Terrestrial biotas and environmental changes during the late Middle Weichselian in north Jylland, Denmark

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Studies of glaciotectonized sub-till lacustrine deposits in Lønstrup Klint and Lodbjerg Klint, northern Jylland, Denmark, show the presence of plant and animal remains from the Middle Weichselian "mammoth steppe". Radiocarbon dates on picked-out plant fragments yield ages around 30 ka BP, and a macrofossil plant assemblage in the lake sediments indicates that uplands were covered by an open, tree-less vegetation with herbs and scattered shrubs. Mean July temperatures were probably at least 6°C lower than at present. The datings suggest a change from marine to glacio-lacustrine environments in Vendsyssel slightly before 30 ka BP. Glacial thrusting and subsequent deposition of the youngest till in the region was connected with the Late Weichselian glacial maximum, the Jylland stade, and glaciation commenced some time after 30 ka BP.

Key words: Middle Weichelian, terrestrial biotas, radiocarbon dating, Denmark.

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Radiocarbon dated plant and animal remains from strongly glaciotectonized and till-covered Middle Weichselian lacustrine sediments have previously been reported from two sites in eastern Denmark (Fig. 1), on Møn (Bennike, Houmark-Nielsen, Böcher & Heiberg 1994, Houmark-Nielsen 1994, Kolstrup & Houmark-Nielsen 1991) and Sejerø (Houmark-Nielsen & Kolstrup 1981). Data from these sites suggest that arctic and subarctic, periglacial tundra and/or steppe vegetation prevailed between 35–25 ka BP. Besides, ten tusks, molars and bones out of fourteen radiocarbon dated finds of mammoth fragments from Weichselian glacial and fluvial deposits in Denmark have yielded finite ages older than 22 ka BP (Aaris-Sørensen, Petersen & Tauber 1990) indicating that the "mammoth steppe" was characterized by the above mentioned vegetation types.

In northern Jylland (Fig. 1), foraminifera faunas of the Skærumhede Series indicate shallow marine, boreo-arctic environmental conditions during the late Middle Weichselian Sandnes interstade (Lykke-Andersen & Knudsen 1991). The youngest ^{14}C-ages on foraminifera from the Sandnes Interstade in Kattegat range from 36 to 31.5 ka BP (Seidenkrantz & Knudsen 1993). Evidence from open sections in Vendsyssel (Jessen 1899, 1936) and numerous borings (Jessen, Milthers, Nordmann, Hartz & Hesselbo 1910, Bahnson, Petersen, Konradi & Knudsen 1974, Fredericia 1988) indicate that marine clay with an arctic mollusc fauna (*Portlandia arctica* Zone, Upper Skærumhede Series) is overlain by waterlain non-marine mud and sand, which at some levels contain conspicuous amounts of plant debris. Thus, this marine environment was succeeded by lacustrine and possibly fluvial conditions. The strongly glaciotectonized state of these partly till covered deposits (Fig. 2) shows that deposition took place before the Late Weichselian glaciation maximum, Jylland Stade (Houmark-Nielsen 1989a).

Other sites in northwestern Jylland (Lodbjerg: Sjørring 1989, Mors: Gry 1979) show that bedded (gla-

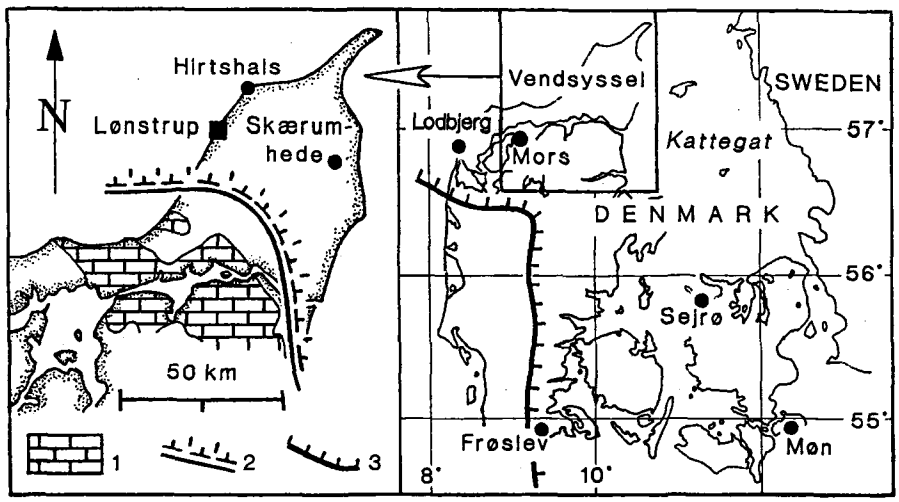

Fig. 1: Key and location map of Lønstrup, Lodbjerg and other sites mentioned in the text. 1: Cretaceous and Tertiary limestone lying higher than 25 m below present sea level (modified from Varv 1992 and Danmarks Geologiske Undersøgelse 1993). 2: Southern and western boundary for deposits of the Skærumhede Sea (from Fredericia 1988). 3: Limit of the Late Weichselian glacial maximum.

cio?)-lacustrine mud and sand may constitute the immediate and often strongly glaciotectonized substratum for the youngest till in the region.

In the present study radiocarbon dating and analyses of macro- and microscopic plant and animal remains from Lønstrup Klint (Sandrende & Nørre Lyngby), and Lodbjerg Klint (Fig. 1) will be discussed. This study adds new information on late Middle Weichselian terrestrial and lacustrine flora and fauna. Moreover, it gives input to the discussion on the change from marine to lacustrine environments as well as new information about the age of the onset of the Late Weichselian glaciation in northern Denmark during the Jylland Stade.

Site descriptions and results

Sandrende, Lønstrup Klint

Jessen (1931, 1936) described the more than 40 m thick succession at Sandrende, Lønstrup Klint, comprising laminated mud with occasional dropstones, gradually replaced upwards by bedded sand and fine gravel (Fig. 2). From sedimentological studies and palaeocurrent analyses Andersen (1961) suggested northward directed infilling of a proglacial lake basin. The succession is younger than the Skærumhede Series and strongly glaciotectonized. It is composed of imbricate thrust-slices piled up in front of a glacier invading the area from the north-northeast (Jessen 1931, Gry 1940), most probably during the Weichselian maximum (Andersen 1933).

The muddy deposits, and especially the bedded sand, occasionally contain high concentrations of plant remains (Jessen 1899, 1936). Hartz (1909) showed that the plant debris is of a composite nature, containing arctic elements as well as interglacial Quaternary and Tertiary species.

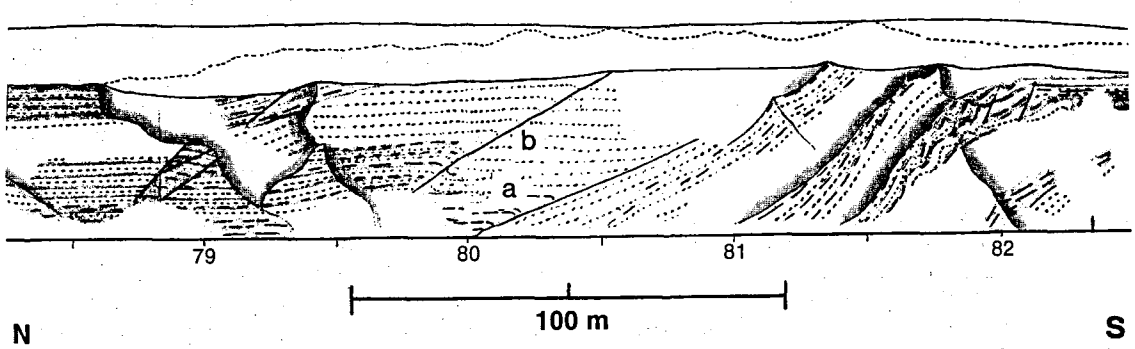

Fig. 2: Sandrende section, Lønstrup Klint (from Jessen 1936). Notations a and b indicate positions of analysed samples and ^{14}C datings. Dashes = laminated mud, dots = bedded sand. No exaggeration of scale.

Table 1. Macrofossils in sample GI 104152

Taxon	Remains
PLANTS	
FUNGI	
Cenococcum geophilum Fries	Few sclerotia
ALGAE	
Nitella sp.	2 oospores
BRYOPHYTA	
Scorpidium cf. *revolvens* (Sw. ex Anonymo) Hedenäs	Shoots common
Scorpidium cf. *scorpioides* (Hedw.) Limpr.	Few shoots
TRACHEOPHYTA	
Selaginella selaginoides (L.) Link	3 megaspores
Thalictrum alpinum L.	1 achene
Ranunculus sceleratus L.	1 achene
Ranunculus sect. *Batrachium*	4 achenes
Papaver sect. *Scapiflora*	3 seeds
Betula nana L.	5 nutlets, 1 female catkin scale
Sagina sp.	2 seeds
?*Draba* sp.	2 seeds
Salix polaris Wahlenb.	2 leaves
Empetrum nigrum L.	1 endocarp
Potentilla cf. *palustris* (L.) Scop.	1 achene
Dryas octopetala L.	1 leaf fragment
Saxifraga oppositifolia L.	4 leaves
Hippuris vulgaris L.	1 fruit
?*Angelica* sp.	1 mericarp
Alisma plantago-aquatica L.	1 seed
Potamogeton natans L.	1 endocarp
Potamogeton filiformis Pers.	1 endocarp
Juncus sp.	1 seed
Carex spp.	20 achenes
?*Poa* sp.	Few caryopses
ANIMALS	
Rhabdocoela indet.	3 coccoons
Oligochaeta indet.	1 coccoon
Coleoptera indet.	Few skeletal remains
Bembidion sp.	1 elytron fragment[1]
Trichoptera	1 lid

In addition, small twigs and a few small pieces of amber and coal were present
[1]Identified by Jens Böcher, Zoological Museum, Copenhagen

Sediments rich in organic detritus from ripple-drift cross-laminated sand taken immediately above the muddy transition zone (a in Fig. 2) consist of plant and animal remains that represent a mixture of dry-ground, wet-ground and aquatic habitats. Amber and coal fragments are derived from pre-Quaternary deposits, but the other fairly well-preserved plant and animal remains provide a fairly consistent ecological and climatic picture and are assumed to be closely related in time to the deposits in which they are found.

The analysed sample (GI 104152, Table 1) is dominated by leafy shoots of brown mosses (Amblystegiaceae), most of which are tentatively referred to *Scorpidium revolvens* (synonym *Drepanocladus revolvens*), and a few to *Scorpidium scorpioides*. These bryophytes are characteristic of wetlands. Remains of vascular plants are rare, but their diversity is quite large, with 21 taxa recorded. In addition, there are a few remains of the soil fungus *Cenococcum geophilium*, of the charophyte *Nitella* sp., and some invertebrates. The mericarp of an Apiaceae, which is referred to ?*Angelica* sp. on morphological grounds, is only 3.2 mm long, as compared to 4.0–8.5 mm in *Angelica archangelica* and 3.5–8.0 mm in *A. sylvestris* (Anderberg 1994).

The dryland vegetation is represented by four dwarf shrubs: *Betula nana, Salix polaris, Empetrum nigrum* and *Dryas octopetala* and by herbs such as *Thalictrum alpinum, Papaver* sect. *Scapiflora* and *Saxifraga oppositifolia*. These heliophytes and the absence of tree species imply that the dry ground areas, were covered by open, treeless vegetation. Wetland vegetation is represented by brown mosses, and by herbs such as *Ranunculus sceleratus* and *Alisma plantago-aquatica*. Several remains of vascular plants that were not iden-

tified at the species level probably also represent wetland taxa; these include *Potentilla* cf. *palustris*, *Juncus* sp. and *Carex* sp.

Aquatic plants and animals comprise *Nitella* sp., *Ranunculus* sect. *Batrachium*, *Hippuris vulgaris*, *Potamogeton natans*, *Potamogeton filiformis*, Rhabdocoela and Trichoptera. These could live in small lakes or along the shore of a larger lake. *Ranunculus* sect. *Batrachium* and *Hippuris vulgaris* could grow in ponds that dried out during the summer. *Nitella* and *Potamogeton filiformis* indicate ion-rich, probably calcareous raw fresh water.

Several of the species, notably *Salix polaris*, *Dryas octopetala* and *Saxifraga oppositifolia* are calciphilous. Their presence probably indicate that raw, unleached, calcareous soils were present in the area. *Papaver* sect. *Scapiflora* is indicative of unstable soil conditions. The brown mosses may point to calcareous wetland habitats, whereas *Potentilla palustris* prefers acid soils.

The flora comprises a number of northern extralimital species that are commonly found in low arctic areas today. However, at least to some degree, these species may have benefitted from the absence of shading trees that may not have had time to immigrate from distant refugia. Several of the plant species recovered show that summer temperatures were not very low. Today *Potamogeton natans*, *Alisma plantago-aquatica* and *Ranunculus sceleratus* only reach the arctic tree line which roughly coincides with a mean temperature of 10°C for the warmest month of the year. Mean July temperatures were probably at least 6°C lower than at present (16°C). Winter temperatures cannot be determined from the data set, but the willow *Salix polaris* is chionophilous and its presence implies areas with snow drifts.

A number of the plant species no longer grow in Denmark. *Salix polaris* is found in northernmost Scandinavia and eastwards, whereas *Dryas octopetala*, *Betula nana*, *Saxifraga oppositifolia*, *Thalictrum alpinum* and *Papaver* sect. *Scapiflora* are found in arctic and alpine areas both north and south of Denmark.

Lodbjerg Klint

At Lodbjerg Klint (Fig. 1) a grey and up to 3–4 m thick till bed (Fig. 3, unit A) with sandy-muddy matrix overlies at least 2 m of lacustrine sediments (units B, C & D). The fabric of the till, striations of clasts and the petrographic composition indicate a direction of ice movement from the north-northeast and deposition of till by a glacier that reached the area from the central parts of Scandinavia (Sjørring 1986). The till gradually overlies beds of diamicton sandwiched by lenses of gravel (Fig. 3, unit B). The diamicts contain clasts of distance transported erratics and show an upward increasing grainsize in matrix. Unit B was deposited by sediment gravity flows and running water in an ice-proximal environment and overlies bedded clay, silt and fine sand with intraclasts of laminated and/or massive clay and silt (Fig. 3, unit C). The mud was probably deposited by gravity flows and suspension in a lake basin and overlie silty clay interbedded with laminated fine sand occasionally fining upwards (Fig. 3, unit D). This succession contains fragments of water mosses (*Drepanocladus*) and unidentified terrestrial plant remains along with few intraclasts of mud. The bedded mud and sand was probably deposited by gravitation, by traction currents and from suspension in a lake basin.

Table 2. Radiocarbon datings Lønstrup and Lodbjerg

Locality	Laboratory No.	Material	$\delta^{13}C$ ‰	^{14}C age years BP
Lønstrup a	Ua-4454	Brown mosses	–29.12	29.190±1415
Lønstrup b	AAR-2265	Plant fragments	–27.3	30.900±530
Lodbjerg	AAR-2616	Plant fragments	–26.7	30.350±410
Nr. Lyngby	AAR-2878	Plant fragments	–27.1	34.700±550
Nr. Lyngby	AAR-2880	Plant fragments	–27.8	39.550±1000
Nr. Lyngby	AAR-2882	Plant fragments	–27.3	36.150±680

The lake sediments at Lodbjerg were preliminary analysed for pollen. As would be expected from such organic-poor sediments the pollen content is very low and the grains are often degraded and deformed. The pollen concentrations reach a maximum of ca. 25,000 grains per cm^3, and this pollen analysed level corresponds to the level where the radiocarbon dated macro remains were found (Table 2).

The pollen flora is dominated by grass (15–35%), sedge (24–40%), pine (10–30%) and unspecified birch pollen. Other frequent types are *Artemisia* and *Salix* together with presumably redeposited grains of *Alnus*, *Carpinus* and *Quercus*. The latter pollen types, especially *Carpinus* suggest that parts of the pollen assemblage may be of Eemian origin. The herb/shrub pollen types together with possibly long-distance transported *Pinus* pollen, the scarce birch vegetation and the low pollen concentrations, imply that a mesic tundra dominated the area around the lake basin.

Radiocarbon dates

Two samples of plant detritus from the lower part of the sand in Lønstrup Klint (a & b, Fig. 2), and one from unit D at Lodbjerg (Fig. 3) were submitted for AMS (^{14}C) measurements (Table 2). To avoid contamination from older plant material, the most well-preserved fragments of brown mosses and vascular plants remains were carefully picked-out and separated from fragments of coal, amber and badly preserved plant remains.

The radiocarbon-ages of the three samples are closeley spaced around 31–29 ka BP which indicates that erosion, transport and deposition of the terrestrial plant remains took place at or after 30 ka BP. The original habitat for the aquatic mosses may, however, have been very close to the finding site. Because it cannot entirely be ruled out that the samples have been contaminated with older carbon due to hardwater errors (aquatic mosses) or old plant debris, the dates at least give maximum ages for the sediments. This indicates that samples from Lønstrup are younger than the youngest ^{14}C ages from the underlying marine sediments (31 ka BP). When the 2σ errors are used the three dates can be as young as 26.360, 29.840, and 29.530 years BP, respectively, which is a further indication that the dates cannot be significantly contaminated. If for example a contamination of 50% "dead" carbon was applied, ^{14}C-ages would increase with 5500 years, suggesting the plant detritus could be as young as 25 ka BP. The fact that less fragile plant detritus can survive several redeposition phases is shown by the ^{14}C dated terrestrial plant material found in the Younger Yoldia caly at Nørre Lyngby (Table 2). The dated material show ages between 34 and 40 ka BP while in situ shells of *Hiatella arctica* of this marine clay show radiocarbon ages younger than 14.5 ka BP (Richardt 1996).

Contamination with younger carbon from penetrating roots is very unlikely since only macrofossils, and not humus, were dated. Although the above mentioned uncertanties with possible influence of old carbon must be taken in consideration, we can conclude that the combination of the painstaking selection of well-preserved plant material and the close resemblance in dating results strongly suggests that the ^{14}C-age of the plant material in the lacustrine/fluvial deposits is close to 30 ka BP.

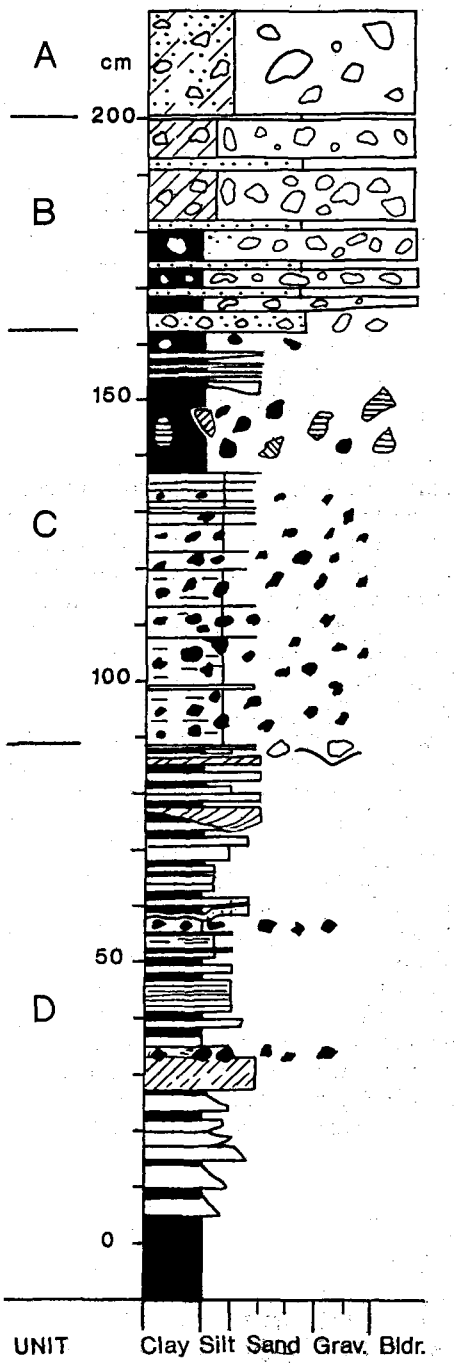

Fig. 3: Lithological log, Lodbjerg. Unit A: Till (lowermost part), Unit B: Iceproximal diamict gravity flows and gravel beds, Unit C: Upper lake sediments with intraclasts of laminated and massive mud, Unit D: Lower lake sediments with bedded mud and fine sand containing plant detritus.

Correlations and discussion

Only a few sites in Denmark contain terrestrial biotas that provide a basis for comparison with the fossil assemblage from Lønstrup. One site that could be roughly comtemporaneous based on AMS and luminescence ages is the Kobbelgård sequence on Møn. This site has been studied by Kolstrup & Houmark Nielsen

(1991) and Bennike et al. (1994), and yielded macrofossil assemblages that show similarities to the one studied here. The assemblages from Møn are richer, both as regards the amount of organic detritus and the number of recovered fossil taxa. This could be due to the size of the depositional basin, the distance from the coast (or an even more remote source area) or other taphonomic factors. Middle Weichselian deposits from Sejerø (Houmark-Nielsen & Kolstrup 1981), Hirtshals (Lykke-Andersen 1981, Odgaard 1982), and Frøslev (Kolstrup & Havemann 1984) are ^{14}C-dated to be 5–15 Ka older than the ones studied here. Most of these sites show evidence of low arctic or subarctic, treeless environments. All taxa of vascular plants from Lønstrup have been recorded from Middle Weichselian deposits in Britain (Godwin 1975), showing that these plants were widespread in NW Europe.

The work of Odgaard (1982) and the ^{14}C ages from Sandrende, Nørre Lyngby and Lodbjerg indicates that a vegetation characteristic of the mammoth steppe surrounded the Older Yoldia sea and local lakes in northern Jylland. Durable plant material may tolerate redeposition giving too high ages compared to the sediments in which it is found, thus the age of the lake sediments at Lodbjerg may be several thousand years younger than 30 ka BP. According to Andersen (1961) the crossbedded sand at Lønstrup Klint, locally showing northward directed palaeocurrents, seems to have a regional distribution and is found in large parts of Vendsyssel. Outcrops of limestone and chalk-rich moraine are only found south and southwest of the area covered by the Skærumhede sea more than 20 km from Lønstrup (Fig. 1). The calcareous wetlands and dry upland habitats which seem to be the source of most plant debris in Lønstrup could therefore have been situated in southernmost Vendsyssel. This implies at least 20 km transport for plant debris from different sources which may enlarge a possible discrepancy between the age of the plant material and the sediment age. However, the presence of rather fragile plant remains from the lacustrine deposits at Sandrende suggets a short and delicate transportation from nearby sources intolerant towards long lasting exposure. Therefore, the age of the sediments in Lønstrup in which the plant detritus is found are probably only insignificantly younger than the ^{14}C-ages.

Our data suggest that the transition from marine to lacustrine conditions in the basin took place close to 30 ka BP. Closing of the northern part of the Norwegian Trench by glacier ice occurred around 30 ka BP (Sejrup, Haflidason, Aarseth, King, Forsberg, Long & Rokoengen 1994) and may have caused the up-damming of a regionally confined lacustrine basin in the Vendsyssel–Kattegat region (Houmark-Nielsen 1989b) in which plant detritus was deposited. This occured in direct coherence with the continuous global sea-level fall in isotope stage 3 (Linsley 1996), transforming previously low-lying marine areas with their fine-grained deposits, into fresh-water basins.

The age of the plant detritus underlying the till at Lodbjerg indicates that the till belongs to the Late Weichselian *maximum*, the complex Jylland stade. Probably, the glaciotectonic deformation in Lønstrup Klint and deposition of till at Lønstrup and Lodbjerg was caused by the same ice advance. Whether this advance is the so-called Norwegian ice (Houmark-Nielsen 1989a) or the Main Weichselian advance reaching the Late Weichselian glacial limit from central Scnadinavia (Fig. 1), or both, is still an open question. Possibly the two ice-advances never separated in the northern-most parts of Denmark as discussed by Houmark-Nielsen (1987).

The time-span between separation of the former marine basin at Lønstrup connected to the Atlantic through the Norwegian Trench and the onset of glaciation in Vendsyssel and Kattegat is unknown. Although deposition of fluvial and lacustrine sediments may have lasted until 26-27 ka BP in Vendsyssel the time of glaciation in northern Denmark can not be estimated from these data. On the other hand, the proposed syntectonic nature for the bedded sand in Sandrende proposed by Pedersen (1986, 1996) disputes a larger time gap between sedimentation and glaciotectonic thrusting in Lønstrup Klint. An indication of ice free conditions on Mors and the surrounding Limfjord area until 22–20 ka BP is based on luminescence datings of lacustrine mud (Petersen & Kronborg 1991, Pedersen 1996). Even though uncertainties exist as to the interpretation of such dates (Mejdahl, Shlukov, Shakhovets, Voskovskaya & Lyashenko 1992), the ages speak in favour of a considerable time-span with deposition of lacustrine sediments in northern Jylland prior to invasion of glaciers. This point of view is supported by the evidence from Lodbjerg, where sedimentation from suspension was succeded by gravity flows with an increasing amount of glacial debris. Further sedimentological and glaciotectonic studies in northern Jylland combined with new radiocarbon datings and analyses of fossil floras and faunas are needed to solve the problem regarding the timing and speed of Late Weichselian glacier movements in northern Denmark, as well as the timing and rate of environmental change from arctic marine environments and subarctic steppe/tundra of the Middle Weichselian to full glacial conditions during the Late Weichselian.

Acknowledgments

Grants from the Natural Science Foundation (SNF) supported parts of the field work and the AMS datings. Bjarni Richter and Jóhann Thorarensen sampled material for pollen and macrofossil analyses at Lodbjerg. Jens Böcher, Zoological Museum, University of Copenhagen kindly assisted in identification of macrofossils. Niels Richardt readily gave radiocarbon datings from Nørre Lyngby at our disposal.

Dansk sammendrag

Glacialtektonisk forstyrrede sø- og flodaflejringer overlejret af till i Lønstrup Klint og Lodbjerg Klint i Nordjylland er analyseret for makroskopiske plante- og dyrerester og pollen. AMS kulstof-14 dateringer af udvalgte planterester har givet aldre på ca 30.000 år før nu, svarende til den sene del af Midt Weichsel (75–25 ka BP).

De makroskopiske planterester fra Lønstrup stammer fra planter der har vokset lokalt. Vedplanter er repræsenteret af dværgbirk, polarpil, revling og dryas, hvortil kommer en række urter, mosser, alger og svampe. Floraen omfatter en række arktiske arter, og det viser, at områder med relativt tør jordbund var dækket af åben, træløs pioner vegetation. Den gennemsnitlige temperatur for årets varmeste måned var mindst 6°C lavere end i dag, svarende til subarktiske eller lavarktiske forhold.

Pollenstudier fra Lodbjerg Klint viser en vegetation domineret af græsser, halvgræsser, fyr og birk, men der findes desuden pollentyper, der antagelig er omlejret fra Eem aflejringer. Pollen af fyr er formentlig fjerntransporteret og vådområder dominerede søbassinets umiddelbare opland.

Midt Weichsel aflejringer der belyser terrestriske naturforhold er tidligere beskrevet fra forskellige steder i Danmark, men de fleste af disse forekomster synes at være ældre end 30 ka BP. Aflejringer fra Klintholm på Møn kan være samtidige med de her beskrevne fra Nordjylland.

Marine Midt Weichsel aflejringer er derimod vidt udbredt i Nordjylland og Kattegat. Den yngste kulstof-14 datering er 31 ka BP. Denne datering, og aldersbestemmelserne i dette arbejde, peger på, at overgangen fra et arktisk marint miljø til isdæmmede, lakustrine forhold fandt sted omkring 30 ka BP. Dateringerne giver desuden en maksimum alder for den sidste nedisning i regionen, Jylland stadialet, hvor det fennoskandiske isskjold nåede hovedopholdslinien, efter først at have passeret Vendsyssel og senere Lodbjerg.

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