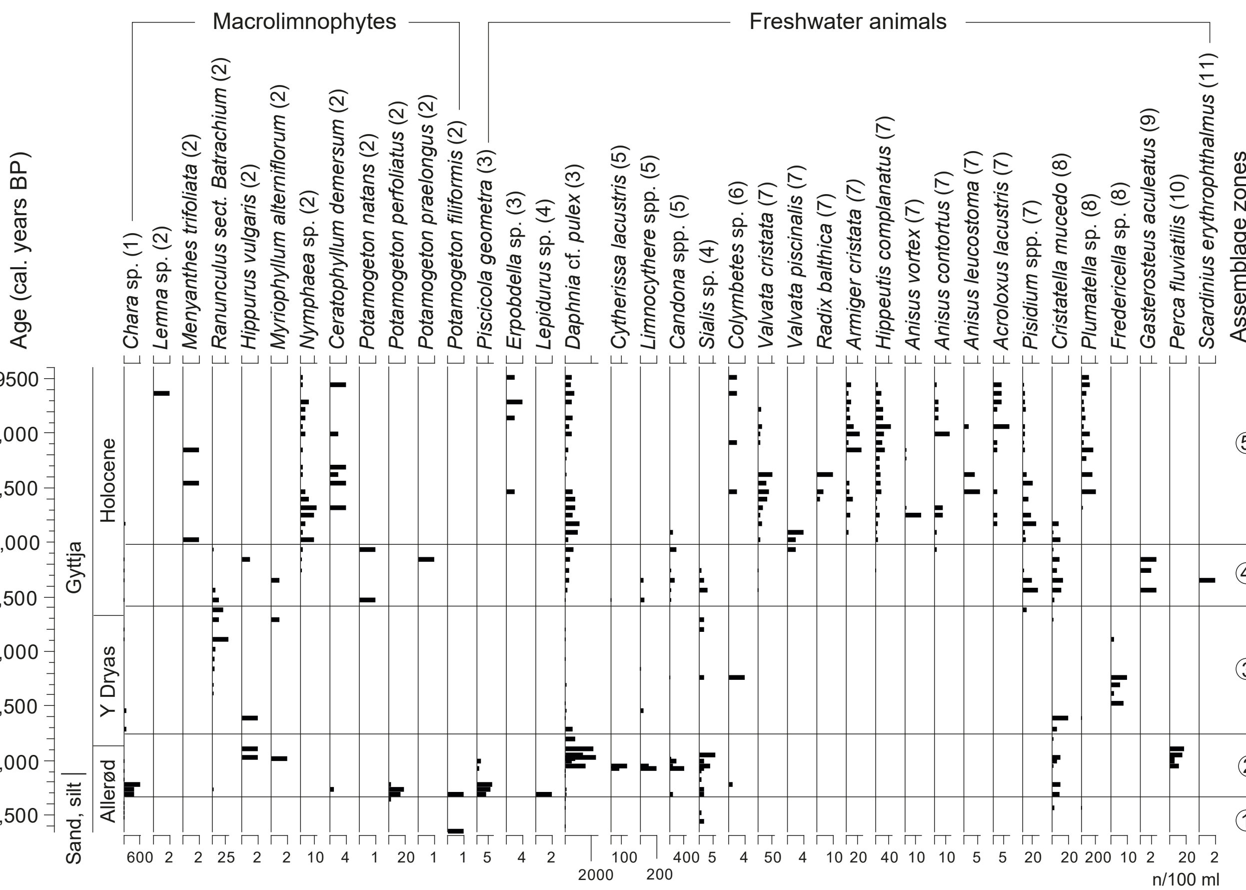

Fig. 4. Simplified macrofossil concentration diagram for Søndre Kobberdam (limnic species). 1: oospores, 2: seeds and fruits, 3: egg cocoons, 4: mandibles, 5: valves, 6: elytra fragments, 7: shells, 8: statoblasts, 9: spines, 10: scales, 11: pharyngeal teeth.

trichopterans, *Sialis* sp., the diving beetle *Colymbetes* sp., *Cristatella mucedo* and *Fredericella* sp.

Zone 4 (11 600–11 000 years BP, 529–503 cm)
In zone 4, only a few remains of terrestrial and telmatic plants are found; they come from *Betula* sect. *Albae*, *Salix polaris*, *Empetrum nigrum*, *Carex* sp. and *Juncus* sp. Water plants include *Ranunculus* sect. *Batrachium* (mainly in the oldest part of the zone) and *Nymphaea* sp. (in the younger part of the zone) in addition to rare occurrences of *Potamogeton natans*, *P. praelongus* and a few other taxa. Freshwater invertebrates include *Daphnia* cf. *pulex*, rare ostracodes, *Sialis* sp., the small bivalve *Pisidium* spp. and *Cristatella mucedo*. Fishes are represented by *Gasterosteus aculeatus* and *Scardinius erythrophthalmus*.

Zone 5 (11 000–9 500 years BP, 503–475 cm)
Zone 5 is characterised by *Betula* sect. *Albae*, *Populus tremula* and *Pinus sylvestris*. Many of the *Betula* sect. *Albae* could be identified to species, and all came from *Betula pubescens*. Herbaceous plants include *Fragaria* sp., *Carex paniculata*, *C. pseudocyperus* and *Cladium mariscus*. Macrolimnophytes include *Nymphaea* sp., *Ceratophyllum demersum*, *Menyanthes trifoliata*. Aquatic invertebrates include the leach *Erpobdella* sp., *Daphnia* cf. *pulex*, diving water beetles (*Colymbetes* sp.) and *Plumatella* sp. Molluscs are represented by a range of gastropod species as well as the bivalves *Pisidium* spp. and *Sphaerium corneum*, the latter represented by a single shell.

Discussion

Zone 1
Zone 1, from *c.* 13 600 to *c.* 13 330 years BP correspond to the early and middle part of the Allerød period, or the Greenland Interstadial 1c (GI-1c) event (Björck *et al.* 1998). The vegetation, with *Dryas octopetala*, *Betula nana*, *Salix polaris* and *Arctostaphylos uva-ursi,* is interpreted as an open pioneer, tundra-like vegetation with dwarf-shrub heaths. *Dryas octopetala* leaves are common in deposits from the early late glacial and the Younger Dryas period in the region (Iversen 1954) and the plant must have been an important component of the vegetation. It thrives on sites with calcareous soils. In addition, *Dryas octopetala* has root nodules that house nitrogen-fixing bacteria, which enables it to grow on raw soils with little nutrients. The water plants *Chara* sp. and *Potamogeton filiformis* are common in late glacial sediments; the latter is mainly a northern species. Mandibles and labra of larvae of *Sialis* sp. (alder fly) are common in late Quaternary lake sediments (Frey 1964).

The soils around the lake, especially on the Højnæsbjerg hill, were unstable, and sand, silt and clay was washed into the lake. The lake water was probably turbid and therefore only supported a sparse flora and fauna. It is also possible that stagnant ice was still present in the basin, which would have led to low water temperatures.

Studies of beetle remains (Coope *et al.* 1998; Lemdahl *et al.* 2014) and chironomid larvae (Heiri *et al.* 2014) from deposits from north-western Europe indicate that summer temperatures during this time period were fairly high. The lack of tree birch during this period may be due to delayed immigration, perhaps due to unstable soils with stagnant ice still present.

Zone 2
Zone 2, from *c.* 13 330 to *c.* 12 780 years BP, corresponds to the middle and late part of the Allerød period and the oldest part of the Younger Dryas, or the GI-1a-b events and the oldest part of the GS-1 event. During zone 2 open woodland with *Betula pubescens* and rare *Populus tremula* developed around the lake. The woodland may have been so dense that the heliophilous dwarf shrubs *Dryas octopetala* and *Betula nana* disappeared from the near vicinity of the lake. The soils around the lake became more stable. The lake housed a rich vegetation of submerged macrolimnophytes, a rich fauna of invertebrates and the fish *Perca fluviatilis*. Remains of *Perca fluviatilis* have previously been reported from Allerød period deposits from Sjælland, Fyn and Jylland (Rosenlund 1976). The flora and fauna indicate that the water in the lake became clearer and warmer. Sedges and *Ranunculus flammula* grew along the shores of the lake. *Ranunculus flammula* remains are extremely rare in Allerød deposits from Denmark.

The Allerød period is commonly considered a period characterised by open forests dominated by *Betula pubescens* in Denmark. However, a recent compilation of the available data by Mortensen *et al.* (2014a) shows that there were marked regional differences in the vegetation in Denmark. Birch forests were restricted to the southern and eastern parts of the country, whereas the north-western parts of Denmark were characterised by shrubs and copses with *Betula nana*. Furthermore, the early part of the Allerød period was characterised by open tundra-like vegetation, and birch forests did not spread until well into the Allerød period. The results from Søndre Kobberdam indicate that also at this site the early part of the Allerød period was characterised by a tundra-like, open, treeless landscape.

During the late part of the Allerød period, *Populus tremula* arrived. There are only a few reports of macrofossils of this species from Allerød layers in Denmark. Hartz (1902) reported a branch from Lundbæk in eastern Jylland and unspecified remains from Skinderbygaard Mose on Bornholm, but at both localities the remains may come from early Holocene deposits. A few more recent finds from eastern Jylland, Fyn, Sjælland and Falster are surely of Allerød age (Nielsen & Sørensen 1992; Fischer *et al.* 2013; Mortensen *et al.* 2014a). The scarcity of finds shows that *P. tremula* was rare in Denmark, and it was probably confined to the southern and eastern part.

The other tree birch species which grows in Denmark, *Betula pendula*, has also been reported from several localities in Denmark, including the Allerød clay pit (Hartz 1902; Jensen 1985). However, Iversen (1954) did not include it in his list of plants found in late glacial deposits in Denmark, and the remains were probably confused with *Betula pubescens*, which can be very variable.

Betula sect. *Albae*, *Populus tremula*, *Potamogeton perfoliatus*, *Ceratophyllum demersum*, *Cristatella mucedo* and *Cytherissa lacustris* are fairly warmth demanding and indicate that the mean July temperature was above 10 °C.

Zone 3

Zone 3, from *c.* 12 780 to *c.* 11 600 years BP, corresponds to the Younger Dryas cold period or the GS-1 event, which is characterised by a return to colder conditions in the North Atlantic region, as illustrated by the $\delta^{18}O$ curve from the GRIP ice core from Greenland (Fig. 2). *Betula nana* and rare *Dryas octopetala* returned to the area and the vegetation became tundra-like again, with *B. nana* dominated dwarf-shrub heaths. The rare occurrence of *Betula pubescens* may indicate that tree birch survived but became very rare. A radiocarbon age of a tree birch stem from Birkerød, also in north-eastern Sjælland, of *c.* 12 350 years BP (K-6151; 10 490 ± 155 ^{14}C years BP) may also indicate that tree birch survived during the Younger Dryas in the region (Mortensen *et al.* 2014a). The find of *Urtica dioeca* is noteworthy because remains of this thermophilous and nutrient-demanding plant are extremely rare in Younger Dryas deposits in Denmark. However, it has been recorded from Younger Dryas layers from southern Sjælland by Fischer *et al.* (2013) and from western Skåne in southern Sweden by Liedberg Jønsson (1988). It requires nitrogen- and phosphorous-rich soil. Maybe there were droppings of reindeer (*Rangifer tarandus*) or other vertebrates near the lake. The common presence in the lower part of the zone of sclerotia of the soil-inhabiting fungus *Cenococcum geophilum* indicates increased soil erosion and unstable soils around the lake (Liedberg Jönsson 1988).

The mean July temperature was probably below 10 °C, and the diversity of limnic organisms decreased strongly, probably due to turbid waters. However, the bryozoan *Fredericella* sp. was fairly common in the middle of the zone; this bryozoan is perhaps the most cold-adapted fresh-water bryozoan. It is common in lakes in northern Norway (Økland & Økland 2001) and the statoblasts can be common in Holocene lake sediments in south-western Greenland (Wagner & Bennike 2012).

Zone 4

The lower boundary of zone 4 is placed at the last occurrence of *Betula nana*; at the same time an increase in the warmth-demanding *Cristatella mucedo* is seen. Surprisingly, there are almost no remains of woody plants in the earliest Holocene sediments. The only exception is *Empetrum nigrum*, which was common in some regions of Denmark during the late Younger Dryas and earliest Holocene (Iversen 1973; Bennike *et al.* 2004; Mortensen *et al.* 2011). The lack of remains of terrestrial plants could perhaps be caused by low lake levels, as has been documented for other lakes in the region (Digerfeldt 1988). Low lake level in Søndre Kobberdam could potentially lead to poor preservation. However, it is also possible that spreading of trees was delayed by the cold event about 11 400 years BP, the Preboreal oscillation (Björck *et al.* 1997; Rasmussen *et al.* 2014). Similarly, at Hasselø in south-eastern Denmark, no remains of tree birch or other trees were reported from earliest Holocene sediments (Mortensen *et al.* 2014b). It is noteworthy that *Salix polaris* is present as late as 11 200 years BP; its presence indicates an open landscape in the first several hundred years after the onset of the Holocene warming. The find represents the first record of this arctic species from the early Holocene in Denmark. However, other arctic species such as *Dryas octopetala* (Andersen 1923) and *Rangifer tarandus* (Aaris-Sørensen *et al.* 2007) have also been recorded from early Holocene deposits in Denmark.

The first tree to appear in the record is *Betula* sect. *Albae* (at *c.* 11 300 years BP), but it took several hundred years before tree birch expanded at the site. The delay in the spreading of tree birch is hardly due to migrational delay from glacial refugia because the tree occurred in the region during the Younger Dryas (Liedberg Jönsson 1988; Mortensen *et al.* 2014a). Perhaps its spread and expansion were delayed by a relatively arid and windy continental climate with strong seasonality, late-spring frost and warm dry summers (Birks & Birks 2014).

Zone 5

The arrival of *Betula* sect. *Albae* was followed by *Populus tremula* and then by *Pinus sylvestris* at *c.* 11 000 years BP, which is one of the earliest *P. sylvestris* ages from Denmark. The area was again forested. The flora at the margin of the lake included the sedges *Carex paniculata*, *C. pseudocyperus* and *Cladium mariscus*; these plants are common in early Holocene deposits in

Denmark. The calciphilous and thermophilous *Cladium mariscus* was a common reed plant in Denmark in the early Holocene, but it has declined due to leaching of the calcareous soils throughout the Holocene and due to decreasing temperatures after the Holocene Temperature Maximum.

The lake supported a species-rich flora and fauna in the early Holocene. *Ranunculus* sect. *Batrachium* was common in the earliest Holocene, and *Potamogeton natans* was also present at an early stage, but soon *Nymphaea* sp. began to dominate, together with *Ceratophyllum demersum*. The early Holocene sediments contain a rich fauna of bivalves and gastropods. *Pisidium* spp. were the first to arrive, soon followed by *Valvata cristata*, *Hippeutis complanatus*, *Valvata piscinalis*, *Anisus contortus*, *Armiger cristata*, *Acroloxus lacustris*, *Anisus vortex*, *Anisus leucostoma* and *Radix balthica* (synonym *Lymnaea peregra*). These species are common in small lakes in Denmark, and the fauna is typical of early Holocene deposits in Denmark (Johansen 1904). However, the record from Hareskovene provides one of the first well dated records of the immigration of these species to Denmark. The early Holocene lake fauna also included *Cristatella mucedo*, *Erpobdella* sp., *Plumatella* sp. and the fishes *Gasterosteus aculeatus* and *Scardinius erythrophthalmus*.

Directly above zone 5, a thin layer of sub-recent leaves of *Fagus sylvatica* was found. We suggest that peat digging transformed a former bog into a lake during the 1800s and estimate that 5000–7000 m^3 of peat may have been removed from Søndre Kobberdam.

Immigration history

According to the local deglaciation chronology, the region became free of active glacier ice between 16 000 and 17 000 years ago (Houmark-Nielsen *et al.* 2012). However, the oldest sediments with plant remains are dated to about 13 600 years BP (Table 1). The lack of older plant remains is best explained by assuming that the landscape was characterised by widespread occurrences of stagnant ice, which meant that the landscape was highly unstable and plants had great difficulties to gain a foothold. If the lake basin formed because of melting of a stagnant ice body, this could also explain the lack of older sediments.

It is a common feature of Danish lakes that sedimentation did not begin until several millennia after the last deglaciation. Similarly, the oldest ages obtained for late glacial plant remains from Denmark are several millennia younger than the last deglaciation (e.g. Bennike & Jensen 1995; Korsager *et al.* 2003; Mortensen *et al.* 2011, 2014b) and the oldest age of reindeer (*Rangifer tarandus*) remains from Sjælland is about 14 000 years BP (Aaris-Sørensen *et al.* 2007). Reindeer was the most common large herbivore during the late glacial in Denmark.

The deglaciated area around Søndre Kobberdam was colonised by pioneer taxa in the early Allerød. The dwarf-shrubs *Dryas octopetala*, *Betula nana* and *Salix polaris* and the herbs *Luzula* sp. and *Juncus* sp. were among the first to arrive. These species are among the first immigrants after the last deglaciation in Denmark (Bennike *et al.* 2004). *Betula pubescens* was the first tree to arrive, with the oldest find dated to *c.* 13 330 years BP. This is somewhat later than at the few other sites in eastern Denmark where the timing of its arrival has been dated to between 13 700 and 13 600 years BP. Unstable soils around Søndre Kobberdam may have delayed the local spread of tree birch. The dating confirms that tree birch did not arrive until the Middle Allerød, as concluded by Mortensen *et al.* (2014a). *Populus tremula* was present in the late Allerød, but it was extremely rare. During the Younger Dryas woodland was replaced by an open tundra landscape with dwarf-shrub heaths with *Betula nana*, *Dryas octopetala*, *Salix* sp. and *Empetrum nigrum*. This landscape type may have persisted from the onset of the Holocene warming until woodland started to dominate about 11 000 years BP. The next new tree to arrive was *Pinus sylvestris*, with the oldest find dated to *c.* 11 000 years BP. Pollen grains of *P. sylvestris* are abundant in late glacial sediments in Denmark, but so far there are no records of macrofossil finds, and the pollen is probably long-distance transported from the south or east. However, *Pinus sylvestris* macrofossils have been reported from late glacial lake sediments from Blekinge in south-eastern Sweden (Wohlfarth *et al.* 2017) and it may be speculated that it was easier for *Pinus sylvestris* to spread to the rocky terrain in Blekinge than to the unstable soft sediment terrain of Sjælland.

Among the reed plants, *Carex rostrata* arrived at Søndre Kobbberdam in the Allerød, and *Carex paniculata* and *Cladium mariscus* in the early Holocene at *c.* 10 800 years BP. The water plants *Ranunculus* sect. *Batrachium*, *Potamogeton perfoliatus*, *Potamogeton filiformis*, *Myriophyllum alterniflorum*, *Hippurus vulgaris* and *Ceratophyllum demersum* arrived in the Allerød; the latter species is new to the late glacial flora of Denmark. The early Holocene flora of water plants includes *Potamogeton natans*. Among animals in the Søndre Kobberdam, *Piscicola geometra*, *Cristatella mucedo* and *Perca fluviatilis* arrived in the Allerød, and during the early Holocene a rich fauna of mollusc became established together with the fishes *Gasterosteus aculeatus* and *Scardinius erythrophthalmus*.

Conclusions

After the last deglaciation of north-eastern Denmark, it took several millennia before vegetation spread, probably due to unstable soils and widespread occurrence of stagnant ice. During the late glacial and early Holocene, the landscape around Søndre Kobberdam in Hareskovene in eastern Denmark changed markedly. The early and middle Allerød landscape was tundra-like and treeless, with pioneer vegetation that included the dwarf-shrubs *Dryas octopetala* and *Betula nana*. During the late Allerød period *Betula pubescens* woodlands with rare *Populus tremula* characterised the area, and the lake supported a rich flora. The lake fauna included the fish *Perca fluviatilis*. During the Younger Dryas a tundra-like vegetation returned, which prevailed during the earliest part of the Holocene. The first trees that spread in the early Holocene was *Betula pubescens*, *Populus tremula* and *Pinus sylvetris*. The early Holocene fauna included a rich and diverse fauna of freshwater molluscs that thrived in the carbonate-rich waters. *Cladium mariscus* and *Carex* spp. grew along the lake shore.

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