Macrofossil studies of Lateglacial sediments from Regstrup, north-west Sjælland, Denmark

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Studies of macrofossils indicate that the vegetation near Regstrup in north-west Sjælland, Denmark, from *c.* 13 600 to 13 500 cal. years BP was dominated by dwarf-shrub heaths. *Betula pubescens* (downy birch) arrived at *c.* 13 500 cal. years BP and became common after *c.* 13 200 cal. years BP. Open forests with *B. pubescens* and *Populus tremula* (aspen) dominated until *c.* 12 500 cal. years BP, indicating that an Allerød-type environment persisted for *c.* 350 years after the cooling at the onset of the Younger Dryas, which is dated to *c.* 12 850 years BP in ice cores from Greenland. Betula nana was common after *c.* 12 500 cal. years BP, indicating a return to a tundra-like landscape with dwarf-shrub heaths. The fauna included *Rangifer tarandus* (reindeer), *Castor fiber* (Eurasian beaver) and possibly *Lemmus lemmus* (Norway lemming). The lake deposits contain remains of many species of aquatic plants and animals, including three species of fish. The flora and fauna indicate that the lake water was fairly nutrient-rich and alkaline.

Keywords: Lateglacial, Allerød, Younger Dryas, vegetation history, fauna history, Denmark.

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Prior to the extension of the Holbæk highway towards the west, Museum Vestsjælland conducted archaeological investigations. South of the village Regstrup, two small basins with Lateglacial sediments were encountered (Fig. 1). During the excavations, a fragment of a small antler and a mandible of reindeer (*Rangifer tarandus*) were found, as well as jaws with teeth of pike (*Esox lucius*), bones and scales of perch (*Perca fluviatilis*) and a leaf of *Dryas octopetala*. The fauna and flora, thus, indicated a Lateglacial age and finds of a scraper of flint and some flint flakes show that hunters visited the area.

The basins probably formed after the last deglaciation by melting of bodies of buried stagnant ice. Plant and animal remains were well-preserved and it was decided to conduct macrofossil analyses of samples that had been collected during the archaeological field work. The samples were taken from open sections from trenches.

Studies of the vegetation history of Denmark go back almost 200 years, but many details of Lateglacial and Holocene vegetation and environmental changes are still poorly known (Bennike & Mortensen 2018). The aim of this paper is to describe and interpret the results of the macrofossil studies of the sediments from Regstrup, from small basins in north-west Sjælland, Denmark. The study is the first radiocarbon dated macrofossil study of Lateglacial deposits from this region (Mortensen *et al.* (2014a). We compare the results with other recent detailed palaeoecological studies of Lateglacial deposits in Denmark (Bennike *et al.* 2004; Mortensen *et al.* 2011, 2014a, b; Fischer *et al.* 2013; Bennike & Mortensen 2018; Wiberg-Larsen *et al.* 2019).

Study area

The studied basins are located in north-western Sjælland, *c.* 9 km south-west of Holbæk (Fig. 1). The basins are small and measure only some tens of metres across. Because of the small size of the basins, they are suitable for plant macrofossil analyses. The sites are located *c.* 32 m above sea level and the basins may have formed as bodies of stagnant ice melted – or perhaps simply as groundwater filled depressions in the glacial landscape. The geographical coordinates of the sites are 55.66°N, 11.61°E (site 1, all samples except JP335) and 55.66°N, 11.64°E (site 2, sample JP 335). The distance between the basins is 1400 m.

The region was glaciated during the last glacial maximum and was deglaciated about 17 000 years BP, according to cosmogenic surface exposure dating of large erratic boulders from the region (Houmark-Nielsen *et al.* 2012). However, bodies of stagnant ice characterised the region for a long time after active glacier ice disappeared. The pre-Quaternary strata of the region are dominated by Paleocene clay, but Danian limestone and Cretaceous chalk is found to the north and east (Håkansson & Pedersen 1992) and the tills in the region are rich in fragments of limestone and chalk. The Regstrup area is dominated by clayey till with small areas of glaciofluvial sand (Milthers 1943) and nowadays by farmland with villages and it has probably been deforested for several millennia. The natural vegetation would probably be *Fagus sylvestris* dominated forests on well-drained soils and *Alnus glutinosa* dominated forests on wet soils. The climate is temperate; the mean July temperature was 16.2°C and the mean annual precipitation was 584 mm during the period from 1961 to 1990 (DMI 2019).

Methods

Profiles through the Lateglacial lake sediments were exposed by excavating trenches through the basins and the sediments were mapped and described by archaeologists from Museum Vestsjælland. Samples were collected from open sections. The samples consisted of a 1 m long sediment monolith and several kg-large bulk sediment samples. The monolith was carefully cleaned, and 50 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 sub-samples on a 0.1 mm sieve. The residues left on the sieves were transferred to petri dishes and analysed using a dissecting microscope. Plant and animal remains were identified using reference material as well as keys and illustrations in various books and scientific papers such as Kaiser (1977), Henderson (1990), Brooks *et al.* (2007) and Rinne & Wiberg-Larsen (2017).

Selected identified macrofossils of terrestrial plants from four levels from the monolith and from one of the bulk samples were dried and submitted for accelerator mass spectrometry (AMS) radiocarbon dating. Dating was carried out at the Ångström Laboratory, University of Uppsala and at Aarhus AMS Centre, Aarhus University. The samples were treated with HCl to remove carbonates and with NaOH to remove humic acids, which may represent contamination

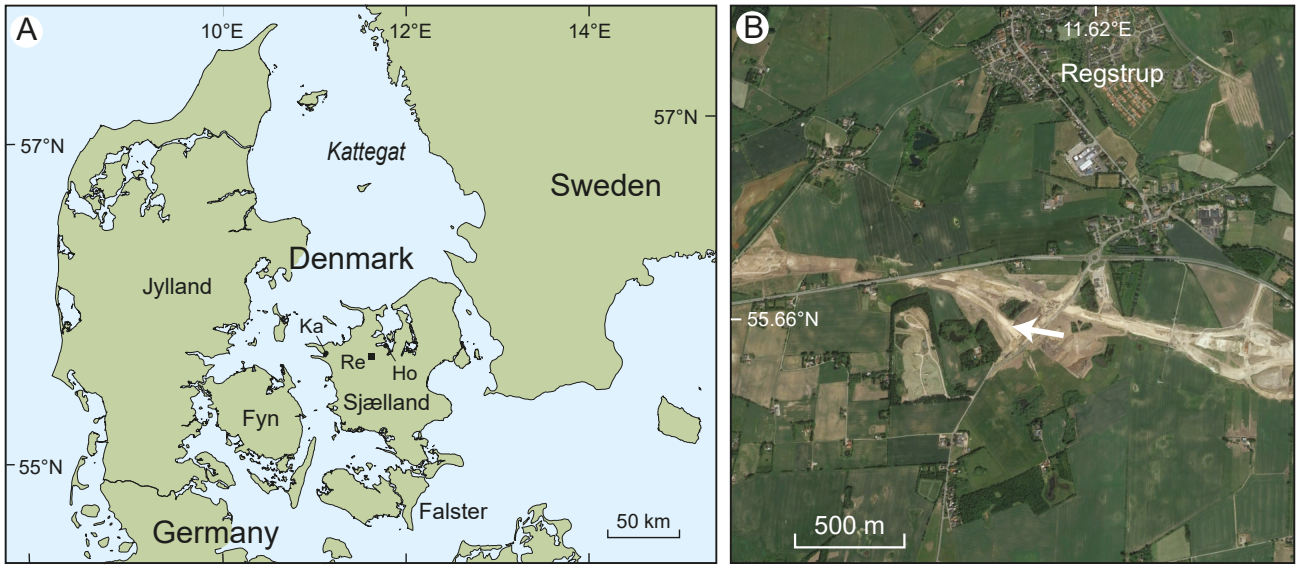

Fig. 1. A. Map of Denmark showing the location of the study sites. Re: Regstrup, Ho: Holbæk, Ka: Kalundborg. **B.** Google Earth satellite image of the study area.

Table 1. AMS radiocarbon age determinations from Regstrup, north-west Sjælland, Denmark
The samples are from site 1, except JP335 that is from site 2

Laboratory number	Depth cm/sample	Layer	Species	Age (^{14}C years BP)[1]	Calibrated age (years BP)[2]	Cal. age (yrs BP)[3]	Cal. age (years BC)[2]
Ua-58868	38–40	8	*Menyanthes trifoliata*	10514 ± 43	12206–12678	12550	10257–10729
Ua-58869	55–56	8	*Betula pubescens*	10663 ± 44	12514–12738	12691	10565–10789
Ua-58870	76–78	9	*Betula pubescens*	10838 ± 44	12728–12833	12766	10779–10884
Ua-58871	96–98	12	*Betula pubescens*	11726 ± 47	13482–13746	13568	11533–11797
Ua-58872	JP 314	10	*Arctostaphylos uva-ursi*	11367 ± 45	13164–13323	13244	11215–11374
AAR-29889	JP 335	6	*Menyanthes trifoliata*	10912 ± 48	12743–12918	12815	10794–10969
Ua-59941	1082x200		*Rangifer tarandus*	5853 ± 33	6560–6746	6674	4611–4797
Ua-59941	1082x200		*Rangifer tarandus*	5775 ± 99	6318–6791	6575	4369–4842

[1]Radiocarbon ages are reported in conventional radiocarbon years BP (before present = 1950; Stuiver & Polach (1977)).
The C ages have been corrected for isotopic fractionation by normalizing to a δ^{13}C value of –25 ‰.
[2]Calibration to calendar years BP/BC is according to the INTCAL20 data (Reimer et al. 2020). [3]Median probability ages.

from younger deposits. A reindeer antler was also dated, using the collogen fraction. The radiocarbon ages were calibrated to calendar years before present (BP) using the CALIB program (Stuiver *et al.* 2021), which calibrates to calendar years according to the INTCAL20 calibration curve (Reimer *et al.* 2020). The widespread occurrence of carbonate-rich glacial deposits in Denmark results in large hard-water effects, and thus it is important to use remains of terrestrial plants or animals for dating. Four samples from the monolith and one sample from the bulk sample were dated (Table 1).

Results and discussion

Sediments, dating and sedimentation rates

The Lateglacial sediments consisted of mineral-rich and organic-rich sediments. The organic-rich sediments were described as peat in the field, but the occurrence of numerous remains of fish and other aquatic animals and plants show that the sediments should be classified as coarse detritus gyttja. The succession at site 1 consisted of sand and gravel, clayey gyttja, calcareous gyttja, detritus gyttja, sandy clay, decomposed peat and clay. At site 2 the succession consisted of grey gyttja, coarse detritus gyttja and decomposed peat.

Four samples from the monolith from site 1 were dated, yielding median probability ages between 12 550 and 13 568 cal. years BP (Table 1). Calibrated ages for the monolith are plotted versus depth in Fig. 2. According to the age–depth curve the sedimentation rate was *c.* 0.25 mm/year in the lower part of the succession, and *c.* 1.52 mm/year in the middle and upper part. The chronology in the middle and upper part of the dated succession is well constrained, whereas the chronology of the lower part of the succession is more uncertain. An endocarp of *Arctostaphylos uva-ursi* from bulk sediment sample JP 314 gave a median probability age of 13 244 cal. years BP, corresponding to the Allerød period. Dating of seeds of *Menyanthes trifoliata* from bulk sample JP 335 from site 2 gave a median probability age of 12 815 cal. years BP, corresponding to an earliest Younger Dryas age (Table 1). Finally, a cast reindeer antler fragment gave a Mid-Holocene age (Bennike *et al.* 2021).

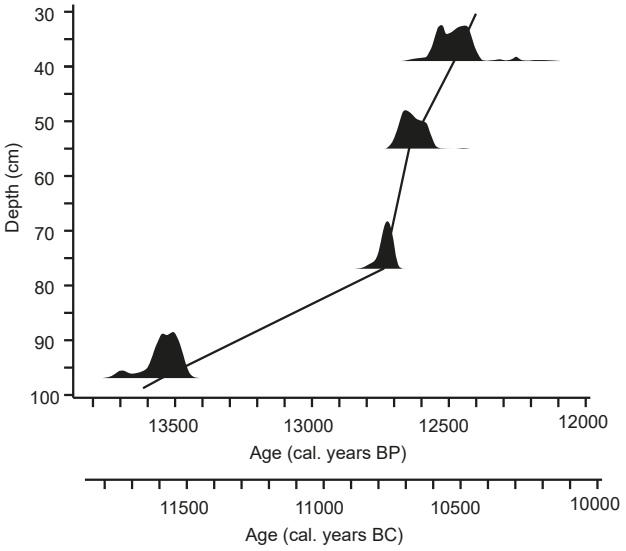

Fig. 2. Age–depth model for the succession from site 1 from Regstrup, north-west Sjælland.

Macrofossils

The results of the macrofossil analyses are presented in a macrofossil concentration diagram (Fig. 3) and in Table 2. The diagram is divided by visual inspection into four local macrofossil assemblage zones that are described and discussed in the following. The upper part of the succession did not contain any macrofossils, hence the diagram only covers *c.* 70 cm.

Zone 1 (13 500–13 600 cal. years BP)

Zone 1 is characterised by the woody plants *Dryas octopetala* and *Betula nana*. In addition, a few remains of *Salix* sp. were found. Herbaceous plants are represented by *Minuartia* sp. and bryophytes are represented by *Distichium* sp. and *Ditrichum* sp., which are often pioneer species on calcareous soils. The bryophyte *Tomentypnum nitens* and the rush *Juncus* sp. often grows in wet soil. Remains of macrolimnophytes are rare and represented by a few endocarps of *Potamogeton natans*, *P. perfoliatus* and *Stuckenia filiformis* (syn. *Potamogeton filiformis*). Aquatic invertebrates are represented by chironomids (head capsules), *Sialis* sp. (alder fly, mandibles) and the small bivalve *Pisidium* sp. Plants and invertebrates began to colonise the small lake and decreasing content of clay, silt and sand in the sediment shows that inwash of minerogenic sediment to the lake decreased. The vegetation around the lake was characterised by dwarf-shrub heaths with *D. octopetala*, *B. nana* and *Salix* sp., with some *B. pubescens*.

Zone 2 (12 650–13 500 cal. years BP)

Betula pubescens remains dominate this zone and in addition, rare remains of *Populus tremula* are found. Remains of *Dryas octopetala* were found in two samples; other woody plants are represented by *Salix* sp. and a single endocarp of *Rubus saxatilis*.

Herbaceous plants are represented by *Minuartia* sp., *Thalictrum alpinum* and *Taraxacum* sp. Plants characteristic of wet soils include *Selaginella selaginoides* that is represented by two megaspores and several species of bryophytes. Aquatic plants are dominated by *Carex rostrata*, in addition fruits of *Ranunculus* sect. *Batrachium* sp., *Hippuris vulgaris* and five species of *Potamogeton* were found. Remains of aquatic invertebrates include egg cocoons of the leaches *Erpobdella* sp. and *Piscicola geometra*, mandibles of the alder fly *Sialis* sp., shells of gastropods and numerous shells of *Pisidium* spp. and statoblasts of the bryozoan *Cristatella mucedo*. The common remains of macrolimnophytes and freshwater invertebrates clearly show that the deposit is of lacustrine origin. The lake housed a rich flora and fauna that indicate that the water was alkaline. Only little clay, silt and sand was washed out into the basin. The vegetation around the lake was dominated by open birch forests with scattered *Populus tremula*, *Dryas octopetala* and other woody plants, herbs and mosses.

Zone 3 (12 500–12 650 cal. years BP)

This zone is also dominated by *Betula pubescens;* in adition remains of *Betula nana* are found and *Populus*

Table 2. Macrofossils in bulk samples from Regstrup, Denmark. The samples are from site 1, except JP335 that is from site 2

	Terrestrial plants															Swamp plants				Aquatic plants																		Aquatic invertebrates								
	Betula nana	*Betula pubescens*	*Populus tremula*	*Salix* sp.	*Arctostaphylos uva-ursi*	*Potentilla* sp.	*Papaver* sect. *Scapiflora*	*Urtica dioeca*	*Selaginella selaginoides*	*Distichium* sp.	*Hylocomium splendens*	*Comarum palustre*	*Climacium dendroides*	*Tomenthyphum nitens*	*Chara* sp.	*Batrachium* sp.	*Menyanthes trifoliata*	*Carex rostrata*	*Alisma plantago-aquatica*	*Nuphar pumila*	*Myriophyllum* sp.	*Hippuris vulgaris*	*Sparganium erectum*	*Potamogeton natans*	*Potamogeton alpinus*	*Potamogeton perfoliatus*	*Potamogeton praelongus*	*Potamogeton obtusifolius*	*Potamogeton pusillus*	*Stuckenia filiformis*	*Erpobdella* sp.	*Piscicola geometra*	*Valvata cristata*	*Valvata piscinalis*	*Hippeutis complanatus*	*Stagnicola palustris*	*Armiger crista*	*Pisidium* sp.	*Cristatella mucedo*
JP 314	–	a	12	–	2	–	–	–	1	–	c	–	1	–	a	–	–	–	–	–	–	1	1	6	–	5	–	–	–	8	2	–	1	1	–	–	2	a	c
JP 320	2	a	–	1	–	–	–	–	–	1	–	–	–	–	r	–	–	a	–	–	1	1	–	–	–	–	–	–	–	1	–	c	c	–	–	–	a	–
JP 321	–	a	–	–	2	–	–	–	1	–	–	–	–	–	1	–	–	a	1	–	1	–	–	c	–	2	–	–	–	r	–	2	1	c	–	–	–	c	a
JP 322	a	a	c	r	–	5	–	–	–	–	r	1	–	–	a	1	a	a	–	–	–	1	2	c	5	–	1	–	–	1	1	–	–	r	2	–	–	r	a
JP 332	2	4	–	–	–	–	–	–	–	–	–	–	–	1	r	1	–	a	–	–	–	–	–	8	–	4	–	–	–	1	–	–	–	c	–	–	–	a	3
JP 334	–	c	1	–	–	–	–	–	–	–	–	–	–	–	r	1	6	c	–	–	1	–	–	3	5	–	–	–	–	–	1	–	–	–	–	–	–	–	r
JP 335	–	c	–	–	–	–	1	6	–	–	–	–	–	–	r	10	2	c	–	1	–	7	–	c	c	–	–	1	c	–	1	1	r	c	–	2	–	c	3

r: rare, c: common, a: abundant

tremula remains are surprisingly common. Herbaceous plants are only represented by two achenes of *Potentilla* sp. Remains of aquatic plants are also in this zone dominated by achenes of *Carex rostrata* and in addition, seeds of *Menyanthes trifoliata* are frequent, whereas *Myriophyllum* sp. remains are rare. *Potamogeton* spp. are represented by the same five species as in zone 2. Invertebrate remains are confined to an egg capsule of *Erpobdella* sp., a few mandibles of *Sialis* sp. and some statoblasts of *Cristatella mucedo*. The vegetation around the lake was still dominated by *Betula* forests, but *Populus tremula* played an important role. Dwarf shrubs and herbs were apparently rare and the forests around the lake may have been so dense that heliophytes became rare.

It should be noted that no remains of *Pinus sylvestris* were recorded. In Danish Lateglacial deposits pollen grains of *Pinus* are often abundant, and it has been proposed that pine had immigrated to Denmark during the Allerød period (Iversen 1947, 1954, 1973). However, so far no macrofossils of pine have been reported (Mortensen *et al.* 2014a) even though macrofossil studies have been conducted from a fairly large number of Lateglacial sites in Denmark. Thus it appears that pine did not grow in Denmark during the Lateglacial.

Zone 4 (12 400–12 500 cal. years BP)

In zone 4 only few remains of *Betula pubescens* were found. Instead, remains of *Betula nana* are common, and *Populus tremula* is missing. A few remains of *Potentilla* sp. and *Selaginella selaginoides* were found. Macrolimnophytes are represented by *Ranunculus* sect. *Batrachium* sp., *Menyanthes trifoliata* and *Carex rostrata* that are found in the lower part of the zone, where *Cristatella mucedo* also occurs. Apparently, macrolimnophyte vegetation disappeared from the lake during zone 4, and the sediment changes from gyttja to poorly sorted gravel that was probably deposited in the lake basin due to solifluction. The vegetation around the lake became more open and tree birch was replaced by dwarf birch; the warmth-demanding *P. tremula* disappeared. The area was, thus, characterised by an open tundra landscape with dwarf shrub heaths, presumably due to cooling during the Younger Dryas period.

The shift from *Betula pubescens* dominated forests with *Populus tremula* to *Betula nana* dominated tundra is dated to *c.* 12 500 cal. years BP. In the Greenland ice cores the shift from the relatively warm Greenland Interstadial 1 to the cold Greenland Stadial 1 is dated to *c.* 12 850 years BP. This raises the following questions: Are the dates from Regstrup too young or did the climate change occur at different times in Greenland and Denmark? Or did birch forests persist for some time into the Younger Dryas period?

There are only few well-dated Lateglacial sites from eastern Denmark. However, Mortensen *et al.* (2014b) studied Lateglacial sediments from Hasselø on Falster and dated the transition from an Allerød-type vegetation to a Younger Dryas-type vegetation to *c.* 12 575 cal. years BP, close to the result from Regstrup.

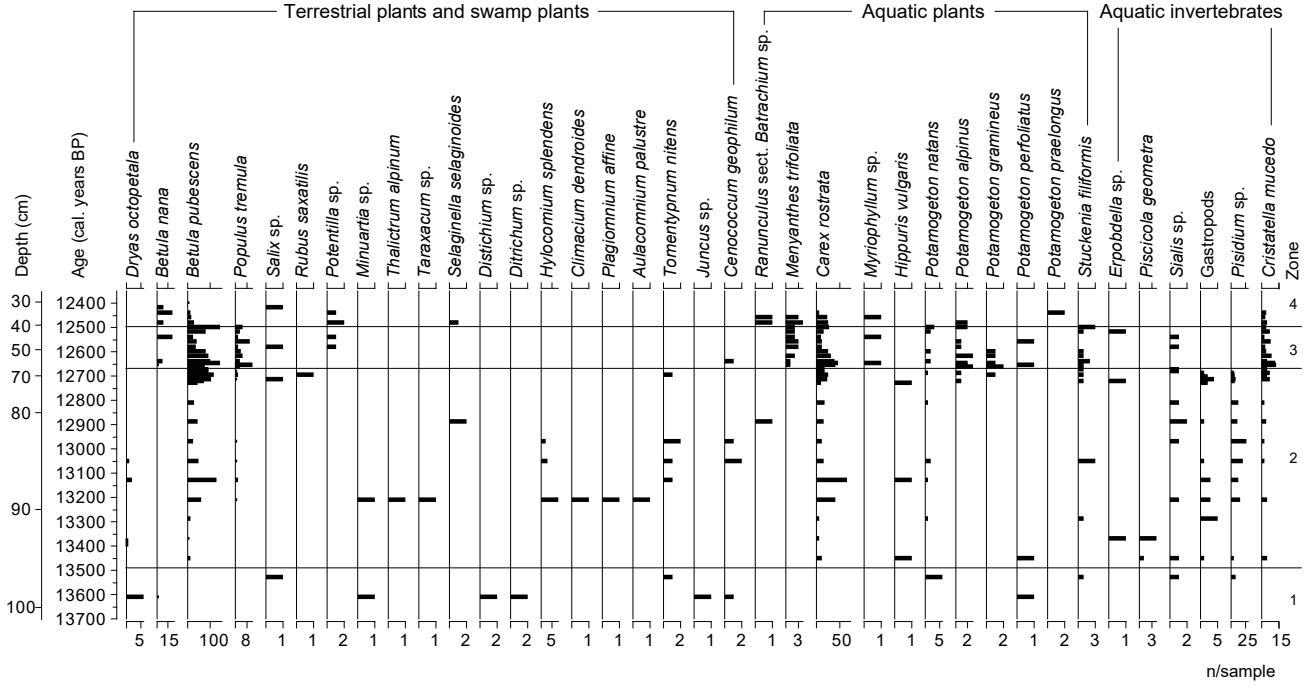

Fig. 3. Simplified macrofossil concentration diagram for site 1 from Regstrup.

Analyses of bulk samples

The results of analyses of large bulk samples appear from Table 2. The common occurrence of fresh water aquatic plants and animals show that the samples consist of detritus gyttja. Because of the large sample size, a number of species was found that did not appear in the monolith samples. Among the plants are *Arctostaphylos uva-ursi*. Endocarps of this dwarf-shrub are fairly frequent in Lateglacial deposits, in particular from the Allerød period. A radiocarbon age of 13 244 cal. years BP was obtained on *A. uva-ursi* endocarps from Regstrup (Table 1).

Achenes of the bog plant *Comarum palustre* are also fairly common in Lateglacial depsoits in Denmark. In contrast, fruits of *Sparganium erectum* have to our knowledge not previously been reported from Lateglacial deposits in Denmark. There is only a single previous record of *Alisma plantago-aquatica* from Lateglacial deposits; from Trollesgave near Holmegårds Mose in southern Sjælland (Fischer *et al.* 2013). The latter two species are relative warm demanding, but it is not surprising that they grew in Denmark because other species with similar temperature requirements have been reported (Johansen 1904; Iversen 1954). Based on beetle remains it is estimated that the mean summer temperature was 9 to 11°C during the Allerød period, and somewhat higher during the Bølling period (Coope *et al.* 1998).

Because remains of *Rangifer tarandus* (reindeer) and *Esox lucius* (pike) were found during the excavation we hoped that more vertebrate remains would turn up in the samples. However, in addition to *E. lucius* remains, we only found a pelvic spine of the small fish *Gasterosteus aculeatus* (stickleback).

The bulk sample JP 335 from site 2 that was dated to 12 770 cal. years BP (early Younger Dryas) was rich in remains of insect larvae (Table 3). The fauna was dominated by head capsules of larvae of chironomids (non-biting midges), but the sample also contained frequent remains of Trichoptera (caddisflies), *Sialis* (alderflies) and oribatid mites. The fauna resembled an invertebrate fauna recorded from submarine Lateglacial lake deposits from the Kattegat (Wiberg-Larsen *et al.* 2019). The lake deposit at site 2 near Regstrup was of limited extent, but the insect fauna indicates that the lake may have been fairly large. The record of *Simulium* cf. *equinum*, confined to running waters, indicates the presence of an inlet stream that might have been fairly large (as this species primarily inhabits larger streams). Several of the taxa such as *Sialis sordida*, *Micropsectra insignilobus*-type, *Micropsectra radialis*-type and *Zalutschia* type B can be classified as northern taxa that indicate lower temperatures than at present, pointing at cooling in the beginning of the Younger Dryas period. *Corynocera ambiqua*, which was the most common chironomid has also been considered an indicator of cold conditions, but the species is common in Denmark at the present (Brodersen & Lindegaard 1999).

Table 3. Arthropod remains from sample JP 335 from Regstrup, Denmark. The sample was dated to *c.* 12 800 cal. years BP

Group	Taxon	Remains	Notes
Oribatida	Oribatidae A, cf. *Hydrozetes*	4 exoskeletons	
	Oribatidae B	7 exoskeletons	Large, dark
Megaloptera	*Sialis sordida* *	4 frontoclypea	
	Sialis sp.	22 mandibles	
Trichoptera, Polycentropodidae	*Cyrnus flavidus*	1 frontoclypeus	
Trichoptera, Phryganeidae	*Agrypnia* cf. *varia*	3 frontoclypea	
Trichoptera, Limnephilidae	*Chaetopteryx sahlbergi/villosa*	1 frontoclypeus	
	Limnephilus A	15 pronotae	The frontal 1/3 part is darker than the rest
	Limnephilus B	5 frontoclypea	*Asynarchus* cf. *lapponicus* *
Simuliidae	*Simulium* cf. *equinum*	1 frontoclypeus	
Chironomidae[1]	*Chironomus anthracinus*-type	21 head capsules	
	Corynocera ambiqua (*)	65 head capsules	
	Micropsectra insignilobus-type *	18 head capsules	
	Micropsectra radialis-type *	3 head capsules	
	Chaetocladius type B	1 head capsule	
	Psectrocladius sordidellus-type	1 head capsule	
	Zalutschia type B *	1 head capsule	

[1] The nomenclature of Chironomidae follows Brooks *et al.* (2007). * Northern taxon.

Notes on selected species

Species living on land

Betula pubescens was represented by numerous nutlets and catkin scales. Hence, bulk samples JP 314 and JP 322 each contained at least 100 nutlets and 50 catkin scales. The rich occurrence of the species shows that the vegetation around the lake was characterised by birch forests during the time period from *c.* 13 200 to *c.* 12 500 cal. years BP. The lowest sample from the monolith contained a few remains of *B. pubescens*; this sample is dated to *c.* 13 600 cal. years BP. At Slotseng in southern Jylland the oldest macrofossils of *B. pubescens* were dated to *c.* 13 500 cal. years BP (Mortensen *et al.* 2011), at Hasselø on Falster to *c.* 13 600 cal. years BP (Mortensen *et al.* 2014b), at Staalsø near Kalundborg in north-west Sjælland to *c.* 13 700 cal. years BP (Mortsensen & Bennike, unpublished data), at Martin Holms Mose on the island of Samsø in central Denmark to *c.* 13 600 cal. years BP (Mortensen *et al.* 2014a), and at Søndre Kobberdam in north-east Sjælland to *c.* 13 330 cal. years BP (Bennike & Mortensen 2018). These ages imply that the species arrived in Denmark during the mid-Allerød. *Betula pubescens* was the first tree species that colonised Denmark after the last deglaciation, however, the species can occur as a fairly large tree, a small tree or a bush, depending on the local growth conditions. It is impossible to determine the growth form from fossil nutlets or catkin scales.

Danish lake deposits rich in remains of *Betula pubescens* are usually referred to the Allerød period. However, the radiocarbon ages from Regstrup show that *Betula pubescens* was also common in the early part of the Younger Dryas period at this site. Mortensen et al. (2014b) showed that the Allerød environment in Falster in south-eastern Denmark continued until *c.* 12 575 cal. years BP before the ecosystem collapsed and was replaced by a Younger Dryas type vegetation. The same appears to be the case in the Regstrup region in north-west Sjælland. It also appears that *Betula pubescens* survived into the Younger Dryas near Birkerød in north-east Sjælland (Mortensen et al. 2014a).

Betula nana was also represented by numerous nutlets and catkin scales. The species does not grow in Denmark anymore, but it occurs in bogs in southern Sweden and is common in heaths in northern Scandinavia and in low arctic regions. Remains of this shrub are common in Lateglacial deposits in Denmark and *Betula nana* was among the first woody plants to immigrate after the last deglaciation. There are also a few Early Holocene finds of this light-demanding species from Denmark (Jensen 1985; Bennike & Jensen 2011).

Populus tremula remains were surprisingly common in the samples from Regstrup. Until now only few fossils of this species were found in Lateglacial deposits in Denmark. A few pollen grains were reported from a clay pit near Ruds-Vedby in western Sjælland (Krog 1954) and a few scattered finds of macrofossils have been reported (e.g., Nielsen & Sørensen 1992; Bennike & Mortensen 2018). All securely dated finds from Denmark come from the Allerød period. However, at Regstrup the species continued to grow until 12 500 cal. years BP, i.e. in the early part of the Younger Dryas period. The beginning of cold conditions is dated to *c.* 12 850 years BP in ice cores from Greenland (Rasmussen *et al.* 2009) and the invertebrate fauna from sample JP 335 also indicate relatively cold conditions at *c.* 12 800 cal. years BP, as mentioned above.

Danish Lateglacial finds of *P. tremula* are confined to the southern and eastern part of Denmark, where summer temperatures are higher than in the north-western part of the country. The samples from Regstrup only contained bud scales – no catkin scales were found. This implies, together with the sparse occurrence of pollen grains reported in earlier studies of Lateglacial deposits that flowering and in particular fruiting were uncommon. Vegetative reproduction is currently common in *P. tremula* near the northern range limit of the species; it was probably also a common phenomenon in Lateglacial populations of the species in Denmark.

A single fruit stone of *Rubus saxatilis* was recorded. The species has previously been reported from Allerød-period layers from the classical Allerød site, from Frihedens Mose and from Hasselø on Falster in south-eastern Denmark (Hartz 1902; Jessen 1920; Mortensen et al. 2014b).

Arctostaphylos uva-ursi was represented by four endocarps. The species is rare in Denmark at present, but common in northern Scandinavia where it grows in dwarf-shrub heaths. Fruit stones of the species are fairly frequent in Allerød layers from Denmark, but it is also recorded from Younger Dryas layers (Bennike & Jensen 1995; Bennike *et al.* 2004a). Five finds from eastern Denmark have been dated to the mid-Allerød (Bennike *et al.* 2020; Bennike unpublished data).

A few leaf fragments of *Dryas octopetala* were found in the lower part of the monolith. *Dryas octopetala* is a common plant in Arctic regions, but the species may also grow in open non-shaded areas south of the Arctic. It prefers carbonate-rich soil and it can thrive in nutrient-poor conditions because it lives in symbiosis with nitrogen-fixating micro-organisms. The species was common in Denmark during the Lateglacial, but the forest in the southern and eastern parts of the country were so dense during the Allerød period that the species almost disappeared. In the north-western part of Denmark, the species was one of the dominating plants throughout the Allerød period (Bennike *et*

al. 2004b; Mortensen et al. 2014a). From north-western Sjælland the species has been reported from Vinde-Helsinge Mose near Gørlev, Ruds-Vedby (Krog 1954) and Raklev near Kalundborg (Bennike & Barry 2009).

Ten small achenes of *Potentilla* could not be identified to species. Most species of *Potentilla* are small herbs that grow in dry soils. The genus *Potentilla* includes many species in Arctic and northern boreal regions.

Papaver sect. *Scapiflora* sp. (arctic poppy) was represented by a single seed. To our knowledge it is the first record of this taxon from Lateglacial deposits in Denmark.

Six achenes of *Urtica dioeca* (common nettle) were found in sample JP 335. The species is rare in Lateglacial Danish deposits (Jensen 1985); it is nitrophilous and indicate nutrient-rich soils. Such soils may have formed locally due to the presence of reindeers or roosting birds.

A single achene belonged to *Comarum palustre* that grows in wet soil in bogs and along lake shores, in boreal or low-arctic climates. The species has been recorded from several Lateglacial sites in Denmark.

Thalictrum alpinum was also represented by a single achene. *Thalictrum alpinum* is a small heliophilous herb that today grows in heaths and copses in arctic and alpine regions (Fig. 4). Achenes of the species are rare in Lateglacial deposits, but they have been reported from Hasselø on the island of Falster in south-eastern Denmark, from sediments dated from 12 600 to 14 200 cal. years BP (Mortensen *et al.* 014b) and from sites in England and elsewhere in north-western Europe (Tralau 1963).

Taraxacum sp. was represented by a fragment of a nutlet. *Taraxacum* is a rare record for Lateglacial deposits in Denmark, but it has likewise been reported from Hasselø, in a sample dated to *c.* 13 700 cal. years BP. *Taraxacum* spp. are today fairly common in arctic regions, often growing in pioneer communities

A few megaspores of the small plant *Selaginella selaginoides* were found, the megaspores are fairly common in Danish Lateglacial deposits. The species grows in moist or wet sites, for example in calcareous mires.

The flora from Regstrup includes the bryophytes *Climacium dendroides*, *Hylocomium splendens*, *Aulacomnium palustre*, *Tomentypnum nitens*, *Calliergon* sp., *Ditrichum* sp., *Distichium* sp., *Plagiomnium affine*, *Bryum* sp. and *Sphagnum* sp. that have previously been recorded from a few Lateglacial sites in Denmark (Jessen 1924; Odgaard 1981). Most of the species grow in mires and several of them, especially *Distichium* sp., are calciphiles. Remains of *Sphagnum* are rare in Lateglacial deposits, presumably because most species of the genus grow in acid soils, which were rare during the Lateglacial.

Rangifer tarandus (reindeer). During the excavation two fragments of *R. tarandus* were found in layer 7. One is a fragment of a lower jaw of an animal that was 5½ to 6½ years old (Magnussen 2019). The other is a fragment of a small, slender cast antler probably from a female reindeer that was found in the uppermost part of layer 7. The antler was dated to *c.* 6600 cal. years

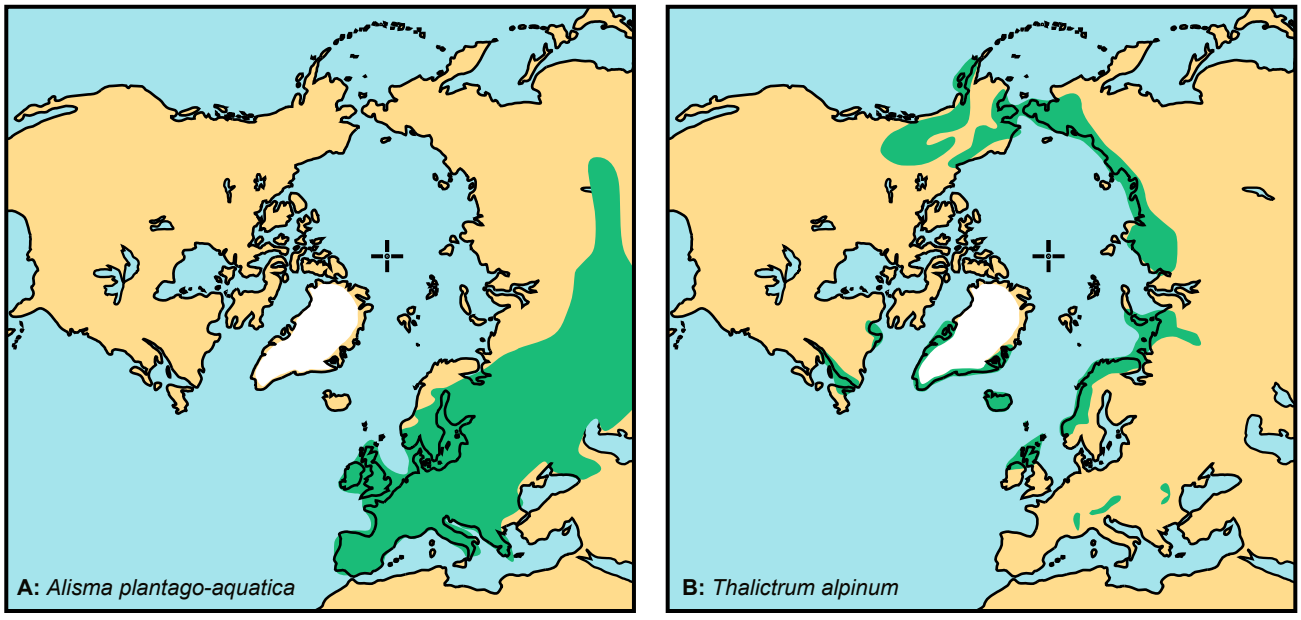

Fig. 4. Modern-day distribution of a warmth-demanding species (**A:** *Alisma plantago-aquatica*) and a cold-adapted species (**B:** *Thalictrum alpinum*), of which remains were found in the Lateglacial sediments from Regstrup. Modified from Hultén & Fries (1986).

BP (Table 1). This most surprising age for a Danish reindeer find was discussed by Bennike *et al.* (2021). The identification based on a visual inspection of the antler fragment was confirmed by protein sequencing by liquid chromatography tandem mass spectrometry (LC-MS/-MS). The reindeer antler may have come to Sjælland from Norway or Sweden as a result of trade.

Layer 7 with the jaw fragment is dated to the Younger Dryas. The former presence of reindeer in Denmark was discussed by Degerbøl & Krog (1959) and by Aaris-Sørensen *et al.* (2007). Radiocarbon dating of reindeer remains shows that the species lived in Denmark during the time period from *c.* 14 500 to 10 300 cal. years BP. This means that it persisted in Denmark into the early part of the Holocene. During this period temperatures were increasing but the increase was interrupted by the cold Preboreal oscillation centred at *c.* 11 400 cal. years BP (Björck *et al.* 1997). Several reindeer remains have previously been reported from north-west Sjælland, but only one find has been radiocarbon dated; it gave an age of *c.* 11 800 cal. years BP (Aaris-Sørensen *et al.* 2007).

Castor fiber (Eurasian beaver) was represented by a lumbar vertebra from layer 8. Two samples of plant macrofossils from this layer yielded ages of *c.* 12 550 and 12 690 cal. years BP (Table 1), corresponding to a mid-Younger Dryas age. Bones of beaver or beaver-gnawed branches have been reported from a few localities with Lateglacial sediments in Denmark. None of these finds are directly dated but they are referred to the Allerød period (Aaris-Sørensen 1995). Thus, the find from Regstrup may be the first record of bones of the species from Younger Dryas sediments. The beaver is primarily a boreal species that lives in rivers and streams, where it constructs dams.

?*Lemmus lemmus* (Norway lemming). A humerus fragment of a small rodent was with hesitation referred to *Lemmus lemmus*. Remains of the species have previously been recorded from Middle and Late Weichselian deposits in Denmark (Bennike *et al.* 1994; Heiberg 1995; Aaris-Sørensen 1995).

Aquatic plants

Three fruits of *Sparganium erectum* were found; the species appears to be new to the Lateglacial flora of Denmark. *Sparganium erectum* is a fairly warmth-demanding spccies but there are scattered finds of it from northern Sweden and northern Finland (Hultén & Fries 1986).

One fruit of *Alisma plantago-aquatica* was recorded, the species is another warmth-demanding plant, extending north almost to the arctic tree line (Fig. 4). It grows in shallow water along the shores of nutrient-rich lakes, in ponds and streams, and it is often one of the first water plants to colonise newly formed ponds (Moeslund *et al.* 1990). The species has been recorded from Lateglacial deposits from Holmegårds Mose in southern Sjælland (Fischer *et al.* 2013).

Three seeds of *Nuphar pumila* were found in JP 335. This species of water-lily is rare in Lateglacial deposits in Denmark (Jensen 1985). It is relatively warmth-demanding, but the geographical range extends to the arctic treeline.

Seven species of pondweeds (*Potamogeton* and *Stuckenia*) were found – all of them have been recorded from Lateglacial deposits in Denmark before (Jensen 1985).

Fruits of *Carex* were abundant in some of the samples. Some of the fruits had the perigynium preserved and could be identified to *Carex rostrata*, and most of the fruits without perigynium probably also belong to this species. The species grows in shallow water in lakes or in mires. Fruits of *C. rostrata* are common in Lateglacial deposits from Denmark.

Aquatic animals

Aquatic invertebrates included gemmules of Spongillidae indet., egg cocoons of leaches (*Erpobdella* sp. and *Piscicola geometra*). These taxa are common in Lateglacial deposits in Denmark.

Cladocerans were represented by ephippia of *Daphnia pulex*, *Simocephalus vetulus* and head shields and shells of *Chydorus sphaericus*. *Daphnia pulex* and *Chydorus sphaericus* remains are common in Lateglacial deposits, whereas *Simocephalus vetulus* remains are rare. Ephippia of *S. vetulus* have previously been reported from southern Sjælland (Poulsen 1944).

Ostracodes were represented by *Candona* sp., *Limnocythere* sp., *Cyclocypris laevis* and *Herpetocypris reptans*. The latter species appears to be new to the Lateglacial fauna of Denmark, but it has been reported from Lateglacial deposits in Germany (Absolon 1973). It is a warmth-demanding species that is found today to the north to Trondheim in Norway (Sars 1925). It mainly lives in nutrient-rich ponds and small lakes rich in macrophytes.

Freshwater molluscs were represented by several species of gastropods and bivalves such as *Valvata cristata*, *V. piscinalis*, *Ampullaceana balthica* (syn. *Radix balthica*, *Lymnaea peregra*), *Stagnicola palustris* (syn. *Lymnaea palustris*), *Gyraulus laevis*, *Hippeutis complanatus*, *Armiger crista*, *Pisidium* spp. and *Sphaerium* sp. All species have previously been recorded from Danish Lateglacial lake deposits (Johansen 1904), although *Stagnicola palustris* only rarely.

Statoblasts of three bryozoan taxa were found: *Cristatella mucedo*, *Plumatella* sp. and *Fredericella* sp. The latter is rarely recorded but the statoblasts are common in lake deposits. The taxa have wide geographical ranges but in the Arctic they are confined to the low arctic.

Finally, remains of three fish species were recorded:

Gasterosteus aculeatus, *Esox lucius* and *Perca fluviatilis*. *G. aculeatus* (three-spined stickleback) was represented by a pelvic spine in sample JP 320. Remains of the species have been reported from the classical Lateglacial Bølling site in Jylland (Rosenlund 1976) and from northern Sjælland (Bennike & Mortensen 2018; Bennike *et al*. 2020). *Gasterosteus aculeatus* can be found in large numbers in shallow, vegetation-rich water of lakes where it is an important prey for larger fish and birds. It is widely distributed in temperate and low-Arctic regions in the northern Hemisphere.

Esox Lucius (pike) was represented by 127 bones, which represent at least four individuals. The total length of the individuals was about 30 to 70 cm. *Perca fluviatilis* (perch) was represented by 454 fragments, of which 400 were scales. Remains of at least three individuals are present in the material – one of them was *c.* 32 cm long, the others somewhat smaller. Both pike and perch have been reported from fairly many sites with Lateglacial deposits in Denmark (Rosenlund 1976; Skousen 2008). Pike and perch may be found in a wide range of habitats, but they are most common in vegetation-rich lakes. They do not occur in the Arctic.

Further discussion

Lateglacial deposits with remains of arctic plants were first demonstrated in Denmark by the Swedish geologist Alfred Nathorst (Nathorst 1914). Later, in a clay pit south of Allerød in northern Sjælland, signs of a warm period during the Lateglacial were found (Hartz & Milthers 1901) and some decades later an older warm period was described from Bølling Sø in Jylland (Iversen 1942, 1954). These warm periods were partly recognised from sedimentological criteria. In the Allerød clay pit, the major part of the Lateglacial sediments consisted of clay, but during the Allerød period organic-rich gyttja was deposited. In Bølling Sø the Lateglacial deposits are dominated by sand and sandy clay and silt, but during the Allerød period gyttja rich in microalgae accumulated. In the Allerød pit the clay layers contained leaves of *Betula nana*, *Dryas octopetala* and other arctic plants, whereas leaves of *Betula pubescens* (downy birch) were found in the gyttja layer. In Bølling Sø the mineral-rich layers contained pollen of *B. nana*, whereas the gyttja layer contained pollen of tree birch, according to Iversen (1942).

The earliest analyses of plant remains from the Lateglacial were based on studies of macrofossils (Hartz 1902), but after the introduction of pollen analysis plant macrofossils have often been ignored. However, plant macrofossils have some advantages compared to pollen: macrofossils can often be identified to species. It is for example not possible to identify pollen grains of *Thalictrum* to species, whereas fruits can be identified. Hence, it is possible to decide if fruits belong to *T. alpinum* or the more warmth-demanding *T. flavum*, both of which occur in Lateglacial deposits in Denmark.

Another problem about pollen analysis is that some species produces vast quantities of pollen and some pollen types are being spread far by the wind. During the Lateglacial when the local pollen production was relatively small this means that a large part of the pollen rain may come from non-local trees. This problem is specially pronounced for *Pinus*, the pollen of which are abundant in Danish Lateglacial deposits, even though no macrofossils of this tree has so far been found.

Pollen grains can also be subject to reworking and redeposition, which may hamper interpretation of Lateglacial pollen diagrams. In Bølling Sø it was estimated that up to 80% of the pollen grains were reworked from older deposits (Iversen 1942). Some types of macrofossils, such as seeds and fruits with hard walls may also be reworked, but usually such fossils become worn. Fragile plant macrofossils such as leaves can hardly survive reworking.

Finally, pollen analysis only gives information about plants that produce pollen and spores. Macrofossil analysis also provides information about the animal life of the past. In the samples from Regstrup, we found remains of many animals, which bear witness about a rich life in and around the former lake basins.

Based on pollen analysis it was proposed that all of Denmark was dominated by birch forests during the Allerød period (Iversen 1973). However, analyses of macrofossils indicate that the northern and western parts of Denmark were dominated by dwarf-shrub heaths with *B. nana* (Mortensen et al. 2014a). Clearly, it is important to conduct analyses from different parts of the country if we want to achieve a better understanding of regional variations in vegetation and fauna that may be determined by differences in climate, soil and immigration history.

Conclusions

The analyses from the basins near Regstrup indicate that the area was covered by open forests during the younger part of the Allerød period and the older part of the Younger Dryas period. The forests were dominated by *B. pubescens*, but *Populus tremula* was also quite common, until it disappeared *c.* 200 years into the Younger Dryas period. The area also housed light-demanding species such as *Dryas octopetala*,

Rubus saxatilis, *Minuartia* sp., *Potentilla* sp., *Thalictrum alpinum* and *Taraxacum* sp. Plants growing on wet and moist ground included several species of bryophytes, *Carex* sp. and *Comarum palustre*. Shallow water near the margin of the basins housed a rich vegetation dominated by *Carex rostrata* and including *Ranunculus* sect. *Batrachium* sp., *Hippuris vulgaris*, *Myriophyllum* sp., *Menyanthes trifoliata*, *Alisma plantago-aquatica* and *Sparganium erectum*. The flora in deeper water included charophytes and several pondweed species. The vertebrate fauna included *Rangifer tarandus*, *Castor fiber* and a small rodent, probably *Lemmus lemmus*.

The basins housed a rich fauna of invertebrates, including two species/genera of leeches, water fleas, ostracodes, larvae of beetles, chironomids, alderflies, caddisflies, gastropods, bivalves and bryozoans. The invertebrates are well-know prey for fish and remains of perch, pike and three-spined stickleback were found.

The common presence of bud-scales of the fairly warmth-demanding plant *Populus tremula* and finds of fruits of *Alisma plantago-aquatica* and *Sparganium erectum*, as well as other finds of warmth-demanding plants in south-eastern Denmark indicates that summer temperatures during the Allerød and early Younger Dryas periods were higher in the southern and eastern parts of Denmark than in the the northern and western parts of the country. Before and after the forested period the area around the basins were characterised by dwarf-shrub heaths with *Dryas octopetala*, *Betula nana*, herbs and mosses.

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