A paleoenvironmental Reconstruction of Magleholm, Vedbæk, based on Molluscs and botanical Macroremains

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ABSTRACT

Magleholm was excavated in 1978, 1983 and 1984 under the direction of E.B. Petersen as part of the Vedbæk project. This paper aims to provide a paleoenvironmental reconstruction of the site based on analysis of molluscs and botanical macroremains from 16 samples, covering 80 cm of a profile from a trench excavated in 1984. The samples primarily reflect the environment at the time of the Mesolithic Ertebølle culture while a few samples in the upper part of the profile reflect the environment during the Early Neolithic Funnel Beaker Culture. Apart from providing information about the vegetation and landscape, the data also illustrate which resources were available to people.

The bottom of the profile consists of practically sterile sand. A major part of the profile, consisting of gyttja that was poor in plant and mollusc taxa, reflects the environment of a brackish lagoon. The uppermost three samples, at least partially corresponding with the Neolithic, show a reduction in salinity, resulting in a more diverse combination of brackish water and freshwater taxa. Most taxa in the upper samples represent taxa of shallow open water, salt marshes and border zones alongside freshwater bodies, while some plant taxa represent vegetation of dryland terrain. While some finds of wood charcoal and carbonised fish remains point to human activity, none of the seeds and fruits in the profile were carbonised.

Comparison with earlier environmental data indicates that this new study on the one hand confirms, and on the other hand complements, results from earlier studies at Magleholm. Since archaeobotanical studies from both the Vedbæk fjord and Mesolithic sites in Southern Scandinavia in general are relatively rare, this study underlines both the potential of and need for additional botanical macroremains analysis at comparable archaeological sites.

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Mesolithic, Neolithic, seeds and fruits analysis; Molluscs; Mesohaline paleoenvironment.

Introduction

Magleholm, located 20 km north of Copenhagen in Denmark (Figure 1), was discovered in 1937 by Avnholt (1944, 61-63) and excavated in 1978, 1983 and 1984 as part of the Vedbæk project (Christensen 2014, 10; Petersen et al. 2015: Table 11:1). This project, led by Erik Brinch Petersen, concerned the excavation of multiple sites located in the former Vedbæk fjord¹ undertaken by the National Museum of Denmark and the University of Copenhagen, which were accompanied in some years by the University of Madison-Wisconsin (e.g. Petersen et al. 1979, 1982, 2015).

The site of Magleholm, located at 5.10 masl on a former hill, was characterized by disturbed settlement traces on the sandy top of the hill and refuse embedded in gyttja and peat layers on the slopes. The zone with refuse on the slopes has been described as an outcast zone. The 66 m² of the trenches from the 1983/1984 excavation, of which 15 m² was excavated systematically, were located on the northern and southern slopes of the hill (Christensen 1982, 98-99; Petersen 1985, 2). Based on flint and pottery finds, the site has been attributed to the Early, Middle and Late Ertebølle Culture as well as the Early Neolithic Funnel Beaker Culture (Christensen 2014, 10-14; Juel and Kjær 2015, 221; Petersen 1982, 148; Petersen et al. 2015: Fig. 13.1). The Ertebølle finds were recovered from gyttja layers while the Funnel Beaker finds were found in the upper gyttja and peat





Figure 1. Location of Magleholm. The former fjord area, indicated with the dark grey line, matches the 5 masl-line. White and dashed line: roads and railway (Figure: graphical department at Moesgaard, after Petersen et al. 2015, 206).

deposits (Christensen 1982, 2014). Six radiocarbon dates, collected primarily to reconstruct the landscape development and shoreline displacement (Petersen et al. 2015, 66), range from *c.*5000 to 2600 BCE (Table 1; Christensen 1982, 93; 2014, 40; Petersen et al. 2015, table 11:2; Sørensen 2014, 134), corresponding with the Atlantic and Subboreal (Christensen 2014, 10-12).

Archaeological analyses of the Vedbæk project published so far focus on the flint, pottery, zooarchaeological remains, human remains, isotope analysis of the human remains, wooden artefacts, molluscs used as artefacts, use-wear analysis, pollen analysis, and the reconstruction of sea levels (e.g. Aaris-Sørensen 1982; Albrethsen and Petersen 1977; Christensen 1982, 2014; Enghoff 1995, 71; Jensen and Petersen 1985; Mørck et al. 1999; Petersen 1982, 1984, 7-13; Petersen et al. 1979, 1982, 2015 and references therein). For Magleholm and various other sites in the Vedbæk area, it is argued that the lithic assemblage included "quite a selection of lithic types with much primary lithic work and debitage", that the archaeozoological assemblage contained "a mixture of marine and forest species" and that there is evidence for occupation during most seasons, though without explicit evidence of occupation during winter, since this is difficult to demonstrate (Petersen et al. 2015, 156).

Further details on Magleholm are scarce. Compared with the other sites studied as part of the Vedbæk project, Magleholm represents a relatively

long cultural sequence (Petersen et al. 2015, 45). The site was subjected to radiocarbon dating and pollen analysis to reconstruct sea levels (Christensen 1982, 2014; Petersen et al. 2015, 20, 68). The presence of domestic animals is demonstrated by a goat bone fragment (Sørensen 2014; Table 1: 3799-3647 BCE, 2σ). The fish assemblage at least during the Mesolithic was dominated by gadids (Gadidae, 70%) and further contained spurdog (Squalus acanthias Linnaeus, 1758, 22%), flatfish (Pleuronectiformes, 5%: particularly European plaice, Pleuronectes platessa Linnaeus, 1758, and flounder, Platichthys flesus Linnaeus, 1758), eel (Anguilla anguilla Linnaeus, 1758, <1%) and some remains of other taxa (Enghoff 1995, 71), indicating the occurrence of marine or brackish conditions (Møller and Carl 2010).

Despite excellent preservation of organic material at multiple sites in the area, botanical macroremains analysis was not undertaken systematically as part of the Vedbæk project including at Magleholm, or is at least not published internationally. One exception is an archaeobotanical analysis from Maglemosegård (c.5500-3600 BCE, Christensen 2014, 39; see also Christensen 1982, 93), carried out by G. Jørgensen (Petersen et al. 2015, 193, no context data presented). Information about finds of seeds and fruits is thus restricted to larger remains found during sieving: It is reported that hazelnut shells (*Corylus avellana* L.) and acorns (*Quercus* sp.), including carbonized remains, were found

Lab. No.	Material	Age	Age	Age	Depth	Sediment	Section	Layer	Excava-	Reference
		(years uncal	(years cl BCE, 2σ)	(years cl BCE, 1σ)	(masl)				tion	
		BP)							year	
K-3151	Wood, Alnus	4390±90	3346 (95.4%) 2886	3314 (3.4%) 3296	2.86	Limnic gyttja	Ø199, N325	layer 9	1978	Petersen et al. 2015
	sb.			3286 (9.3%) 3240						
				3104 (55.6%) 2904						
K-3150	Wood	4250±90	3261 (0.3%) 3251	3010 (4.7%) 2982	3.65	Limnic gyttja	Ø199, N325	layer 9	1978	Christensen 2014
			3100 (94.9%) 2572	2934 (27.5%) 2838						
			2513 (0.3%) 2504	2816 (36.1%) 2668						
K-4178	Wood	4650±85	3636 (82.0%) 3312	3618 (6.2%) 3586	2.86	Gyttja rich in	Ø200, N317,45	layer 3		Christensen 2014
	(branch),		3298 (0.7%) 3285	3530 (62.1%) 3348		detritus				
	Alnus sp.,		3272 (0.2%) 3269			and Ruppia				
	charred		3241 (12.5%) 3103			fruits				
OxA-27117	OxA-27117 Bone, Capra	4961±34	3894 (2.0%) 3880	3772 (51.0%) 3702					1978	Sørensen 2014
	sb.		3799 (93.4%) 3647	3680 (17.3%) 3656						
K-3149	Wood	6180 ± 100	5357 (0.5%) 5347	5293 (6.2%) 5265	3.15	Sand	Ø199, N315,50	layer 6	1978	Petersen et al. 2015
			5332 (93.3%) 4881	5218 (62.1%) 5000						
			4872 (1.7%) 4846							
K-3148	Worked	6270 ± 100	5473 (4.4%) 5428	5331 (40.5%) 5204	2.40 -	Sandy gyttja	Ø199, N318-	layer 8	1978	Petersen et al. 2015
	poom		5416 (91.0%) 4996	5178 (27.8%) 5064	2.70		320			

Table 1. Magleholm, radiocarbon dates from profile Ø 199 (Christensen 1982, 93).

at multiple sites, as well as remains of crab apple (Malus sylvestris Mill.) (Petersen et al. 2015, 82; no details per site). On the one hand, one can argue that botanical macroremains analysis was still developing within archaeology in the 1970s and early 1980s. On the other hand, sampling of botanical macroremains at wetland sites had already started in Europe at this time (e.g. Bakels 1981; Becket 1978a,b; Behre 1969, 1976; Casparie et al. 1977; Gaillard and Lemdahl 1988; Göransson 1988; Jacomet et al. 1989; Körber-Grohne 1967; Out 2010, 2012; Out and Dörfler 2017; Schlichtherle 1990), also by scholars in Denmark (Fredskild 1969; Troels-Smith 1960). Pollen analysis was incorporated in the Vedbæk project, and such data are available for Magleholm (Christensen 2014, 13-14).

This paper presents new identifications of seeds and fruits as well as molluscs from sixteen sediment samples from a profile at the site of Magleholm. The aim of the study is to reconstruct the environment and natural vegetation at the site and to assess whether there is evidence of handling of plants by people. Most of the analysed samples cover the Mesolithic while the uppermost samples cover the Early Neolithic.

Paleogeography of the Fjord and Stratigraphy of Magleholm

During the Boreal and Early Atlantic, a lake was present in the Vedbæk area, as indicated by the presence of gyttja, containing freshwater molluscs, on top of the glacial sand (Christensen 1982, 98). The gyttja sequence was covered by peat rich in seeds of bogbean (Menyanthes trifoliata L.). This lake had a size comparable to that of the fjord at the time of the highest sea level. Depending on the location, the thickness of the lake deposits varies widely, from a few tens of cm up to 2 m (Christensen 2014, 6). The lake deposits are not documented in the earlier published profile from Magleholm (Christensen 1982, 6).

The Mid-Holocene development of the Vedbæk area is characterized by the gradual rise of the relative sea level, which resulted from a global eustatic sea-level rise (Bennike et al. 2023, 449; Christensen 1982, 2014; Petersen 1982, 141). As a result

of this gradual rise, salt water flooded the Vedbæk valley in the early 7th millennium BCE, creating a shallow inlet with numerous islands and peninsulas (Petersen 1984, 8; Petersen et al. 2015, 20). At the entrance of the fjord a beach ridge formed, leaving open only a narrow entrance to the fjord (Petersen et al. 2015, 23), resulting in the development of a lagoon. Stratigraphically, the changes in the landscape can be observed as a sharp transition from peat to marine gyttja (marine gyttja: see Discussion). At Magleholm, located in the western and relatively sheltered part of the Mesolithic Vedbæk fjord, this gyttja layer was c.1 meter thick. It was further noted that at Magleholm, especially on the island's east side, this gyttja contained layers of sand, gravel and stones, indicating a relatively dynamic environment in comparison with other sites in the fjord (Christensen 2014, 10).

The sea reached its highest level in the area during the middle Holocene. Some prehistoric sites in the Vedbæk region were submerged at this time but Magleholm always remained an island during the Atlantic and Subboreal. The maximum sea level was a result of the eustatic sea level rise on the one hand and the glacio-isostatic land uplift on the other hand. Due to the latter, sites in certain parts of Denmark that were coastal sites during the Atlantic, including Magleholm, are now located above sea level (Christensen 1982, 94; Petersen 1984, 7; Petersen et al. 2015, 44-45).

Between 3850 and 3700-3600 BCE (date according to Christensen 2014, 40, based on palynology and radiocarbon date K-4178, see also Table 1), a detritus gyttja layer was deposited containing some Funnel Beaker pottery sherds (Christensen 2014, 11). This layer, only observed at Magleholm, was earlier interpreted as a subboreal transgression (Christensen 2014, 11; see also discussion). Pollen and macroremains analyses indicated the presence of tasselweed (*Ruppia* sp.) in these deposits (Christensen 2014, 10).

Shortly after 3500 BCE or at least before 3000 BCE (date according to Christensen 2014 40, based on radiocarbon dates K-3150 and K-3151, see also Table 1), the connection of the lagoon to the sea closed (earlier interpreted as a regression of the sea level), resulting in the deposition of coarse limnic detritus gyttja in what became a freshwater lake 100-150 m wide and 1 km long. These

freshwater deposits have particularly been found further away from the former lagoon edges and have also been attested at Magleholm (Christensen 1982, 98-99, 2014, 10-14, layer 3 and layer 9/upper part layer 3). In the northern and southern trenches of Magleholm, a calcareous gyttja was observed on top of the marine gyttja and beneath the limnic detritus gyttja, at the bottom containing small individuals of cockle (*Cardium* sp., now called *Cerastoderma* sp.) and mud snails (*Hydrobia* sp.), indicating a transitional brackish environment (Christensen 1982: 91, 98, 99: layer 10, Christensen pers. comm. 2025).

The limnic gyttja is covered by peat, representing the paludification of the freshwater lake (infill with marsh vegetation). At many places the peat has degraded due to dehydration and cultivation practices (Christensen 2014, 6).

Materials and Methods

The Samples: their Context, History and Analysis

In 1984, L.B.M. Verhart of the National Museum of Antiquities in Leiden, the Netherlands, participated in the excavation of Magleholm and collected 16 sediment samples from the south profile of trench 2, covering 85 cm. After collection the samples were taken to the Netherlands and subsequently sieved and analysed by W.J. Kuijper, at that time working at the archaeobotanical laboratory at the Faculty of Archaeology of Leiden University. In 2023, W.J. Kuijper handed the resulting documentation over to W.A. Out.

With the exception of sample 1, which is twice as thick as the others, all samples had a height of c.5 cm and a volume of c.200 cm³. Since the main focus of the analysis concerned the molluscs, the samples were sieved with a 0.5 mm sieve, implying that the smallest seeds and fruits, for example those from *Juncus* sp. (rushes) may be lost. Interpretation of the molluscs is based on Gittenberger et al. (2004), Glöer (2002), Götting (2008), Kuijper (2000) and Muus (1967). The nomenclature of the molluscs is based on Gittenberger et al. (2004) and Welter-Schultes (2012). The seeds and fruits were identified using the reference collec-

tion of the Faculty of Archaeology, Leiden University. The nomenclature of the seeds/fruits is based on Duistermaat (2020). The analysed molluscs are stored at Naturalis Biodiversity Centre, Leiden, the Netherlands. The majority of the botanical macroremains were discarded after analysis since the assemblage did not contain rare taxa or other finds that were considered relevant to preserve.

Context of the investigated Profile and Layers

The profile drawing of the investigated samples mentions the south profile of trench 2, referring to the dy-line (diagonal trench?) and mentions 74 (m?) as a location marker. The sample location is estimated to be located c.10 meter from the earlier shore of the fjord (notes W.J. Kuijper 1984). Generally, the layers can be interpreted as refuse layers (Christensen 2014, 10) and as an off-site zone, since the gyttja layers represent the fjord rather than the dry island. Based on Christensen (2014, Fig. 7), the disturbance at the bottom of the peat layer above the investigated samples is interpreted as resulting from removal of Neolithic find material. It is not clear precisely how the studied profile relates to the profile where the radiocarbon dates presented in Table 1 were taken (further discussed below).

Results

Studied Profile

Figure 2 and Table 2 show the sampled profile and descriptions of the layers. The lowest sample consisted of glacial sand with scattered stones. The sediment of the remaining samples consisted of gyttja. Peat was present above the samples.

The identifications of molluscs, seeds and fruits, and other finds from Magleholm, trench 2, are shown in Figure 3. Samples throughout the profile contained sand and charcoal, suggesting that the entire analysed profile may correspond with periods of human activity. Small flint fragments were particularly present in the lower part of

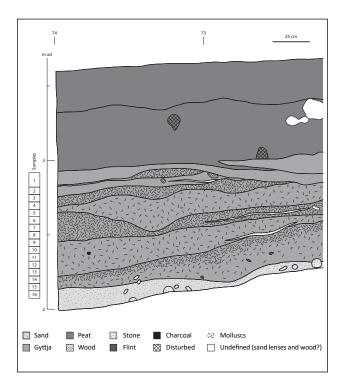


Figure 2. Magleholm, trench 2, south profile, dy-line. The samples were collected at "74" (m?) (Figure: graphical department at Moesgaard, after a drawing by L.B.M. Verhart).

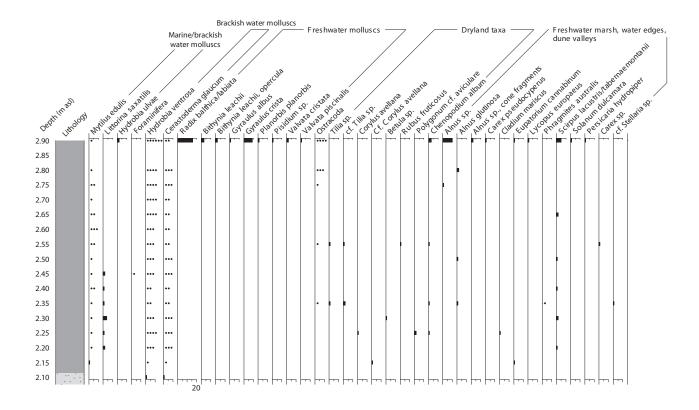
the profile (samples 11, 12, 15 and 16 at 2.07-2.17 and 2.27-2.37 meter above sea level). Carbonised fish remains and carbonised culms were observed in two different samples (at 2.27-2.37 masl). Especially the lower samples contained leaf fragments and buds. Finally, various samples contained small uncarbonized fish remains, which are expected to belong primarily to small fishes, e.g. the common goby (*Pomatoschistus microps* Krøyer, 1838), that may have ended up naturally at the sample location.

Molluscs, Foraminifera and Ostracods

Most layers present in the studied profile contained molluscs, some more than others. The top of the layer at 2.12-2.22 masl (samples 14-15) was particularly rich in molluscs. This may indicate that apart from molluscs' growth, there was little sedimentation. The top of the layer at 2.27-2.47 (samples 9-13) was rich in broken molluscs. In other layers, the shells were mostly found as complete single shells. Shell fragmentation primarily

Depth (masl)	Sample nr.	Sediment	Description
2.82-2.92	1	Gyttja	1: coarse gyttja containing few molluscs. Thin layer with molluscs at the transition of samples 1 and 2, after 50 cm wedging out in a thicker layer with many molluscs
2.77-2.82	2	11	2-3: gyttja containing few molluscs and some wood fragments
2.72-2.77	3	"	3-4: gyttja containing many molluscs
2.67-2.72	4	"	4-5: gyttja containing some molluscs
2.62-2.67	5	11	5-9: gyttja containing many molluscs. Sand lens
2.57-2.62	6	"	
2.52-2.57	7	"	
2.47-2.52	8	"	
2.42-2.47	9	"	9-13: gyttja containing some molluscs. Top of this layer: many
			broken molluscs
2.37-2.42	10	"	
2.32-2.37	11	"	
2.27-2.32	12	"	
2.22-2.27	13	"	
2.17-2.22	14	"	14-15: gyttja, top rich in molluscs. Flint and stones present.
			Charcoal fragment. Sand lens
2.12-2.17	15	"	
2.07-2.12	16	Grey sand.	16 and below: sand; stones present
		Glacial deposits	

Table 2. Magleholm, trench 2, south profile, description of the studied layers and samples.



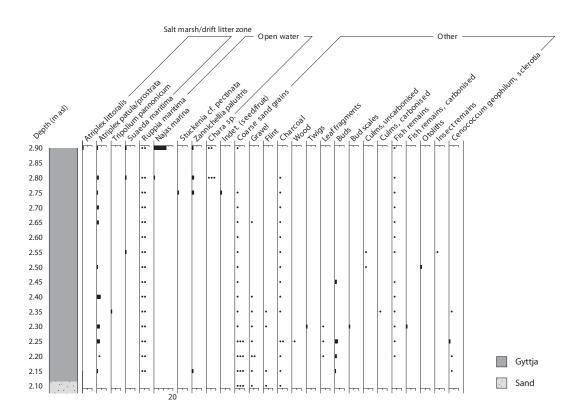


Figure 3. Magleholm, trench 2, the identifications of molluscs, botanical macroremains and remaining finds (absolute numbers). Depth: meter above sea level. Sample 1 is located at the top of the sample series and sample 16 at the bottom (see also Table 2). Note the larger sample volume of sample 1. Scale of x-axis if not indicated: 0-10. Bars: counted quantities. Dots: estimated quantities: • = some, • • = some tens, • • • = many tens, • • • • = some hundreds, • • • • • = many hundreds, • • • • • • = thousands (Analysis: W.J. Kuijper. Figure: graphical department at Moesgaard).



Figure 4. Sample 14, containing lagoon cockles, sand and pebbles (Photo: W. Kuijper).

resulted from sampling and sieving. Paired shell valves were rare; these have been reported for levels 2.27-2.32, 2.72-2.77 and 2.82-2.92 masl (samples 12, 3 and 1).

The lowest sample from the sand layer contained single fragments of mud snail and cockle shells that are considered intrusive and did not contain any seeds or fruits. The gyttja sample directly above the sand layer contained more mollusc remains but was relatively poor in molluscs compared to the other samples.

In the majority of the remaining gyttja samples, the mollusc fauna is poor in taxa and rich in individuals. Three mollusc taxa were present in all these samples: the common mussel (Mytilus edulis Linnaeus, 1758), the spire snail (Hydrobia ventrosa Montagu, 1803, also called Ecrobia ventrosa Montagu, 1803) and the lagoon cockle (Cerastoderma glaucum Bruguière, 1789) (Figure 4). The constant presence of these taxa as well as the practical absence of obligate marine taxa indicate that brackish conditions prevailed.

The common mussel, represented by few remains per sample in the lower half of the profile (until and including sample 8 at 2.47-2.52 masl) and tens of remains in the upper half of the sample, occurs in marine and brackish water environments.

The spire snail, present with up to hundreds and even thousands of shells per sample, occurs in shallow, calm, brackish water zones without tide or with small tidal amplitudes. It tolerates relatively extreme conditions and tolerates both influxes of freshwater as well as weekly and yearly fluctuations of saltwater. At 2.82-2.92 masl (sample 1 at the top of the sample series), both juvenile and adult individuals were reported, which indicates their local presence. At 2.77-2.82 masl (sample 2), the shells of the spire snail were found deposited in layers. Also, the sediment at 2.72-2.77 (sample 3) contained layers of unspecified shells.

The shells of the spire snail regularly showed holes caused by either the bristleworm (*Polydora ciliata* Johnston, formerly *Polidora ligni* Webster) or the boring sponge (*Cliona celata* Grant) (Cadée and



Figure 5. Sample 1, containing shells from the brackish- and freshwater molluscs spire snail (common), common pond snail (see text), Nautilus ramshorn, ramshorn snail and flat valve snail, Leach's Bithynia and a pea mussel (Photo: W. Kuijper).

Wesselingh 2005, 40-42; Muus 1967, 91). Thickenings on the inner sides of the shells indicate that the organism affected living spire snails.

The lagoon cockle, represented by tens of shells, lives in stagnant or slowly flowing waters and is characteristic of brackish water environments. It can survive periods of fresh or marine water supply, but under true marine conditions it is replaced by the common cockle (*Cerastoderma edule* Linnaeus, 1758) – a taxon which was not found at Magleholm. At 2.82-2.92 masl and 2.67-2.77 masl, thus in the top of the sample series, both juvenile and adult individuals of the lagoon cockle have been reported, and at 2.72-2.77 masl, doublets, including empty doublets, have been reported, which all indicates their local presence.

Apart from the common mussel, two more mollusc taxa were found that are characteristic of marine or brackish waters: the rough periwinkle (*Littorina saxatilis* Olivi, 1792) and the mud snail (*Hydrobia ulvae* (Pennant, 1777), synonym *Peringia ulvae* (Pennant, 1777)). The rough periwinkle was found

at 2.17-2.47 masl (samples 9-14). At 2.27-2.32 masl (sample 12), both juvenile and adult individuals were present, indicative of local occurrence. One of the samples that contained finds of the rough periwinkle (sample 9 at 2.42-2.47 masl) also contained foraminifera, unicellular organisms that occur in brackish and marine environments. The mud snail was present at 2.82-2.92 masl (upper sample 1).

The upper layer at 2.82-2.92 masl (sample 1) stands out from the other samples because it contains not only taxa indicative of marine or brackish conditions that are present in all gyttja samples, but also a variety of freshwater molluses present in small quantities. This concerns the common pond snail (Radix balthica/labiata interpreted as R. balthica (Linnaeus, 1758)), Leach's Bithynia (Bithynia leachii (Sheppard, 1823)), the white ramshorn (Gyraulus albus (O.F. Müller, 1774)), the Nautilus ramshorn (Gyraulus crista (Linnaeus, 1758)), the ramshorn snail (Planorbis planorbis (Linnaeus, 1758)), a pea mussel (Pisidium sp.), the flat valve snail (Valvata cristata (O.F. Müller, 1774)) and the common

valve snail (*Valvata piscinalis* (O.F. Müller, 1774)) (Figure 5). These taxa were not present in a single, thin layer, but were mixed with the shells of brackish and marine water taxa. Many of the freshwater taxa were represented by juveniles, implying that they may have been transported via small freshwater streams into the lagoon.

The ostracods at 2.32-2.37, 2.52-2.57 and 2.72-2.92 masl (samples 11, 7 and the upper three samples), which not only occurred as single carapaces (shells) but also as doublets in samples 11, 2 and 1, do not give direct information about the salinity of the environment. They may represent taxa that live in freshwater, brackish water and/or saltwater conditions.

Plant Macroremains and green Algae

The seeds and fruits from Magleholm were well-preserved. The ecological group that is quantitatively dominant in the studied profile is the group of salt marsh taxa and water plants that tolerate brackish conditions. The species that occurs in all samples except from the sand sample at the bottom of the profile is beaked tassel-

weed (Ruppia maritima L.), a pioneer water plant of shallow brackish water (max. depth 70 cm), which tolerates changes in salinity but does not occur in the sea, represented by tens of fruits per sample (Figure 6). The taxon flourishes in stagnant to slow-flowing water with limited water level changes, such as the low water table zone of areas affected by tide. Peduncles (culms) of up to 4 cm have been found, indicating that the species occurred locally. The occurrence of beaked tasselweed together with horned pondweed (Zannichellia palustris L.), spiny naiad (Najas marina L.), fennel pondweed (Stuckenia pectinata (L.) Börner) and stonewort (Chara sp.), as is the case in the upper three samples at 2.72-2.92 masl, points to the presence of the plant community of the Ruppion maritimae. This community occurs in shallow, clear, calm, brackish water under mesohaline to polyhaline conditions (Iversen 1934, 24; Schaminée et al. 1995, 29-30).

Similar to tasselweed, fruits of common/spear-leaved orache (*Atriplex patula* L./*prostrata* Boucher ex DC.) were found in relatively many samples. Based on the common presence at Magleholm of taxa that indicate brackish or marine conditions, these fruits are interpreted as spear-leaved orache,

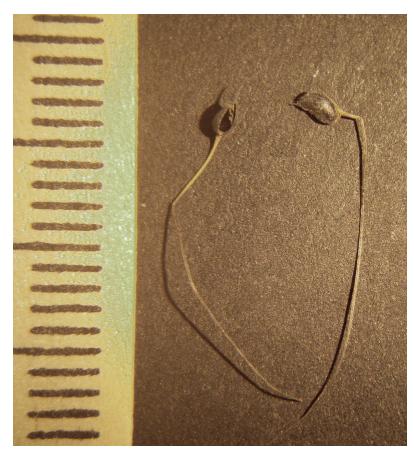


Figure 6. Beaked tasselweed, dried, but very well preserved (Photo: W. Kuijper).

a species that occurs on open, moist, nitrate-rich terrain and at drift litter zones on the beach and in salt marshes.

Other salt marsh taxa whose fruits occur occasionally in the profile are sea aster (*Tripolium pannonicum* (Jacq.) Dobrocz., formerly *Aster tripolium L.*, 2.32-2.37 masl, sample 11), annual seablite (*Suaeda maritima* (L.) Dumort, 2.52-2.57 masl, 2.77-2.92 masl, samples 7, 2 and 1) and grassleaf orache (*Atriplex littoralis L.*, 2.82-2.92 masl, sample 1). Annual seablite is usually found in the intertidal zone and in salt marshes. Since only small quantities are present, these seeds may have been transported with marine influxes occurring during relatively extreme high-water events.

A second group represented by the seeds and fruits in the profile are taxa indicative of alder carr, water edges, freshwater marshes and (to some degree) dune valleys, including common alder (Alnus glutinosa (L.) Gaertn.), cyperus sedge (Carex pseudocyperus L.), great fen-sedge (Cladium mariscus (L.) Pohl), hemp-agrimony (Eupatorium cannabinum L.), European bugleweed (Lycopus europaeus L.), common reed (Phragmites australis (Cav.) Steud), lakeshore bulrush or softstem bulrush (Schoenoplectus lacustris (L.) Palla or tabernaemontani (C.C.Gmel.) Palla), bitter nightshade (Solanum dulcamara L.), water pepper (Persicaria hydropiper (L.) Delarbre), sedge (Carex sp.) and possible chickweed (cf. Stellaria sp.). Of these, cyperus sedge, great fensedge, European bugleweed, reed, bulrush, bitter nightshade and hemp-agrimony tolerate brackish or slightly brackish conditions, while hemp-agrimony can also be found on beaches (Weeda et al. 1988-1994). In contrast, alder explicitly does not tolerate brackish conditions. Bulrush is found in six different samples throughout the profile. The remaining taxa are also found throughout the profile, but only sporadically and hardly ever with more than three taxa in a single sample. The largest number of taxa from this group of water edges, freshwater marshes and dune valleys occur at 2.82-2.92 masl in sample 1 at the top of the profile, which also contains freshwater molluscs and a larger diversity of water plants.

A third group of plants represented in the profile are plants of dryland terrain, including both woodland taxa such as lime (*Tilia* sp.), birch (*Betula* sp.), European hazel (*Corylus avellana*) and blackberry (*Rubus fruticosus* L. agg.) as well as taxa of open, nutrient-rich terrain such as white goosefoot (*Chenopodium album* L.) and possibly trodden terrain (*Polygonum* cf. *aviculare* L.). Some of these taxa occur particularly in the lower and middle part of the profile at 2.22-2.27 masl (sample 13), 2.32-2.37 masl (sample 11) and 2.52-2.57 masl (sample 7).

Discussion

Environment

In a major part of the profile (samples 15-4, 2.07-2.72 masl), the mollusc fauna, with the common mussel, the spire snail and the lagoon cockle as dominant taxa, as well as the common plant taxa beaked tasselweed, bulrush and orache, indicate the presence of a brackish lagoon, with predominantly annual variations in salinity caused by seasonal variation in the freshwater supply and evaporation. The water was calm, clear and shallow, with a depth of c.0.5 m. The presence of the common mussel indicates that the water body was connected to the open sea.

The assemblage at 2.72-2.82 masl (upper samples 2 and 3) includes a greater diversity of salt marsh plants, water plants that tolerate both brackish and freshwater conditions, and ostracods, than the samples below at 2.12-2.62 masl, indicating that an environmental change occurred. The upper 10 cm of the profile (sample 1) contains freshwater molluscs and taxa of water edges, freshwater marshes and dune valleys, including taxa that do not tolerate brackish conditions, and indicate a decrease in the salinity of the lagoon.

With the exception of only a few remains and taxa, the taxa of dry terrain are mostly found in the lower half of the studied profile (at 2.22-2.57 masl, samples 13-7) that represent two different stratigraphical layers. Although it is not clear what the size of the Magleholm island was at this time, these taxa could represent the vegetation on the island, thus indicating erosion and rolling or washing down of seeds and fruits. Alternatively, it may concern remains of vegetation at other dryland patches in the lagoon transported via water.

The upper 10 cm of the profile (2.82-2.92 masl, sample 1) contain relatively many seeds and fruits of taxa of water edges, freshwater marshes and, to some degree, vegetation of dune valleys, including common alder. Such vegetation may have occurred on the slopes of Magleholm island or elsewhere along the borders of the lake. The seeds and fruits may also have been part of a drift litter zone deposited by water (Cappers 1993). In any case, the sample represents a thanatocoenosis, i.e. remains of taxa that did not all live contemporaneously at the same spot but instead represent multiple habitats, since alder does not tolerate brackish conditions while some of the molluscs that occurred locally are indicative of brackish water environments. Considering the thickness of the sample (10 cm) and the occurrence of shells in layers, another explanation for the coexistence of freshwater and brackish water taxa is that periods and/or influxes of more and less brackish water alternated.

Indications of human Impact

The macroremains assemblage contains various edible taxa, including hazelnut, blackberry, sea aster, annual seablite and water pepper, amongst others. However, none of the seeds and fruits were found in a carbonized state, fragmented in such a way that demonstrates handling by people in the past, or found in a context, quantity or concentration that assures deposition by people. While people thus potentially may have used various of the taxa present, there is no explicit evidence of such use. The best indications that the investigated profile intersects refuse layers comes from the finds other than molluscs and seeds and fruits, such as the presence of sand lenses in the gyttja that may have resulted from either storms or erosion of the island, and small fragments of flint and the remains of charcoal present in most samples. A flint fragment (0.0183 g) from 2.32-2.37 masl (sample 11) was possibly worked.

Comparison with earlier published Information about Magleholm

Despite the lack of radiocarbon dates from the studied profile, which may potentially become available when a site report about Magleholm appears, and despite it being unclear how the earlier studied profile and the new profile relate to each other precisely, the analysed data and data from earlier published profiles from Magleholm can be compared with each other. The brackish gyttja in the investigated profile, with a thickness of 60 cm, may correspond with the earlier described marine gyttja layer, which was c.1 m thick elsewhere at Magleholm. The investigated samples indicate a brackish rather than a true marine environment, but there was indeed a connection to the open sea, and the earlier description "marine" can probably primarily be interpreted as opposite to limnic, i.e. freshwater conditions. Whether the earlier reported subboreal transgression, dated between 3850 and 3700-3600 BCE and registered at Magleholm only (Christensen 2014, 11), is present in the studied profile is not clear. Elsewhere in the profile, at 50 cm distance from the analysed samples, a layer rich in molluscs is present between the layers of samples 1 and 2 and perhaps this layer represents the transgression phase. Concerning the earlier reported transgressions and regressions, it should be noted that today the interpretation that large fluctuations as have been observed in the Vedbæk fjord represent oscillations of the global sea level changes is subject to discussion (see e.g. Yu 2003, 16 and the discussion in Bennike et al. 2023, 449).

The upper part of the profile at 2.72-2.92 masl, *i.e.* the three upper samples, represent a gradual transition of the lagoon to a freshwater lake. However, since the upper sample still contains taxa indicative of brackish conditions, this sample must predate the closing of the connection with the sea that was dated to "shortly after 3500 BCE or at least before 3000 BCE" (Christensen 2014, 12). The peat present above the investigated profile matches the peat found in earlier studies at Magleholm and represents the infill of the freshwater lake.

The earlier pollen analysis of Magleholm aimed to date samples and layers and focused much on whether these pre- or postdated Landnam phases. Tasselweed was regularly found, as well as dinoflagellates (*Hystrix* sp.), confirming the brackish conditions. Similar to the current study, the pollen analysis does not show dominance or frequent occurrence of obligate marine plant taxa. Also the Chenopodiaceae and Asteraceae, which may include salt marsh taxa, do not reach include high percentages.

Short Comparison with other Locations

Brackish waters commonly occurred along the Danish coast during the middle Holocene. Locations from which macroremains and mollusc data are available and that point to environmental conditions that are comparable to Magleholm include e.g. Brabrand fjord (eastern Jutland), Syltholm (Lolland) and Gilleleje (northern Sjælland). Brabrand fjord had an open connection to the sea between 7500 BCE (8500 cal BP) and 3500-900 BCE (5200-2900 cal BP). The mollusc assemblage contained taxa of marine and brackish conditions, while the macroremains assemblage was characterized by scarce finds of particularly tasselweed and additionally a few remains of horned pondweed (Bennike et al. 2022, 111-112). At the coastal zone of Syltholm, slightly more saline conditions occurred during the Middle Holocene than at Magleholm (Bennike and Jessen 2023, 37-39; Bennike et al. 2023: phase with tasselweed, horned pondweed, charophytes, mud snail, cockle, periwinkle and common mussel). At Gilleleje, beaked tasselweed and spiny naiad dominate the macroremains sample from a profile dating to 5100-5300 BCE, but the frequent presence of the common cockle indicates that the environment must have been more affected by the sea than at Magleholm. Like at Magleholm, also at this location the samples show a combination of taxa from a brackish water environment and dryland taxa (Henriksen and Jessen 2014, 2015).

Conclusions and wider Perspective

The analysis of molluscs and botanical macroremains presented above provides a paleoenvironmental reconstruction of the Mesolithic and

Neolithic site of Magleholm in the Vedbæk fjord. The sample location, located at c.10 m distance from the shore of a brackish water lagoon that ultimately changed into a more freshwater environment, can be interpreted as an off-site location. Indications of human activity include small pieces of flint, charcoal, carbonized fish and carbonized culms. The botanical macroremains give information about the vegetation present in the larger area, including salt marsh vegetation of the brackish lagoon, woodland vegetation and later also vegetation of water edges, freshwater marshes, beaches and dune valleys. Although the environmental reconstruction of Magleholm is based on data from only a single sample column, the data are relatively consistent and compatible with earlier environmental reconstructions of the lagoon. While the plant data from Magleholm hardly provide concrete evidence of plant use, they do give information about the vegetation types present in the fjord, the environment that the people living at Magleholm experienced on a daily basis and the plant resources that were available to them (cf. Schepers 2014).

Since the publications by Zvelebil (1994) and Mason and Hather (2002), the number of macrobotanical analyses of Mesolithic sites has shown a strong increase all over Europe (e.g. Antolín et al. 2016; Bishop 2021; Bishop et al. 2014, 2015; Deforce et al. 2013; Jensen et al. 2024; Lagerås et al. 2021; Lopez-Doriga 2016; Out 2009; Ptáková et al. 2021). On the one hand, macrobotanical studies in Denmark, also of Mesolithic sites, have a long history (e.g. Broholm 1924, 19-20), but on the other hand, information on plant use in the Mesolithic in this region is still relatively scarce, as recently discussed in a review by Termansen et al. (2024). Data from coastal Mesolithic sites are even rarer. The present study from Magleholm, although having its limitations because of the absence of more precise context information, thus makes an important contribution, even more since there are hardly any other botanical data sets available from the Vedbæk fjord. Hence, this study underlines both the potential of and need for additional botanical macroremains analysis at comparable archaeological sites. Additional archaeobotanical analyses of other Mesolithic sites in Scandinavia, as well as sites that cover both

Mesolithic and Neolithic occupation phases, would be highly relevant, for example to shed light on the use of both food plants and those that provided raw materials, as well as on the character and extent of human impact on the vegetation and how this interplay developed through time, to get a better understanding of former societies and cultural processes (e.g. Bakels and Van Beurden 2001; Bakels et al. 2001; Holst 2010; Kubiak-Martens et al. 2015; Out 2008a, b; Out and Verhoeven 2014; Schepers and Bottema 2020; Sørensen and Karg 2014; Wolters 2016; see also Blaesild et al. 2024; Groß et al. 2018). In this respect, the current PhD project by Signe Sangill Termansen at Aarhus University, focusing on submerged coastal Mesolithic sites, is expected to provide an important contribution to the understanding of plant use in Southern Scandinavia.

In the case of future excavations of similar Mesolithic and Neolithic sites with partially waterlogged deposits, it would, in so far the presence of undisturbed deposits allows, be relevant to combine an off-site environmental study like this and palynological analysis, ideally including multiple cores, with analysis of grid sampling and analysis of both carbonized botanical macroremains of samples from the slopes and dry parts of the dune, analysis of samples of carbonized and uncarbonized, worked and unworked wood, and, for example, phytolith and starch analysis of food crusts, grinding stones and/or dental calculus from human teeth. Applying such a multi-proxy approach within the framework of a wider archaeological study could give a reconstruction of the use of a broad range of plants, covering the use of plants, including wild plants, for food, fuel and craft, while it could also contribute to the understanding of activity zones, the function of archaeological features, and depositional and taphonomical processes. Given the scarcity of archaeobotanical data so far, especially from Mesolithic sites, future excavations have a strong potential to gather a wealth of new data.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Notes

1 The Vedbæk water body was not always a fjord but was connected to the sea during the period studied in the project (discussed further below).

References

Aaris-Sørensen, K., 1982. Jæger og byte. Søllerødbogen 1982, 131-138.

Albrethsen, S.-E. and Petersen, E.B., 1977. Excavation of a Mesolithic cemetery at Vedbæk, Denmark. *Acta Archaeologica* 1976, 47, 1-28.

Antolín, F., Berihuete, M. and López, O., 2016. Archaeobotany of wild plant use: Approaches to the

- exploitation of wild plant resources in the past and its social implications. *Quaternary International* 404(A), 1-3. https://doi.org/10.1016/j.quaint.2016.01.029
- Avnholt, A., 1944. Oldtidsminder og Oldtidsfund i Søllerød Kommune. Søllerødbogen 1944, 41-72.
- Bakels, C.C., 1981. Neolithic plant remains from the Hazendonk, Province of Zuid-Holland, The Netherlands. *Zeitschrift für Archäologie* 15, 141-148.
- Bakels, C.C. and Beurden, L.M. van, 2001. Archeobotanie. *In*: L.P. Louwe Kooijmans, ed. *Archeologie in de Betuweroute. Hardinxveld-Giessendam Polderweg* (Rapportage Archeologische Monumentenzorg 83). Amersfoort: Rijksdienst voor het Oudheidkundig Bodemonderzoek, 325-378.
- Bakels, C.C., Beurden, L.M. van and Vernimmen, T.J.J., 2001. Archeobotanie. *In*: L.P. Louwe Kooijmans, ed. *Archeologie in de Betuweroute. Hardinxveld-Giessendam De Bruin* (Rapportage Archeologische Monumentenzorg 88). Amersfoort: Rijksdienst voor het Oudheidkundig Bodemonderzoek, 369-434.
- Becket, S.C., 1978a. The environmental setting of the Meare Heath Track. Somerset Levels Papers 4, 42-46.
- Becket, S.C., 1978b. Paleobotanical investigations at the Difford's 1 site. *Somerset Levels Papers* 4, 101-106.
- Behre, K.-E., 1969. Untersuchungen des botanischen Materials der frühmittelalterlichen Siedlung Haithabu (Ausgrabung 1963-1964) (Die Ausgrabungen in Haithabu 2). Neumünster: Wachholtz, 7-55.
- Behre, K.E., 1976. Die Pflanzenreste aus der frühgeschichtlichen Wurt Elisenhof. Frankfurt am Main: Lang.
- Bennike, O., Astrup, P.M., Odgaard, B.V., Pearce, C. and Wiberg-Larsen, P., 2022. Holocene development of Brabrand Fjord, eastern Jylland, Denmark. *Bulletin of the Geological Society of Denmark* 70, 105-115. https://doi.org/10.37570/bgsd-2022-70-07
- Bennike, O. and Jessen, C., 2023. Environmental changes after the last deglaciation, southern Lolland, Denmark. *In*: D. Groß and M. Rothstein, eds. *Changing identity in a changing world*. Leiden: Sidestone Press, 33-42.
- Bennike, O., Philipsen, B., Groß, D. and Jessen, C., 2023. Holocene shore-level changes, southern Lolland and the Femern Belt, Denmark. *Journal of Quaternary Science* 38(3), 440-451. https://doi.org/10.1002/jqs.3479
- Bishop, R.R., 2021. Hunter-gatherer carbohydrate consumption: plant roots and rhizomes as staple foods in Mesolithic Europe. *World Archaeology* 53(2), 175-199. https://doi.org/10.1080/00438243.2021.2002715
- Bishop, R.R., Church, M.J. and Rowley-Conwy, P.A., 2014. Seeds, fruits and nuts in the Scottish Mesolithic. *Proceedings of the Society of Antiquaries of Scotland 143*, 9-71. https://doi.org/10.9750/psas.143.9.71
- Bishop, R.R., Church, M.J. and Rowley-Conwy, P.A., 2015. Firewood, food and human niche construction: the potential role of Mesolithic hunter-gatherers in actively structuring Scotland's woodlands. *Quaternary Science Reviews* 108, 51-75. https://doi.org/10.1016/j.quascirev.2014.11.004

- Blaesild, P., Hallgren, F., and Nielsen, A.B. 2024. Early Holocene vegetation development at Mesolithic fen dwelling sites in Dagsmosse, south-central Sweden, and its implications for understanding environment—human dynamics at various scales. *Palaeogeography, Palaeoclimatology, Palaeoecology* 641, 112106. https://doi.org/10.1016/j.palaeo.2024.112106.
- Broholm, H.C., 1924. Nye fund fra den ældste stenalder, Holmegaard og Sværdborgfundene. *Aarbøger for Nordisk Oldkyndighed og Historie*, 1-144.
- Cappers, R.T.J., 1993. Seed dispersal by water: a contribution to the interpretation of seed assemblages. Vegetation History and Archaeobotany 2, 173-186. https://doi.org/10.1007/bf00198588
- Casparie, W.A., Mook-Kamps, B., Palfenier-Vegter, R.M., Struijk, P.C. and Zeist, W. van, 1977. The palaeobotany of Swifterbant. *Helinium* 17, 28-55.
- Cadée, G.C. and Wesselingh, F.P., 2005. Van levend schelpdier naar fossiele schelp: tafonomie van Nederlandse strandschelpen. *Spirula* 343, 36-52.
- Christensen, C., 1982. Havniveauændringer 5500-2500 f.Kr. i Vedbækområdet, NØ-Sjælland. *Dansk Geologisk Forening, Årsskrift for 1981*, 91-107.
- Christensen, C., 2014. Havniveauændringer 6000-3000 f.Kr. i Vedbæk-området, NØ-Sjælland fortsatte geobotaniske undersøgelser i årene 1982-1990. *Nationalmuseets Naturvidenskabelige Undersøgelser NNU-rapport* 2014-15.
- Deforce, K., Bastiaens, J., Van Neer, W., Ervynck, A., Lentacker, A., Sergant, J. and Crombé, P., 2013. Wood charcoal and seeds as indicators for animal husbandry in a wetland site during the Late Mesolithic–Early Neolithic transition period (Swifterbant culture, ca. 4600-4000 B.C.) in NW Belgium. *Vegetation History and Archaeobotany* 22, 51-60. https://doi.org/10.1007/s00334-012-0354-2
- Duistermaat, H., 2020. Heukels flora van Nederland. Groningen: Natural Biodiversity Centre/Noordhoff.
- Enghoff, I.B., 1995. Fishing in Denmark during the Mesolithic period. *In*: A. Fischer, ed. *Man and Sea in the Mesolithic. Coastal settlement above and below present sea level* (Oxbow Monograph 53). Oxford: Oxbow Books, 67-74.
- Fredskild, B., 1969. Nordboernes landnam under mikroskop. Nationalmuseets Arbejdsmark 1969, 46-58.
- Gaillard, M-J. and Lemdahl, J., 1988. Plant macrofossil analysis (seeds and fruits) at Skateholm-Järavallen, southern Sweden. A lagoonal landscape during Atlantic and early Sub-Boreal time. *In*: L. Larson, ed. *The Skateholm project I. Man and environment.* Stockholm: Almqvist and Wiksell, 34-38.
- Gittenberger, E., Janssen, A.W., Kuijper, W.J., Kuiper, J.G.J., Meijer, T., Van der Velde, G. and Vries, J.N. de, 2004. De Nederlandse zoetwatermollusken recente en fossiele weekdieren uit zoet en brak water. Leiden: Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij, European Invertebrate Survey Nederland.
- Glöer, P., 2002. Die Süßwassergastropoden Nord- und Mitteleuropas (Die Tierwelt Deutschlands 73). Hackenheim: ConchBooks.

- Göransson, H., 1988. Neolithic man and the forest environment around Alvastra pile dwelling. Lund: Lund University Press.
- Götting, K-J., 2008. Meeres-Gehäuseschnecken Deutschlands (Die Tierwelt Deutschlands 80). Hackenheim: ConchBooks.
- Groß, D., Zander, A. Boethius, A., Dreibrodt, S., Grøn, O., Hansson, A., Jessen, C., Koivisto, S., Larsson, L., Lübke, H. and Nilsson, B., 2018. People, lakes and seashores: Studies from the Baltic Sea basin and adjacent areas in the early and Mid-Holocene. *Quaternary Science Reviews* 185, 27-40. https://doi.org/10.1016/j.quascirev.2018.01.021
- Henriksen, P.S. and Jessen, C., 2014. Naturvidenskabelige undersøgelser af mesolitiske kystaflejringer ved Kulturhavn Gilleleje. *Nationalmuseets Naturvidenskabelige Undersøgelser NNU-rapport* 2014-86 (A9265).
- Henriksen, P.S. and Jessen, C., 2015. De naturvidenskabelige undersøgelser af kystaflejringer ved Kulturhavn Gilleleje. *Museum Nordsjællands Årbog* 2015, 95-88.
- Holst, D., 2010. Hazelnut economy of early Holocene hunter-gatherers: A case study from Mesolithic Duvensee, northern Germany. *Journal of Archaeological Science* 37(11), 2871-2880. https://doi.org/10.1016/j.jas.2010.06.028.
- Iversen, J., 1934. Studien over vegetationen i Ringkøbing Fjord for Hvide Sande-kanalens aabning 1931. In: A.C. Johansen, H. Blegvad and R. Spärck, ed. Ringkøbings Fjord naturhistorie i brakvadsperioden 1915-1931. Copenhagen: Høst, 18-35.
- Jacomet, S., Brombacher, C. and Dick, M., 1989. Archäobotanik am Zürichsee (Berichte der Zürcher Denkmalpflege, Monographien 7). Zürich: Füssli.
- Jensen, C.E., Hamre, E., Lempiäinen-Avci, M., Panagiotakopulu, E., Macphail, R. and Elo, R., 2024. Submerged Mesolithic plant remains reveal lush thermophilous woodland on remote isle off the SW-Norwegian coast. *Quaternary International* 713, 1-20. https://doi.org/10.1016/j.quaint.2024.10.003
- Jensen, H.J. and Petersen, E.B., 1985. A functional study of lithics from Vænget Nord, a Mesolithic Site at Vedbæk, N. E. Sjælland. *Journal of Danish Archaeology* 4, 40-51. https://doi.org/10.1080/0108464x.1985.10589934
- Juel, C. and Kjær, A., 2015. The earliest Neolithic at Vedbæk fjord, Denmark. An overlooked horizon. In: E.B. Petersen, J.H. Jønsson, C. Juel and A. Kjær, eds. Diversity of Mesolithic Vedbæk (Acta Archaeologica 86). Oxford: Wiley, 217-225. https://doi.org/10.1111/j.1600-0390.2015.12068.x
- Körber-Grohne, U., 1967. Geobotanische Untersuchungen auf der Feddersen Wierde, vol 1. Wiesbaden: Franz Steiner.
- Kubiak-Martens, L., Verbruggen, F., and Kooistra, L. I., 2015. Archaeobotany: landscape reconstruction and plant food subsistence economy on a meso and microscale. *In*: J.M. Moree and M.M. Sier, eds. *Twenty meters deep! The Mesolithic period at the Yangtze Harbour site Rotterdam Maasvlakte, the Netherlands. Early Holocene landscape development and habitation*. Rotterdam: Bureau Oudheidkundig Onderzoek Rotterdam, 223-286.

- Kuijper, W., 2000. De weekdieren van de Nederlandse brakwatergebieden (Mollusca). Nederlandse Faunistische Mededelingen 12, 41-120.
- Lagerås, P., Broström, A. and Svensson, N.-O., 2021. Insamling av ätlige växter och ved under mesolitikum. *In*: E. Rudebeck and M. Anglert, eds. *At leva vid Vesan*. Malmö: Holmbergs, 139-160.
- Lopez-Doriga, I., 2016. La utilización de los recursos vegetales durante el Mesolítico y Neolítico en las costa Atlántica del peninsula Ibérica. Santander: PhD thesis Universidad de Cantabria, Department of Ciencias Históricas.
- Mason, S. and Hather, J.G., 2002. *Hunter-Gatherer Archaeobotany: Perspectives from the Northern Temperate Zone*. London: University College London. https://doi.org/10.4324/9781315427171
- Møller, P.R. and Carl, H., 2010. Atlas over danske saltvandsfisk. Dyr i natur og museum 2010, nr. 1.
- Mørck, P.B., Casati, C., Hansen, F., Riis, K.M., Sørensen, L. and Kristensen, J.T., 1999. Vedbæk ældste stenalderboplads. *Søllerødbogen* 1999, 7-31.
- Muus, B.J., 1967. The fauna of Danish estuaries and lagoons. Meddelelser fra Danmarks Fiskeri og Havundersøgelser Ny Serie 5(1).
- Out, W.A., 2008a. Neolithisation at the site Brandwijk-Kerkhof, the Netherlands: natural vegetation, human impact and plant food subsistence. *Vegetation History and Archaeobotany* 17(1), 25-39. https://doi.org/10.1007/s00334-007-0108-8
- Out, W.A., 2008b. Gathered food plants at Dutch Mesolithic and Neolithic wetland sites. *In*: S. Baker, M. Allen, S. Middle and K. Poole, eds. *Conference proceedings Food and drink in archaeology: a postgraduate conference*. Totnes: Prospect Books, 84-95.
- Out, W.A., 2009. Sowing the seed? Human impact and plant subsistence in Dutch wetlands during the Late Mesolithic and Early and Middle Neolithic (5500-3400 cal BC). Archaeological Studies Leiden University 18. Leiden: Leiden University Press. https://doi.org/10.5117/9789087280727
- Out, W.A., 2010. Integrated archaeobotanical analysis: Human impact at the Dutch Neolithic wetland site the Hazendonk. *Journal of Archaeological Science* 37(7), 1521-1531. https://doi.org/10.1016/j.jas.2010.01.012
- Out, W.A., 2012. What's in a hearth? Seeds and fruits from the Neolithic fishing and fowling camp at Bergschenhoek, the Netherlands, in a wider context. *Vegetation History and Archaeobotany* 21(3), 201-214. https://doi.org/10.1007/s00334-011-0338-7
- Out, W.A. and Dörfler, W., 2017. The best of both worlds: Human impact and plant subsistence at the Middle and Late Neolithic semi-agricultural site of Hekelingen III (2900-2500 BC). *Quaternary International* 436(B), 41-63. https://doi.org/10.1016/j.quaint.2015.11.081
- Out, W.A. and Verhoeven, K., 2014. Late Mesolithic and Early Neolithic human impact at Dutch wetland sites: the case study of Hardinxveld-Giessendam De Bruin. *Vegetation History and Archaeobotany* 23(1), 41-56. https://doi.org/10.1007/s00334-013-0396-0

- Petersen, P.V., 1982. Stenalderbopladser under Vedbæk by. Søllerødbogen 1982, 139-152.
- Petersen, P.V., 1984. Chronological and regional variation in the Late Mesolithic of Eastern Denmark. *Journal of Danish Archaeology* 3, 7-18. https://doi.org/10.1080/0108464x.1984.10589909
- Petersen, E.B., Alexandersen, V., Petersen, P.V. and Christensen, C. 1979. Vedbækprojektet. Ny og gammel forskning. Søllerødbøgen 1979, 21-29.
- Petersen, E.B., Jensen, H.J., Aaris-Sørensen, K. and Petersen, P.V., 1982. Vedbækprojektet. Under mosen og byen. *Søllerødbogen 1982*, 117-152.
- Petersen, E.B., 1985. Magleholm. Arkwologiske udgravninger i Danmark katalog 1984.
- Petersen, E.B., Jønsson, J.H., Juel, C. and Kjær, A., 2015. *A Diversity of Mesolithic Vedbak* (Acta Archaeologica 86(1)). Oxford: Wiley. https://doi.org/10.1111/j.1600-0390.2015.12048.x
- Ptáková, M., Šída, P. and Kovačiková, L., 2021. What was on the menu? Mesolithic cooking and consumption practices in inland central Europe based on analysis of fireplaces. *Quaternary International* 586, 90-104. https://doi.org/10.1016/j.quaint.2021.01.017
- Schaminée, J.H.J., Weeda, E.J. and Westhoff, V., 1995. De vegetatie van Nederland 2. Wateren, moerassen, natte heiden. Leiden: Opulus Press.
- Schepers, M., 2014. Wet, wealthy worlds: The environment of the Swifterbant river system during the Neolithic occupation (4300-4000 cal BC). *Journal of Archaeology in the Low Countries* 5, 79-106.
- Schepers, M. and Bottema-Mac Gillavry, N., 2020. The vegetation and exploitation of plant resources. In: D.C.M. Raemaekers and J.P. de Roever (eds). *Swifterbant S4 (the Netherlands): Occupation and exploitation of a Neolithic levee site (c.4300-4000 cal. BC)*. (Groningen Archaeological Studies 36). Groningen: Barkhuis, 51-76. https://doi.org/10.2307/j.ctv13nb6ns.8
- Schlichtherle, H., 1990. Siedlungsarchäologie im Alpenvorland I. Die Sondagen 1973–1978 in der Ufersiedlung Hornstaad-Hörnle I. Befunde und Funde zum Frühen Jungneolithikum am westlichen Bodensee (Forschungen und Berichte zur Vor- und Frügeschichte Baden-Württemberg 36). Stuttgart: Theiss. https://doi.org/10.29091/9783752002034
- Sørensen, L., 2014. From hunter to farmer in Northern Europe. Migration and adaptation during the Neolithic and Bronze Age (Acta Archaeologica 85(2)). Oxford: Wiley.
- Sørensen, L. and Karg, S., 2014. The expansion of agrarian societies towards the north new evidence for agriculture during the Mesolithic/Neolithic transition in Southern Scandinavia. *Journal of Archaeological Science* 51, 98-114. https://doi.org/10.1016/j.jas.2012.08.042
- Termansen, S.S., Astrup, P.M., Out, W.A. and Johannsen, N.N., 2024. Rebooting the study of forager plant economies: The potential of submerged archaeological sites. *Environmental Archaeology*, 1-12. https://doi.org/10.1080/14614103.2024.2393015
- Troels-Smith, J., 1960. The Muldbjerg dwelling place: an early neolithic archaeological site in the

- Aamosen bog, West-Zealand, Denmark. *Annual Report of the Board of Regent of the Smithsonian Institution* 1959, 577-601.
- Weeda, E.J., Westra, R., Westra, C. and Westra, T., 1988-1994. Nederlandse oecologische flora. Wilde planten en hun relaties 1-5. Amsterdam: KNNV.
- Welter-Schultes, F., 2012. European non-marine molluscs, a guide for species identification. Göttingen: Planet Poster Editions.
- Wolters, S., 2016. Die pflanzlichen Makroreste der Mesolithstation Friesack. *In*: N. Benecke, B. Gramsch and Jahns, S., eds. *Subsistenz und Umwelt der Feuchtbodenstation Friesack 4 im Havelland: Ergebnisse der naturwissenschaftlichen Untersuchungen*. Brandenburg: Brandenburgisches Landesamt für Denkmalpflege und Archäologisches Landesmuseum, 189-203.
- Yu, S., 2003. The Littorina transgression in southeastern Sweden and its relation to mid-Holocene climate variability. Lund: Doctoral Thesis Lund University, Department of Geology.
- Zvelebil, M., 1994. Plant use in the Mesolithic and its role in the transition to farming. *Proceedings of Prehistoric Society* 60, 35-74. https://doi.org/10.1017/s0079497x00003388