Last Interglacial (Eemian) hydrographic conditions in the southeastern Baltic Sea, NE Europe, based on dinoflagellate cysts

Martin J. Head[a,*], Marit-Solveig Seidenkrantz[b], Zofia Janczyk-Kopikowa[c], Leszek Marks[c,d], Philip L. Gibbard[a]

[a] Godwin Institute for Quaternary Research, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK
[b] Department of Earth Sciences, University of Aarhus, DK-8000 Århus C, Denmark
[c] Polish Geological Institute, Rakowiecka 4, PL-00-975 Warsaw, Poland
[d] Institute of Geology, Warsaw University, Zwirki i Wigury 93, PL-02-089 Warsaw, Poland

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Abstract

A rich organic-walled dinoflagellate cyst and pollen record from the Licze borehole in northern Poland has been used to reconstruct the hydrographic history of the southeastern Baltic Sea during the Last Interglacial (Eemian Stage, Late Pleistocene). Warm, saline waters (ca. 10–15 psu) entered the site from the North Sea within the first few hundred years of the Eemian, corresponding to the *Pinus–Betula* (E1) or *Pinus–Betula–Ulmus* (E2) regional pollen assemblage zones (RPAZ). By about 300 years (beginning of RPAZ E3), dinoflagellate cyst assemblages were already indicating summer sea-surface salinities in excess of about 15 psu and temperatures that perhaps exceeded 27°C. Warm and saline conditions of 15–20 psu or more, at least twice present levels, persisted throughout the early Eemian. A rise in sea level at Licze appears to correlate with a similar event in eastern Denmark, as both coincide with the increase in *Corylus* (ca. 750 years into the interglacial). This sea-level rise might therefore have a basinwide extent, and appears to correspond to an opening of the Danish Belts. There is little if any evidence of arctic waters throughout the sequence. Whereas dinoflagellate cysts reflect sustained high salinites within the upper water column, a concomitant increase in abundance of the chlorococcalean alga *Pediastrum* within the *Carpinus–Corylus–Alnus* (E5) RPAZ indicates an escalating freshwater input, presumably from the proto-Vistula whose mouth was nearby. This suggests the development of a thin, seasonal, low-salinity surface layer below which dinoflagellates lived in more saline waters. Increasing fluvial influence suggests shallowing through RPAZ E5. This study is the first to document dinoflagellate cysts from the Eemian of the southeastern Baltic Sea, and reveals a flora with distinctive Lusitanian/Mediterranean affinities.
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1. Introduction

The Last Interglacial (equivalent to the Eemian Stage, and approximately to Marine Isotope Substage 5e; Kukla et al., 2002) began at about 130 ka with the retreat of glaciers that had extended over much of northern Europe in Saalian times. As a consequence the Baltic Sea region was left isostatically depressed, and rising global sea level at the start of the Eemian led swiftly to the establishment of marine conditions (Liivrand, 1984, 1991; Kalnina, 2001). Surface water temperatures and salinities soon exceeded those of today, and in addition to a narrow seaway across northern Germany, two main portals developed: one connecting to the North Sea in the Danish area, and another that linked the Baltic Sea to the White Sea by means of a seaway across the Karelian Isthmus in Russia (Fig. 1). This Karelian seaway was until recently thought to have permitted free exchange between the Baltic and White seas (e.g., Donner, 1995, fig. 6.1), but is now considered to have been too restricted for this to have happened (Funder et al., 2002).

The present study focuses on marine, organic-walled dinoflagellate cysts and other aquatic palynomorphs in the Licze borehole (19°07′45″E, 53°44′45″N), located about 5 km to the west of Prabuty in northern Poland (Figs. 1

*Corresponding author. Tel.: +44-1223-339751; fax: +44-1223-333392.

E-mail address: mh300@cam.ac.uk (M.J. Head).

Fig. 1. Eemian hydrography and geography of the Baltic Sea region during maximum inundation in the early Eemian (based on Funder et al., 2002). The present study area is marked, along with other Eemian sites mentioned in the text. RK = Ristinge Klint, M = Mommark.
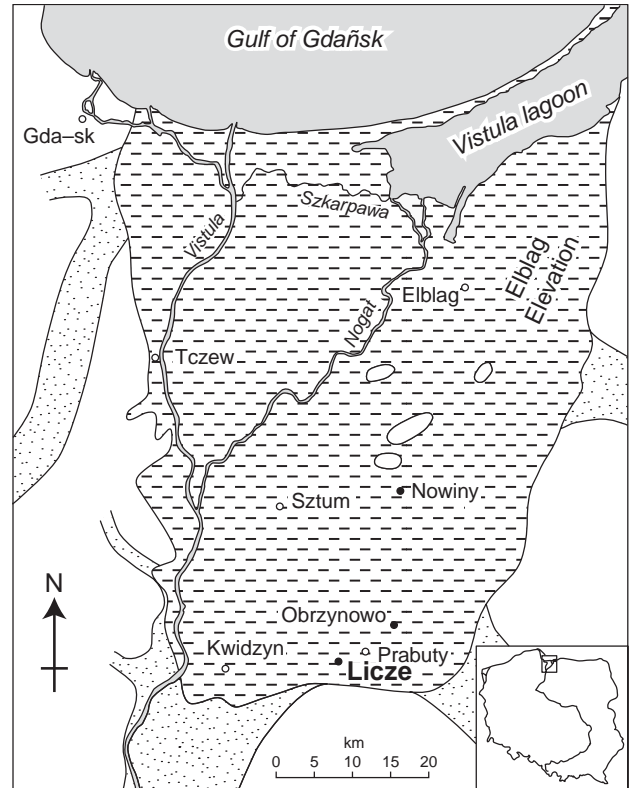

Fig. 2. Sketch of the Lower Vistula region, northern Poland with the marine limit of the Eemian sea and location of the Licze, Nowiny and Obrzynowo boreholes (solid dots) and nearby towns (open dots). The extent of marine Eemian deposits (horizontal shading) and coeval fluvial deposits (stippling) is also shown.

and 2). The specific aims of our study are to understand the nature and timing of marine transgression into the southeastern Baltic Sea during the early Eemian, and to assess whether the Karelian seaway influenced surface water conditions by facilitating the inflow of arctic waters. Summer upper-water-column salinity and temperature are reconstructed accordingly, but because the proto-Vistula entered the sea nearby during Eemian times, it has been necessary to differentiate as far as possible between local and regional influences on hydrography. Pollen stratigraphy and its correlation to the well-dated pollen record at Bispingen in northern Germany (Müller, 1974; Field et al., 1994) provides a tentative chronostratigraphic control for the Licze borehole.

This study is part of a larger investigation into the Eemian of both the Licze core and a nearby core at Obrzynowo (Fig. 2). The mollusc faunas have been published by Makowska (2001) whereas publications on the foraminifera, ostracods and diatoms are forthcoming. Previous studies of dinoflagellate cysts from the Eemian of the Baltic Sea are limited to the Gulf of Bothnia (Eriksson et al., 1999), Denmark (Head and Gibbard, 2000) and to a brief general account (Head et al., 2001) and short taxonomic study (Head, 2003). The present work is therefore the first to document Eemian dinoflagellates in detail from the southeastern Baltic.

2. Dinoflagellate cysts

Dinoflagellates are almost exclusively unicellular protists, and include both autotrophic and heterotrophic species (Fensome et al., 1993). Dinoflagellates are mostly planktonic, but unlike diatoms have a motile stage in their life cycle that allows them to control and optimise their position in the water column (Levandowsky and Kaneta, 1987). Many dinoflagellates produce a resting cyst (as a strategy for over-wintering in mid to high latitudes) whose wall is generally very resistant to degradation, and the geological record of dinoflagellates is based on these species (Head, 1996). Owing to the sensitivity of dinoflagellates to salinity, temperature, and nutrient levels over a wide range of environmental parameters, and to the high preservability of the cysts, the Quaternary record of dinoflagellate cysts is becoming increasingly used for reconstructing sea-surface conditions (Dale, 1996; Rochon et al., 1999; Matthiessen and de Vernal, 2001; Dale and Dale, 2002).

3. Present hydrography

The present day Baltic Sea is one of the world's largest bodies of brackish water, with surface salinities generally not exceeding 10 psu. Summer sea-surface temperatures are generally above 19°C over most of the southern and eastern Baltic Sea (Bundesamt für Seeschiffahrt und Hydrographie, 2002), largely due to water stratification. The Gulf of Gdansk is characterised by a highly dynamic hydrography (Pastuszak, 1995), and is strongly influenced by freshwater outflow from the Vistula, the largest freshwater source entering the Baltic Sea in the area. Surface water salinity reaches about 8 psu, but lower salinities averaging about 4.0 psu are found close to the mouth of the Vistula. Sea-surface temperatures in the Gulf of Gdansk reach between 19°C and 24°C during summer (Nowacki and Jarosz, 1998). In the outer part of the Gulf of Gdansk during summer, a thermocline is established at about 20 m and halocline at about 70 m, but in the inner parts of the bay a freshened surface layer 1 or 2 m deep results from discharge from the Vistula (Nowacki and Jarosz, 1998).

4. Geological and palaeoenvironmental background

An embayment of the Baltic Sea occupied the Lower Vistula region in northern Poland during Eemian time (Figs. 1 and 2). This embayment was 40–65 km wide and reached 70–75 km inland to the south of the present Gulf of Gdansk. It was fed by the proto-Vistula, which was presumably the largest of several rivers entering the Baltic Sea from the south during the Eemian. Marine Eemian silts and clays in the Lower Vistula region reach up to 10 m thick, and include pollen, mollusc shells, ostracods and foraminifera. These Eemian marine deposits are underlain by late Saalian glaciolacustrine clays and silts, and are overlain by late Eemian and Early Vistulian (=Early Weichselian) fluvial sands with thin peat intercalations.

The marine Eemian sediments of this region occur both as glaciodislocated and undisturbed in-situ deposits. They were first described by Roemer (1864) and Berendt (1866), and have since been studied repeatedly from boreholes and escarpments along the Lower Vistula valley (Makowska, 1979, 1986, and references therein) where they represent the Tychnowy Sea transgression of Polish literature (Makowska, 2001; Makowska et al., 2001). They are also widely known from boreholes and outcrops in the Elblag Elevation (Fig. 2) to the east of the Lower Vistula delta, where they have been dislocated intensively by subsequent ice movement and undoubtedly derive from the bottom of the Lower Vistula embayment.

Eemian marine sediments have also been noted recently from north-westernmost Poland near Sliwin and Rewal (Krzyszkowski et al., 1999). These deposits consist of fine-grained sand to sandy silt and shell detritus, and represent a beach or lagoonal facies.

However, it is in the Lower Vistula region that Eemian marine sequences are most complete. Here, evidence from shoreface and deeper-water molluscs, particularly from Elblag and the Nowiny borehole (Makowska, 1986; Funder et al., 2002; Fig. 2), depicts a protected embayment in which sea-surface salinities and temperatures were considerably higher than today, resulting from an early connection to the North Sea. In the Nowiny borehole, marine incursion began at the onset of the *Quercus–Fraxinus–Ulmus* regional pollen assemblage zone (RPAZ E3) of Mamakowa (1988, 1989) and lasted until some time into the *Picea–Abies–Alnus* zone (RPAZ E6) (Makowska, 1986). Molluscs, including the foreshore/tidal zone species *Retusa umbilicata*, indicate that salinity culminated in RPAZ E3 where it periodically rose above 30 psu, which is more than 20 psu higher than present, although surface-water salinity was in general probably not higher than 25 psu. High salinities persisted from RPAZ E3 until the end of the *Carpinus–Corylus–Alnus* zone (RPAZ E5; Makowska, 1986; Funder et al., 2002). It is also noteworthy that the occurrence of Lusitanian mollusc species indicates a winter sea-surface temperature of about 9°C, which is 6°C warmer than today (Funder et al., 2002).

Eemian marine sequences within the Lower Vistula region have been studied from numerous boreholes, but only those drilled within the mapping project of the Detailed Geological Map of Poland on the scale 1:50,000 were fully cored. This project was initiated in the early 1950s and is co-ordinated by the Polish Geological Institute in Warsaw. These boreholes create a network of key sites that elucidate the regional Quaternary stratigraphy, and shed new light not only on marine ingressions during the Eemian but also on glacial episodes during the Vistulian (Weichselian) (Makowska, 1976, 1979, 1986).

The Licze borehole, drilled in 1995 as an integral part of this scheme, is situated just 5–7 km offshore of the southernmost limit of the embayment of the Eemian Baltic Sea (Fig. 2). Mapping was completed by Makowska et al. (2001), the Licze borehole contributing to the Prabuty sheet.

5. Sedimentology and palaeoecology of the licze borehole

The Licze borehole is located on a morainic plateau at 87 m above sea level, and the Quaternary sequence is 168 m thick (Fig. 3). The sedimentology and lithostratigraphy of this borehole are based on Zawidzka (1997) and Makowska et al. (2001), and the palaeoecology uses evidence from molluscs (Makowska, 2001). These studies are summarised below and in Fig. 3.
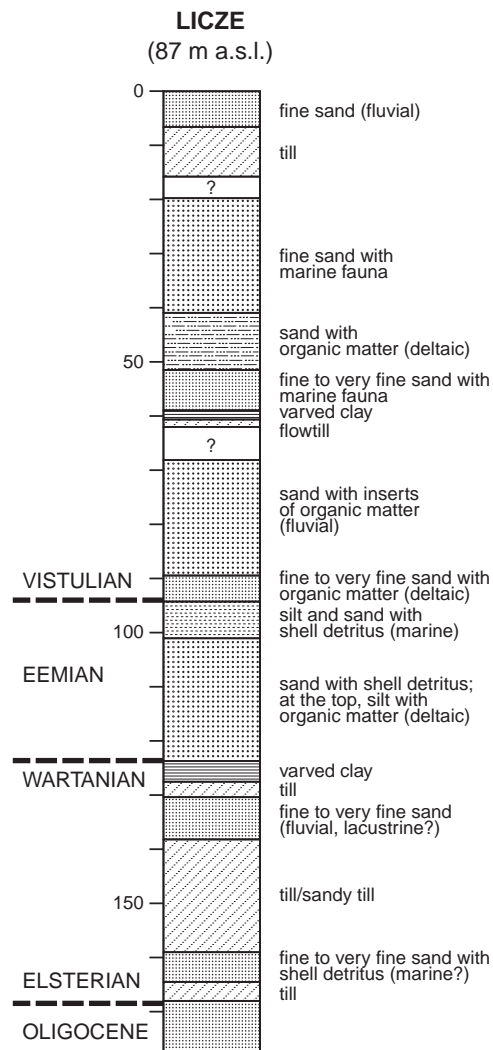
LICZE
(87 m a.s.l.)

Fig. 3. Quaternary stratigraphy and lithology of the Licze borehole.

The Quaternary sequence starts with tills of Elsterian and then Wartanian (late Saalian) age, as indicated by the petrography of clasts within the 4–10 mm range. The tills are intercalated with fine-grained and very fine-grained sand. At 128.20 m the Wartanian sequence contains a 4.5-m-thick glaciolacustrine varved clay. This is overlain at 123.70 m by a unit consisting of two sets of deltaic vari-grained sands containing some localised admixture of fine gravel. This unit, which is 22.20 m thick, is interpreted from sedimentological and lithostratigraphic evidence to represent the Eemian (Makowska et al., 2001). It is characterised by medium-rounded quartz grains; and among the heavy minerals, garnet (36–53%) is more abundant than amphibole (22–35%). The base of the unit is marked by gravel and pebbles, passing upwards into medium- and fine-grained sands, commonly with an admixture of plant detritus and single fragments of freshwater mollusc shells. At the top these sands pass into silts, peaty silts, peats and peaty mudstones of lakes, oxbow lakes and bogs, with freshwater mollusc shells (Makowska et al., 2001). In particular, between 101.65 and 101.50 m, shells including *Valvata piscinalis*, *Planorbis planorbis*, *Bithynia tentacula*, and *Pisidium* sp. indicate a freshwater mollusc community living in a small or large, shallow lake (Makowska, 2001).

An overlying unit of sands, from 101.50 m to about 97.60 m, is interpreted from sedimentology to mark the onset of marine conditions, these sands including clay balls at the base and being regarded as beach deposits (Makowska et al., 2001). The lowest molluscan indication of marine conditions occurs at 100.50 m with fragments of the marine species *Hydrobia ulvae*, *Bittium reticulatum*, *Chrysallida spiralis*, *Macoma balthica*, *Mytilus edulis*, *Venerupis aurea senescens*, and *Cerastoderma edule* (Makowska, 2001). Between 100.50 and 98.00 m, freshwater molluscs are gradually replaced by marine species, but the presence of broken shells and occasional gravel and clay balls indicates redeposition and led Makowska (2001) to interpret this unit as representing a beach facies.

A marked marine transgression is indicated by silt and silty sand between 98.40 m and 97.60 m, with abundant mollusc shells occurring particularly between 98.10 and 97.60 m. Lower energy conditions are indicated by the deposition of finer-grained sediments between 97.60 and 94.50 m. These sediments are principally silt, with local development of silty sand or clay, and contain abundant fragments of mollusc shells that are dissipated or concentrated in horizontal layers about 1 mm thick. Shell fragments are more common towards the bottom of the unit. The sediment is horizontally laminated, locally deformed, dark grey to greenish-grey in colour, and is bituminous at the top. The heavy mineral content between 97.20 and 95.20 m varies dramatically (e.g. up to 61% garnet and more than 6% zircon), with a rapid increase in chlorites (13%) and biotite (18%) at the top. Marine mollusc shells are common to 94.55 m, with 21 species reported, among which are the marine species *Cerastoderma edule*, *Corbula gibba*, *Venerupis aurea senescens*, *Mytilus edulis*, *Nassarius reticulatus* (as *Nassa reticulata*), *Bittium reticulatum* and *Rissoa membranacea*, and the brackish *Ventrosia stagnorum* and *Hydrobia ulvae*. Above 95.20 m, a marine regression is indicated by sandy interbeds and a poorer marine mollusc assemblage (12 species only). At 94.51 m the presence of a freshwater snail *Anisus spirorbis*, accompanied by *Valvata piscinalis*, already indicates a very shallow lake nearby. Fine fragments of marine mollusc shells are also present (Makowska, 2001).

Deltaic fine-grained and very fine-grained sand is present at 94.50 m. This unit is 9.6 m thick and contains well-rounded quartz sand grains, as well as plant detritus and peats in which mollusc shells are absent. It was considered by Makowska (2001) from sedimen-

tological evidence to represent Early Vistulian deposition. Overlying this unit are two other alluvial series composed of medium-grained sands with inserts of organic matter. These sediments are capped by tills of Middle and Late Vistulian age containing rafts of glaciolacustrine, fluvial and marine sediments.

6. Material and methods

6.1. Sampling

The Licze borehole was continuously cored although some discrete intervals, which are marked on the pollen diagram (Fig. 4), were lost during drilling. Samples were first taken for pollen analysis, and represent the exact levels shown on the pollen diagram (Fig. 4). Bulk samples representing contiguous intervals were subsequently taken from the core, with each sample then being subsampled for different analyses. For these bulk samples, those taken above 98.50 m each represent a 10 cm interval. Those taken below 98.50 m represent a 20 cm interval, except for the lowest sample (101.50–101.75 m) that represents a 25 cm interval. Each subsample is plotted using the mean depth for its respective bulk sample (Figs. 6 and 7) but its precise depth is unknown within its respective 10-, 20-, or 25-cm interval. Subsamples of a particular bulk sample will therefore not represent exactly the same level. All depths cited in this paper are uncorrected core depths.

6.2. Pollen and age determinations

Most samples processed for pollen analysis were treated with 10% HCl, 7% KOH, $KJ + CdJ_2$ separation (solution density ca. 2.0) and Erdtman's acetolysis. The pollen of trees, shrubs and terrestrial herbaceous plants was used as the total sum for percentage calculations. The proportion of aquatic plant pollen, spores, plankton and redeposited sporomorphs was computed in relation to this basic sum. A total of 31 samples (spaced between 6 and 50 cm apart) was analysed from the interval 97.85–88.65 m, and results are presented in the pollen diagram (Fig. 4). This diagram is based on counts of at least 500 pollen grains per sample, except for the sample at 89.75 m which is based on a count of 215 pollen. Sediments below this interval were subjected only to qualitative analysis owing mostly to low recovery of pollen.

The resulting local zonation, which is based on a visual inspection of the pollen diagram (Fig. 4), is correlated to the regional pollen assemblage zonation for Poland (Mamakowa, 1988, 1989) and to the well-dated pollen zonation of northern Germany (Müller, 1974) (Fig. 5).

Samples at 101.63, 101.40, 101.00, 99.40, and 98.80 m were analysed for pollen using residues prepared for dinoflagellate cyst analysis. Because these residues have been sieved at 10 μm, some smaller pollen grains may have been lost. The pollen counts are therefore not directly comparable with other pollen data for this borehole.

6.3. Dinoflagellate cysts and other aquatic palynomorphs

Twenty-eight pre-dried sediment samples from the Licze core were processed (Fig. 7), each weighing 3.1 g for the two lowest samples (101.63 and 101.40 m), between 8.8 and 23.7 g for the 10 superjacent samples (101.00 m–98.35 m), and between 3.1 and 3.5 g for the upper 16 samples (98.05–94.55 m). Following the addition of *Lycopodium* tablets (batch no. 938934 = 10,679 spores per tablet; 1 tablet per gram for upper 16 samples; variable for lower samples) to determine palynomorph concentrations, samples were treated with 7% cold HCl for 2 h, 48% cold HF for 4 days, and 7% cold HCl for 2 h; with water washes between and after acid treatments. Residues were then sieved using a 10 μm polymer mesh, stained with safranin o, and one or two microscope slides were made. Remaining residue was sonicated for about 30 s, re-sieved, and a further one or two microscope slides were made. Slides were mounted using glycerine jelly.

To determine the abundance of non-pollen aquatic palynomorphs, slides were counted at between $300 \times$ and $500 \times$ magnification until more than 200 dinoflagellate cysts had been enumerated. Wherever possible, slides containing unsonicated residue were used for counting. An additional slide, usually of sonicated residue, was traversed under lower magnification to detect any rare taxa.

Four dinoflagellate cyst zones (LDf 1–4) were recognised, and are based principally on a visual inspection of Figs. 6 and 7. The dinoflagellate cysts and other aquatic palynomorphs are illustrated comprehensively in Figs. 8–13. The Appendix gives raw data for all samples in which cysts were sufficiently abundant to count. Dinoflagellate cyst nomenclature follows Head (1996), Williams et al. (1998) and Head (2003).

7. Results of pollen analysis

7.1. Local pollen zonation

A continuous sequence of pollen spectra within the interval 97.85–88.65 m (Fig. 4) is described below. However, pollen and spores were also obtained from the lower part of the borehole below 97.85 m, in coarser, sand-dominated sediments. These lower pollen spectra

Licze – Trees, Shrubs & Summary
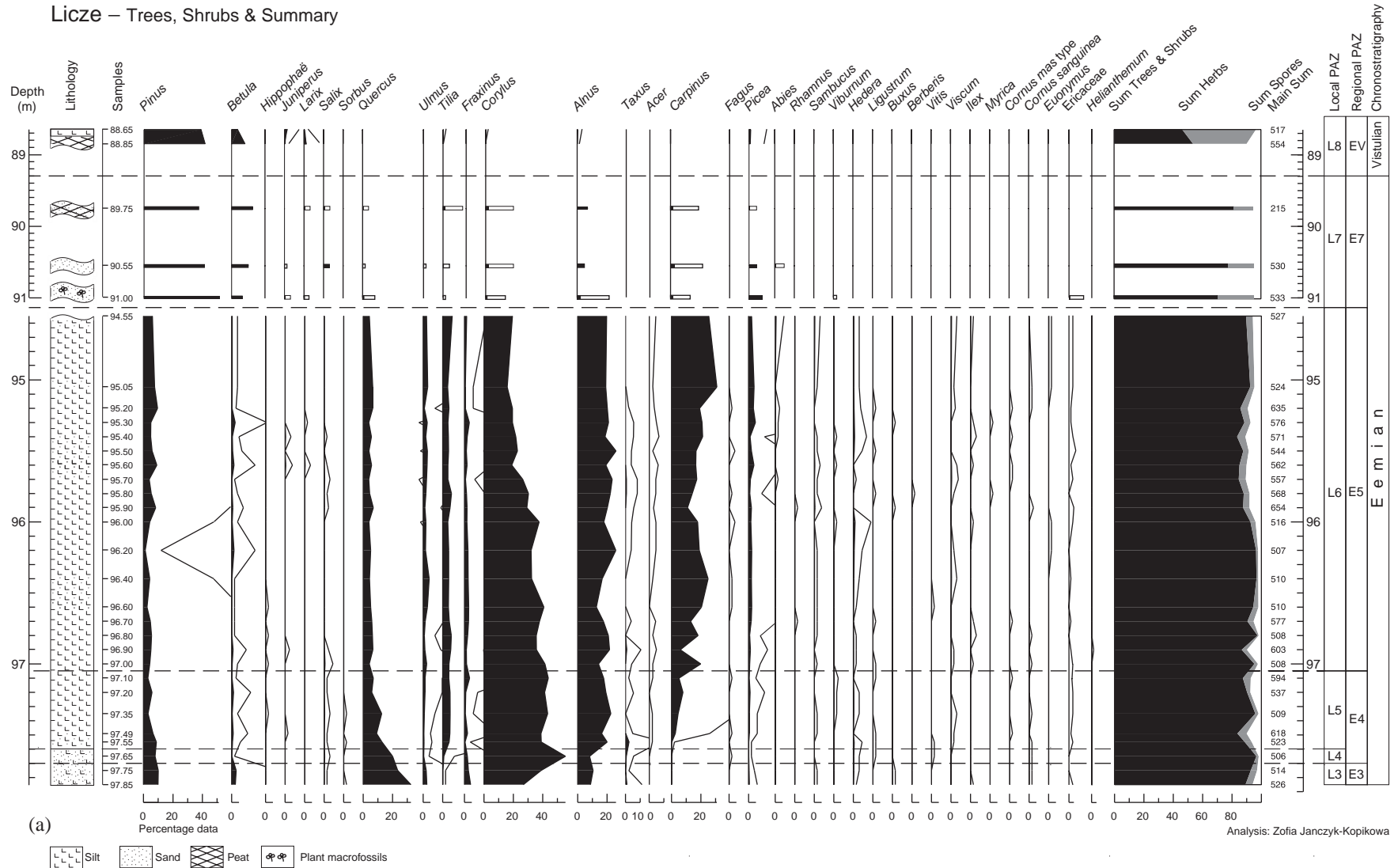

(a)

Analysis: Zofia Janczyk-Kopikowa

Fig. 4. Pollen diagram for the Licze borehole, showing (a) trees, shrubs and summary diagram; and (b) herbs, sporophytes, aquatic plants, fungi and plankton. Black-filled lines indicate percentage abundance and white-filled lines give ×10 exaggeration (i.e., per mill abundance). The local pollen assemblage zones (LPAZ) are based on the present study, and the regional pollen assemblage zones (RPAZ) are those of Mamakowa (1988, 1989).
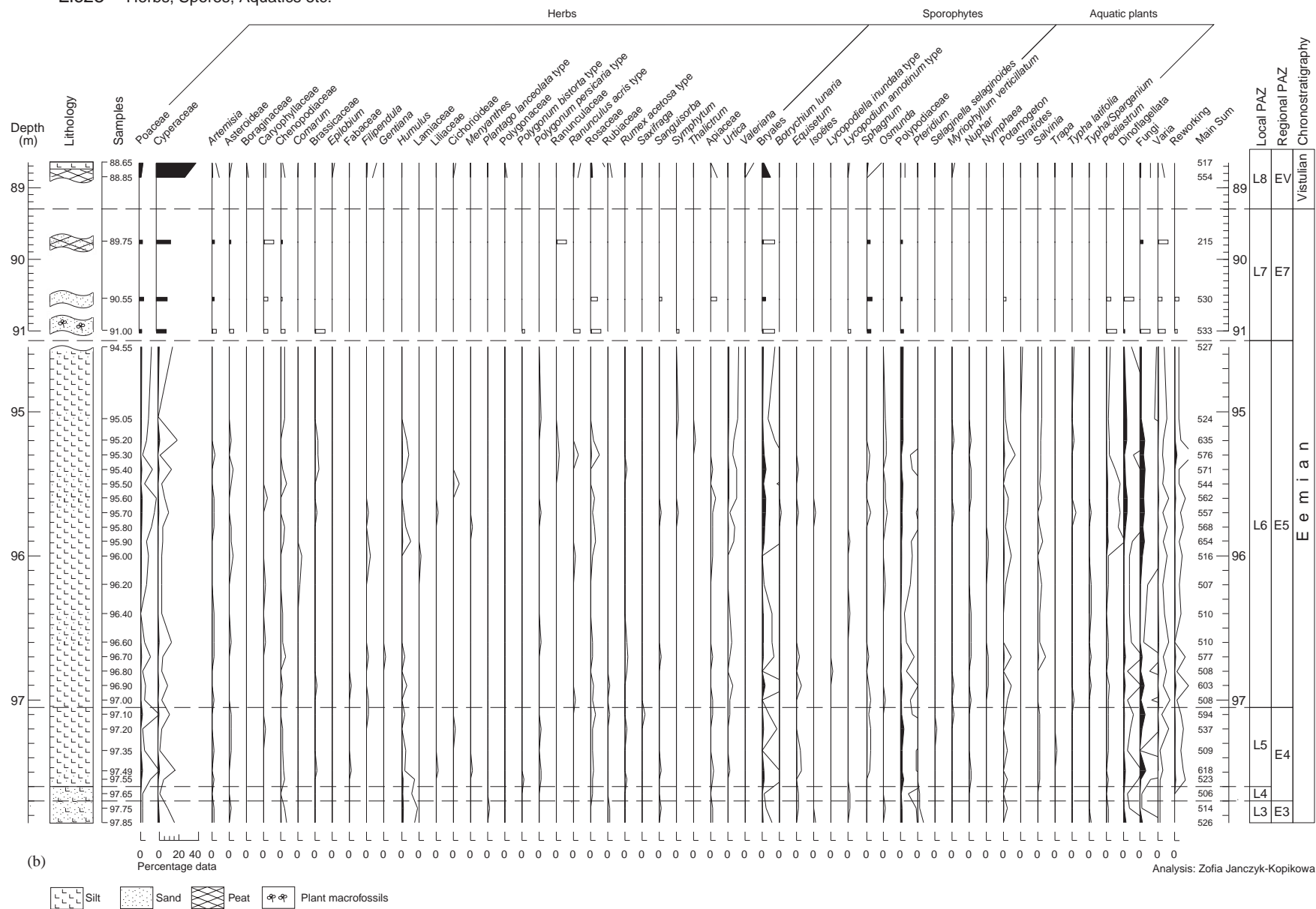
Fig. 4 (continued).

Turner & West 1968	Jessen & Milthers 1928	DENMARK Andersen 1961, 1975	Müller 1974	N. GERMANY Menke & Tynni 1984	POLAND Mamakowa 1988, 1989	LICZE This study	Stage
	i	EW 1 — Poaceae Ericales	—11000—	WF 1 — NAP – Ericales	EV 1 — Gramineae *Artemisia Betula nana*	L 8	Early Vistulian
Post-temperate	h	E 7 — *Pinus – Picea Betula*	VI	VII — *Pinus*	E 7 — *Pinus*	L 7	N
		—8500—					
		E 6 — *Picea – Pinus Alnus*	V	VI — *Pinus – Picea Abies*	E 6 — *Picea – Abies Alnus*	not sampled	A
Late-temperate	g	E 5 — *Picea – Carpinus Alnus*	—7000— IV	V — *Carpinus – Picea*	E 5 — *Carpinus Corylus Alnus*	L 6	I
Early-temperate	f	E 4 — *Quercus – Tilia Corylus – Alnus*	—3000— IIIc	IVb — *Corylus – Taxus Tilia*	E 4 — *Corylus – Quercus Tilia*	L 5	M
			IIIb	IVa — Mixed Oak Forest *Corylus*		L 4	E
	e	E 3 — *Quercus Fraxinus*	—750— IIb	III — *Pinus* – Mixed Oak Forest	E 3 — *Quercus Fraxinus Ulmus*	L 3	
						L 2	E
	d	E 2 — *Betula – Pinus Ulmus*	—300— IIa	II — *Pinus – Betula*	E 2 — *Pinus – Betula Ulmus*		
Pre-temperate	c	E 1 — *Betula*	I	I — *Betula*	E 1 — *Pinus – Betula*	L 1	
			—0—				

Fig. 5. Proposed correlation of local pollen assemblage zones (LPAZ) L1–L8 for the Licze borehole with regional pollen assemblage zonation (RPAZ) schemes for Denmark, northern Germany and northern Poland based on Jessen and Milthers (1928), Andersen (1961, 1975), Müller (1974), Menke and Tynni (1984), Mamakowa (1988, 1989), and the scheme of Turner and West (1968). The ages of zonal boundaries in the zonation of Müller (1974) are in years from the Saalian/Eemian Stage boundary. Adapted from Zagwijn (1996), Kristensen et al. (2000) and Turner (2000).

are not amenable to fully quantitative analysis or comprise a continuous sequence, but they provide important information on the age of the sediments and of the marine transgression. They are assigned to local pollen assemblage zones (LPAZ) L1 and L2, as follows.

Spectra from samples at 101.63, 101.40, 101.00, and 99.40 m depth are assigned to LPAZ L1. Spectra from a sandy silt sample at 101.63 m and a clayey silt sample 101.40 m are strongly dominated by *Pinus* with subordinate *Betula* pollen. The spectrum at 101.40 m contains 98% *Pinus*, 1% *Betula*, and 1% Cyperaceae. The spectrum at 101.00 m contains 82% *Pinus*, 3.8% *Picea*, 3.8% Cyperaceae, 0.9% *Quercus*, 0.9% *Betula*, 0.5% *Ulmus*, and 0.9% herbs. A pollen spectrum from 99.40 m is very strongly dominated by *Pinus*, but contains a few grains of *Betula*, *Picea* and herbs.

A spectrum from 98.80 m depth, despite being strongly dominated by *Pinus* (80% of the total sum),

contains significant values of *Quercus* (11%) as well as *Corylus* (2%) and *Betula* (2%) pollen. This spectrum is assigned to LPAZ L2.

Within the interval 88.65–97.85 m, quantitative analysis of 31 samples has enabled six local pollen assemblage zones (LPAZ L3–8) to be distinguished (Fig. 4). In LPAZ L3–5 the sequence is dominated by the pollen of deciduous forest trees, particularly *Quercus* and *Corylus*, and accompanied by *Tilia*, *Ulmus*, *Fraxinus* and *Taxus* and increasing frequencies of *Alnus*. Of the shrubs *Ligustrum*, *Vitis*, *Viscum* and *Ilex* pollen are particularly well represented. LPAZ L3 is dominated by *Quercus* which decreases and is replaced by *Corylus*. LPAZ L4 (base at ca. 97.70 m) is distinguished by the peak of *Corylus* pollen and reducing frequencies of *Quercus*. The base of LPAZ L5, at ca. 97.60 m, is placed at the initial appearance of *Carpinus* pollen, the arrival at low frequencies of *Picea* pollen, and the marked
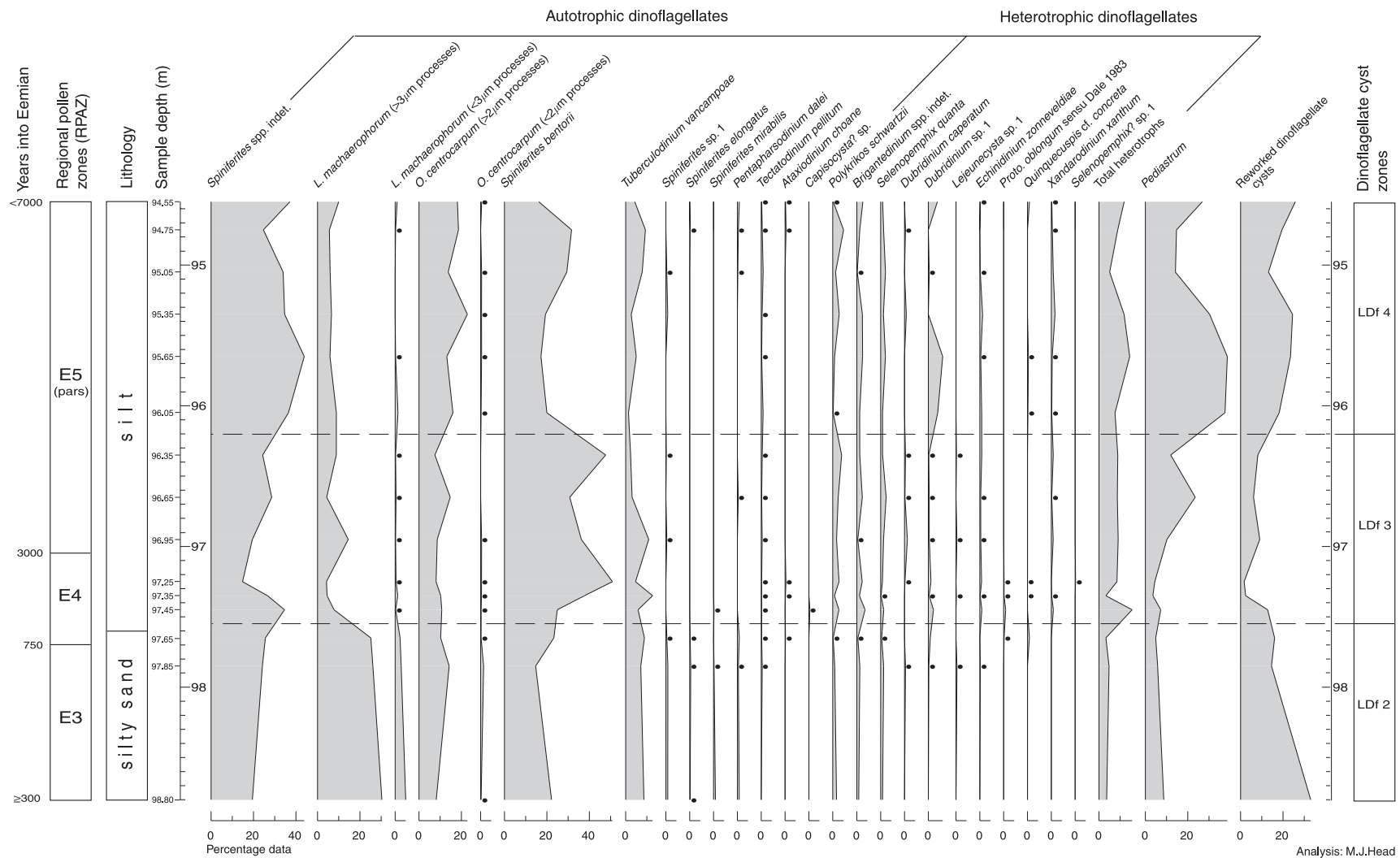
Fig. 6. Relative abundance of dinoflagellate cysts and other selected taxa from the Licze borehole. *Pediastrum* and reworked dinoflagellate cysts are expressed as a proportion of total in situ dinoflagellate cysts. Solid dots indicate rare occurrences (0.5% or less). Dinoflagellate cyst zone LDf 1 is not shown (see Fig. 7). Regional pollen assemblage zones (RPAZ) are those of Mamakowa (1988, 1989) as recognised in the present study. Each sample represents a 10- or 20-cm interval of core and is plotted by its mean depth (see text for details).
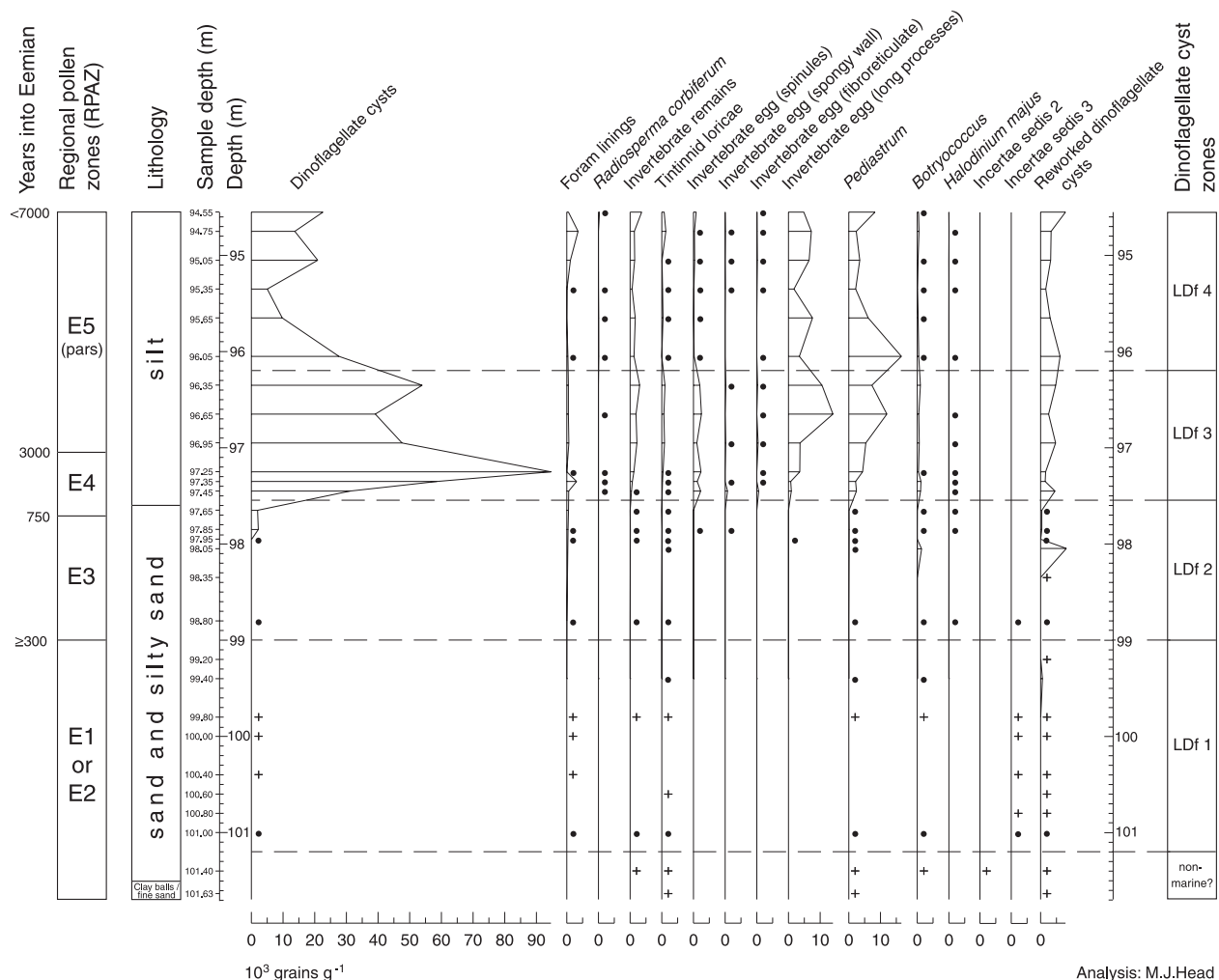
Fig. 7. Concentrations (specimens per gram dry weight of sediment) of all non-pollen aquatic palynomorph groups counted in the Licze borehole. Solid dots indicate low concentrations (500 or less per gram). A cross (+) indicates the presence of a taxon within a sample for which concentrations were not calculated. Regional pollen assemblage zones (RPAZ) are those of Mamakowa (1988, 1989) as recognised in the present study. Each sample represents a 10-, 20-, or 25-cm interval of core and is plotted by its mean depth (see text for details).

increase in *Alnus* pollen. This biozone also includes the first substantial occurrence of *Tilia* and, among the shrubs, Ericaceae pollen.

LPAZ L6, the base of which is placed at ca. 97.05 m, shows an apparently lengthy period of a stable

assemblage dominated by high frequencies of *Carpinus* pollen. It is accompanied by the pollen of other thermophilous trees such as *Alnus* and *Corylus*, but with low frequencies of *Quercus*, *Tilia*, *Fraxinus*, *Acer* and *Ulmus*. The pollen of thermophilous shrubs, notably

Fig. 8. Dinoflagellate cysts from the marine Eemian of Licze. Various magnifications. (a, b) Cyst of *Polykrikos schwartzii* Bütschli 1873, upper and mid foci; length incl. processes 92 µm; sample 27(1)L38/3; depth 95.30–95.40 m. (c, d) *Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) (specimen with processes of normal length), upper and mid foci; central body max. dia. 51 µm; sample 52(2)J30/1; depth 97.80–97.90 m. (e, f) *Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) (specimen with short processes), upper and mid foci; central body length 54 µm; sample 19(2)T21/1; depth 94.50–94.60 m. (g–i) *Operculodinium centrocarpum* sensu Wall and Dale (1966), upper, mid, and lower foci; central body max. dia. 34 µm; sample 27(2)Q46/0; depth 95.30–95.40 m. (j, k) *Operculodinium centrocarpum* sensu Wall and Dale (1966) (specimen with short processes), left lateral view at upper and mid foci; central body max. dia. 39 µm; sample 43(1)U35/0; depth 96.90–97.00 m. (l–n) *Ataxiodinium choane* Reid 1974, upper, mid, and lower foci, length including periblast 46 µm; sample 21(1)P19/0; depth 94.70–94.80 m. (o–q) *Ataxiodinium choane* Reid 1974, upper, slightly lower and mid foci; length including periblast 42 µm; sample 46(2)H28/1; depth 97.20–97.30 m. (r, s) *Spiniferites* sp., upper and mid foci; central body length 43 µm; sample 24(2)J13/4; depth 95.00–95.10 m. (t) *Spiniferites* sp., mid focus; central body max. dia. 35 µm; sample 30(3)T26/1; depth 95.60–95.70 m.
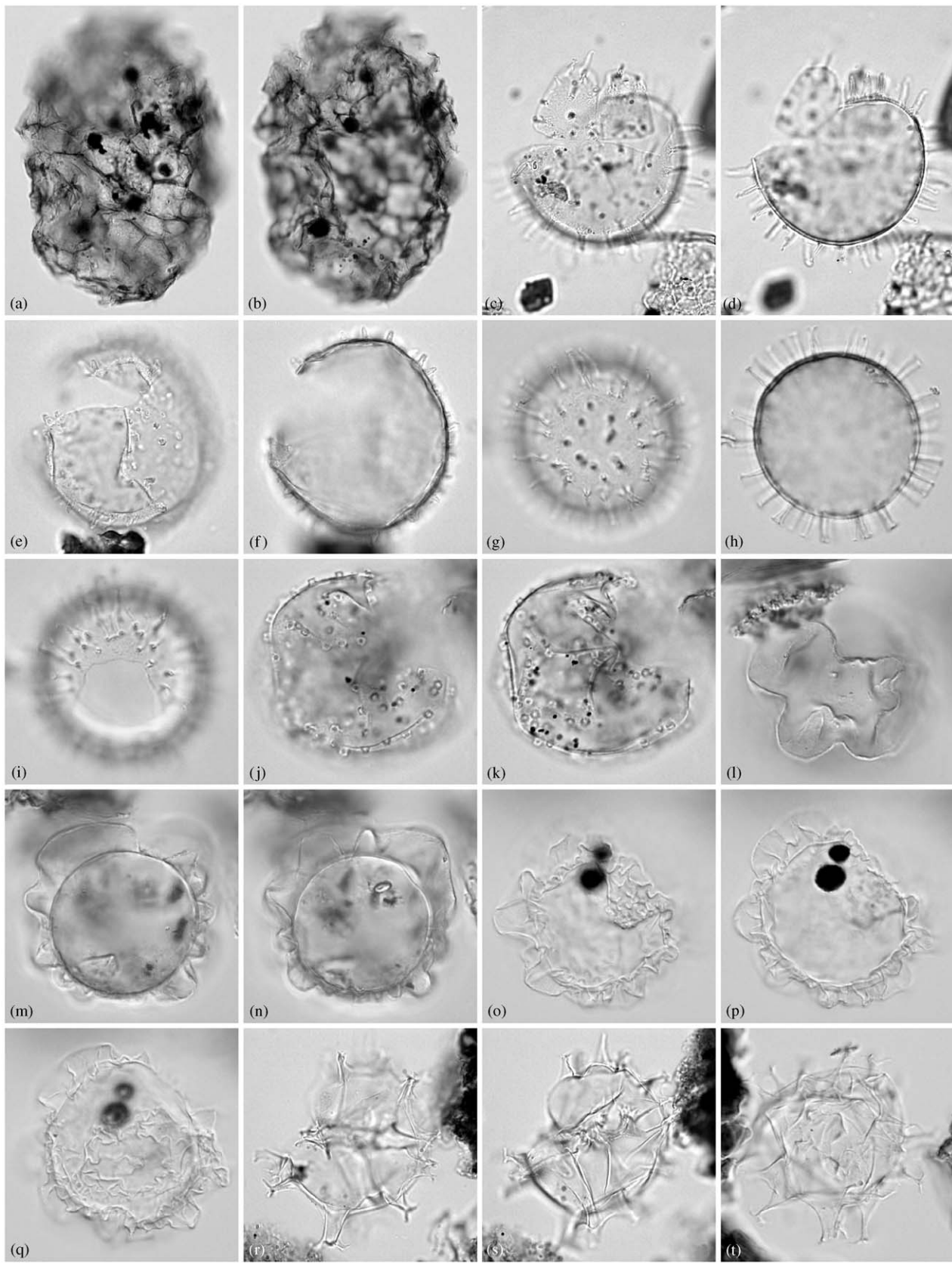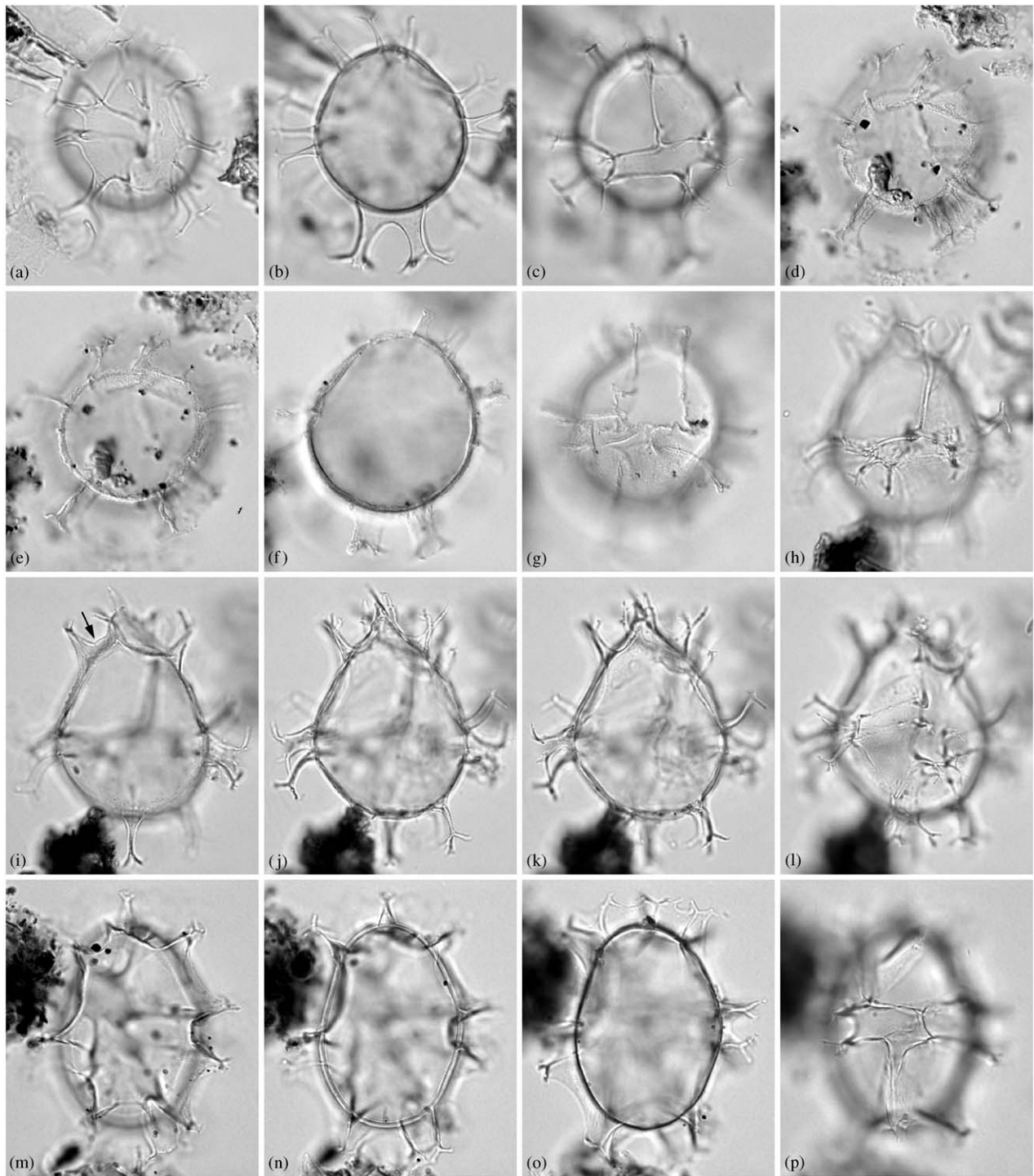
Fig. 9. Dinoflagellate cysts from the marine Eemian of Licze. Various magnifications. (a–c) *Spiniferites* sp., upper, mid, and lower foci; central body length 38 μm; sample 27(2)K24/0; depth 95.30–95.40 m. (d–g) *Spiniferites* sp. 1, upper through lower foci, showing dense invaginations of outer wall layer covering the central body; central body length 41 μm; sample 52(1)S45/2; depth 97.80–97.90 m. (h–l) *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale 1970, upper through lower foci; note small trabecula marked by arrow in (i) which is a rare but sometimes elaborately developed feature of this species in the Eemian of the Baltic, and is probably related to low salinity; central body length 63 μm; sample 47(3)Q40/0; depth 97.30–97.40 m. (m–p) *Spiniferites elongatus* Reid 1974, upper through lower foci; endoblast length 46 μm; sample 50(1)K31/0; depth 97.60–97.70 m.

including *Buxus*, remains present throughout the zone. Coniferous tree pollen such as *Pinus*, *Picea*, *Taxus* and *Abies* are present throughout in low numbers. Herbs remain very poorly represented, with only Poaceae present in low frequencies. Spores of Bryales, Polypodiaceae and fungi occur throughout.

The change to LPAZ L7 is placed in the interval between samples at 94.55 and 91.50 m. It corresponds to a change in sedimentation from sandy silt to sand with plant macrofossils, and then to sand overlain by sandy peat. This facies change indicates the transition from marine to non-marine sedimentation, and is marked by the predominance of the pollen of coniferous trees, particularly *Picea* and *Pinus*. These conifer pollen replace the pollen of deciduous taxa in preceding zones and are accompanied by increasing frequencies of *Betula* pollen. However, *Carpinus* still occurs throughout the biozone, together with *Alnus* pollen. Of the herbs *Artemisia*, Chenopodiaceae, Caryophyllaceae, *Ranunculus acris* type and Cyperaceae are all well represented. Of the lower plants, Polypodiaceae, Bryales and *Sphagnum* spores are abundant.

The base of the uppermost LPAZ L8 is placed at ca. 89.30 m within a gap in core recovery. The lower sample (at 88.85 m) is a peat, and the higher sample (at 88.65 m) is a silt. LPAZ L8 is characterised by the increased dominance of *Pinus* and *Betula* coniferous forest, accompanied by minor numbers of *Picea* and *Larix* pollen. The pollen of boreal climate herbs and Cyperaceae, Poaceae and Rosaceae occur throughout, while *Sphagnum* spores derived from the peat bog are also present.

7.2. Local vegetational development as indicated by the pollen sequence

The pollen record shows that the vegetational history at Licze began with the colonisation of the region by pre-temperate (sensu Turner and West, 1968) boreal forest, dominated by *Pinus* and subordinate *Betula* on the freshly deglaciated topography. The arrival and rise to dominance of deciduous forest indicates the development of a temperate climate. *Quercus* and subsequently *Corylus* are distinctly dominant, with subordinate *Ulmus*, *Fraxinus*, *Alnus*, *Taxus* and, at the end of LPAZ L4, *Tilia* whose expansion reflects its establishment as an important secondary element in the diverse forest flora that occupied the adjacent landscape. The immigration of *Carpinus* in LPAZ L5 apparently led to the displacement of *Quercus* as the forest dominant in LPAZ L6. The late-temperate *Carpinus–Picea–Corylus* forest appears to have been a stable assemblage that colonised the region throughout the main accumulation of the marine, silt-dominated sequence at Licze (LPAZ L6). This forest grew on dry interfluve areas, which in places included acidic soils. By contrast, the extensive floodplains of the Vistula in the hinterland were colonised by the considerable representation of *Alnus* and associated wetland herbs and notably Polypodiaceae ferns.

The substantial change in sedimentation from marine sandy silts to coarser, non-marine sediments also marks a return to the predominance of coniferous forest, dominated by *Pinus*, but accompanied by *Picea*, *Taxus* and *Betula* (LPAZ L7). However, this transition represents a coring gap of 3.55 m (94.55–91.00 m), and the timing of coniferous forest establishment within this long interval is not known. Nonetheless, LPAZ L7 may mark a deterioration in climate but also a deterioration in soil conditions with the widespread development of acidic soils in the district. In addition, the occurrence of *Sphagnum* spores indicates that acid bogs developed in moist depressions. The appearance of open, herb-dominated clearings in the landscape is indicated by increased numbers of *Artemisia*, Asteroidae and Chenopodiaceae pollen. It may be speculated that the opening of forests that marks the change to LPAZ L7 led to increased surface runoff, thereby giving rise to the deposition of coarser sediments. This was perhaps associated with greater seasonal contrast, and consequently higher river discharges.

Finally, the rise to dominance of *Pinus*, together with *Betula* and *Juniperus* shrubs, and boreal-climate herbs represent the continued climatic deterioration that signals the initial phase of the early-glacial climate. During this phase (LPAZ L8), forest is replaced by herb-dominated vegetation represented mostly by Cyperaceae, but with significant proportions of Poaceae and Rosaceae. It is possible that trees continued to occur in copses within sheltered areas such as valley bottoms during this phase, and that tree pollen was entering by river. However, it is also possible that reworking of regolith during this phase led to the inwashing of contained pollen and spores.

7.3. Correlation

Notwithstanding the development of the Licze sequence in marine and fluvial sediments, rather than lacustrine sediments for which the regional pollen zonation schemes have been developed in Poland (Janczyk-Kopikowa, 1991), the sequence can be correlated with those of the Last Interglacial (Eemian Stage) in northern Poland (Mamakowa, 1988, 1989). Moreover, through the recognition of the standard northern Polish biozones, it can also be equated with those from neighbouring areas in western Europe, e.g., Herning (Jessen and Milthers, 1928), Hollerup (Andersen, 1961, 1975; Björck et al., 2000), Bispingen (Müller, 1974), northern Germany (Menke and Tynni, 1984) and localities described by Zagwijn (1996), on the following criteria (Fig. 5):

(1) According to Mamakowa (1989, p. 53) the characteristics of the vegetational succession at Imbramowice, southwestern Poland are "the expansion of
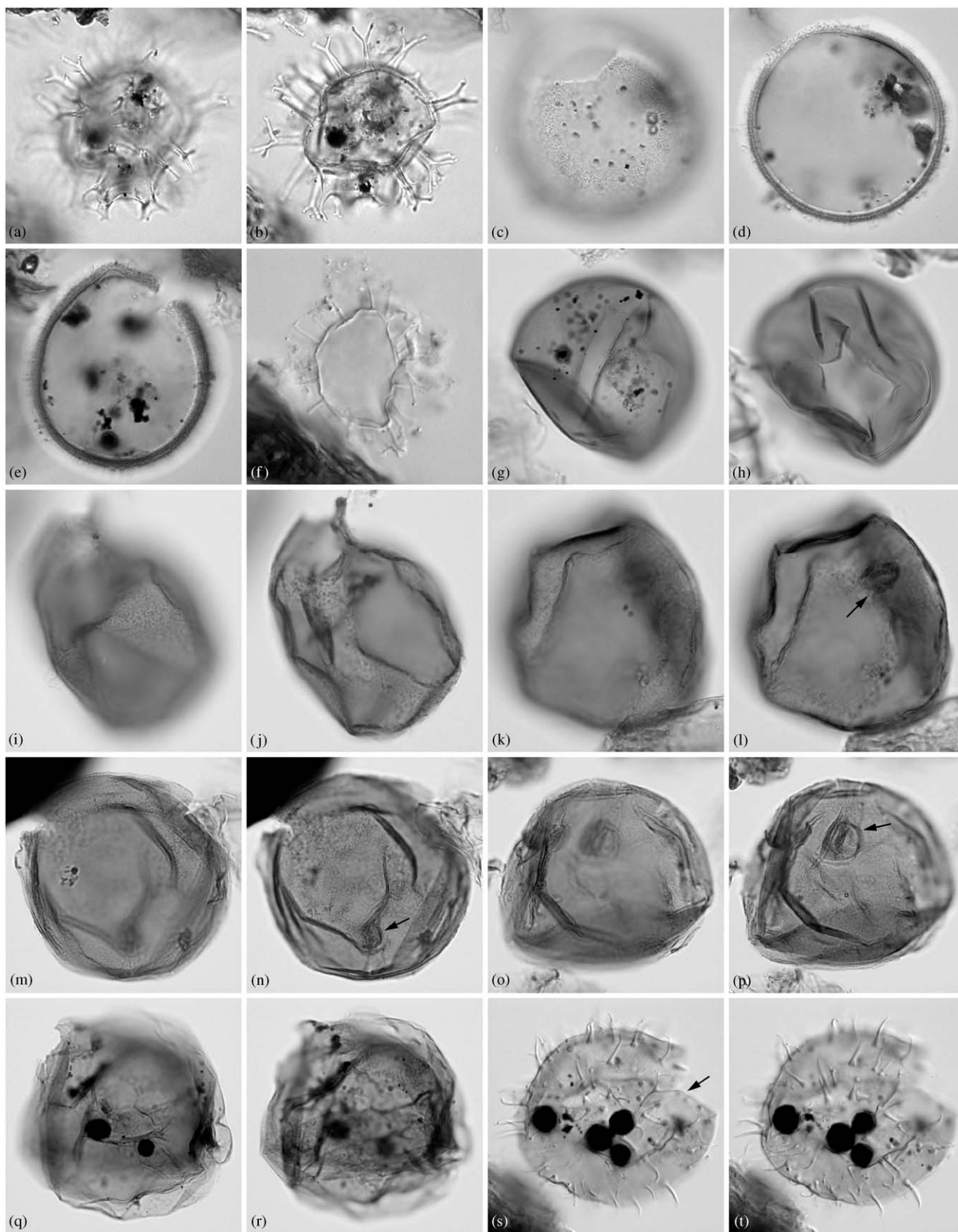
trees and hazel in the following order: *Betula–Pinus*, *Ulmus*, *Quercus–Fraxinus*, *Corylus*, *Alnus*, *Taxus*, *Tilia*, *Carpinus*, *Picea–Abies* and the high *Corylus* values''. In particular, the substantial rise in the *Corylus* pollen curve, early in the mixed oak forest phase, is quite unlike other interglacial developments. Imbramowice serves as the type section for an Eemian Polish regional zonation that is based on the analysis of 99 sites including several marine sections near Licze.

(2) The progressive increases in *Pinus*, *Quercus*, *Corylus* and *Tilia* pollen are typical of the Eemian Stage in Poland and neighbouring north Germany. In the Holsteinian (Mazovian) of Poland, *Ulmus*, *Tilia* and *Alnus* are abundant in the first half of the interglacial, together with very high frequencies of *Picea*, and the late arrival of *Carpinus*. Earlier, pre-Holsteinian, temperate stages are characterised by high frequencies of *Ulmus*, quite unlike those of the younger events (Janczyk-Kopikowa, 1991).

(3) The early arrival together of *Picea* and *Carpinus* pollen is again typical of the Eemian Stage in Poland, and again both are well represented at Licze.

Taken together, this evidence indicates that the Licze interglacial sediments are of Eemian age. Moreover, the succession (Figs. 4 and 5) can be zoned directly using the scheme of Mamakowa (1988, 1989) for northern Poland, and indeed with that of Jessen and Milthers (1928) developed for Denmark and northwest Germany. Equally the succession can be zoned using Andersen's later scheme (1961, 1975) for the lacustrine Eemian parastratotype locality at Hollerup (see also Björck et al., 2000). Proposed correlations for the sequence of local pollen assemblage (bio-) zones shown on Figs. 4 and 5 and are as follows:

LPAZ L1 comprises four discontinuously sampled pollen spectra at 101.63, 101.40, 101.00, and 99.40 m. Spectra from 101.63, 101.40, and 101.00 m represent a pre-temperate vegetational phase equivalent to Mamakowa's (1988, 1989) Eemian regional pollen assemblage zones (RPAZ) E1 (*Pinus–Betula*) or E2 (*Pinus–Betula–Ulmus*). The spectrum from 99.40 m with its strongly *Pinus*-dominated assemblage also suggests equivalence to RPAZ E1 or E2.

LPAZ L2 comprises a single sample at 98.80 m. Despite the dominance of *Pinus*, significant values of *Quercus*, *Corylus* and *Betula* together indicate that this spectrum represents the early part of RPAZ E3, and most probably to the earliest phase of *Quercus* expansion (earliest E3).

LPAZ L3 is equivalent to Mamakowa's RPAZ E3 (*Quercus–Fraxinus–Ulmus*). LPAZ L4 is equivalent to the earliest part of the *Corylus–Quercus–Tilia* RPAZ E4, based on the peak level of *Corylus*. LPAZ L5 can be equated with the remainder of RPAZ E4. LPAZ L3–L5 therefore represent the climatic optimum of the Eemian Stage.

LPAZ L6 is equivalent to RPAZ E5 (*Carpinus–Corylus–Alnus*) on the basis of the abundance of *Carpinus* pollen. Likewise, the predominance of coniferous forest in LPAZ L7 suggests that it should represent RPAZ E7 (*Pinus*). The absence of spectra yielding an assemblage equivalent to RPAZ E6 (*Picea–Abies–Alnus*) suggests that the unrecovered sediment between 94.55 and 91.00 m was deposited at least partly during this phase. Finally, the boreal forest and increasing non-tree pollen assemblage in LPAZ L8 suggests that it represents the initial phase of the Vistulian (Weichselian) Stage, the base of which occurs at ca. 89.30 m depth in the core.

Thus overall, nearly the whole Eemian Stage vegetational development is represented in the pollen record, from the discontinuous sequence in the coarse sediments representing RPAZs E1 or E2–E3, into the continuous profile through RPAZs E3–E5, and returning finally to coarser sediments with a discontinuous sequence representing RPAZs E7–EV1. It is important to note that RPAZ E6 is missing (see below).

Fig. 10. Dinoflagellate cysts from the marine Eemian of Licze. Various magnifications. (a, b) *Spiniferites mirabilis* (Rossignol, 1964) Sarjeant 1970, antapical view, upper and slightly lower foci, central body max. dia., 42 μm; sample 48(4)R15/1; depth 97.40–97.50 m. (c, d) *Tectatodinium pellitum* Wall 1967, upper and mid foci; length including luxuria 49 μm; sample 50(1)M28/2; depth 97.60–97.70 m. (e) *Tectatodinium pellitum* Wall 1967, mid focus showing apical protuberance; length including luxuria 57 μm; sample 47(3)L18/0; depth 97.30–97.40 m. (f) Cyst of *Pentapharsodinium dalei* Indelicato and Loeblich III 1986, mid focus; central body max. dia. 22 μm; sample 21(1)P42/4; depth 94.70–94.80 m. (g, h) *Brigantedinium* sp., probably *B. cariacoense* (Wall, 1967) Lentin and Williams 1993, upper and lower foci; maximum diameter 50 μm; sample 24(2)S11/3; depth 95.00–95.10 m. (i, j) *Dubridinium caperatum* Reid 1977, apical view at upper and slightly lower foci showing coarse granulation beneath thin, closely appressed outer wall layer; maximum diameter 47 μm; sample 27(1)N44/1; depth 95.30–95.40 m. (k, l) *Dubridinium caperatum* Reid 1977, apical view at upper and slightly lower foci, arrow showing apical pore complex; maximum diameter 46 μm; sample 43(1)T49/4; depth 96.90–97.00 m. (m, n) *Dubridinium* sp. 1, antapical? view at upper and lower foci; note finely granulate inner wall layer and thin, loosely appressed outer wall layer; arrow showing apical pore complex; maximum diameter 60 μm; sample 34(2)Q51/1; depth 96.00–96.10 m. (o, p) *Dubridinium* sp. 1, apical? view at upper and lower foci, arrow showing apical pore complex; maximum diameter 56 μm; sample 40(2)O23/4; depth 96.60–96.70 m. (q, r) *Dubridinium*? sp. 2, upper and mid foci; note finely granulate inner wall layer and thin, loose outer wall layer; archeopyle uncertain; maximum diameter 52 μm; sample 47(3)S46/0; depth 97.30–97.40 m. (s, t) *Echinidinium zonneveldiae* Head 2003, upper and mid foci; surface bears sparsely scattered spinules and solid, acuminate processes; arrow indicates theropylic archeopyle; central body max. dia. 50 μm; sample 37(2)D49/0; depth 96.30–96.40 m.
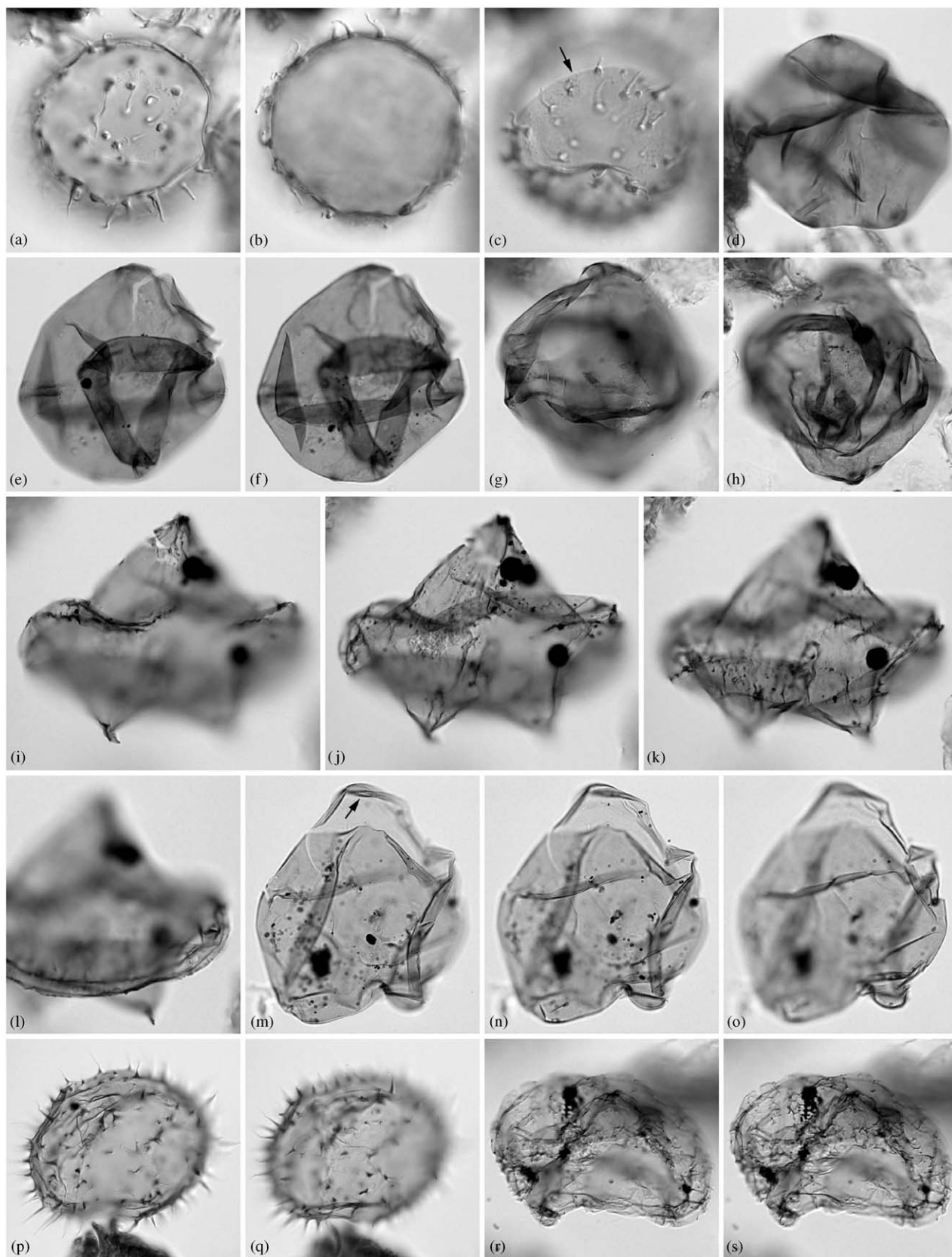
Table 1
Age model, hydrographic events, and estimated sedimentation rates for the Licze borehole sequence

Event	Core depth (m)	Age (years)
Eemian/Vistulian (Weichselian) Stage boundary	ca. 89.30	ca. 11,000
Oldest E7 sediments	91.00	>8500
E6 sediments	Sampling gap	7000–8500
Youngest E5 sediments	94.55	<7000
End of marine conditions	94.55–91.00	
Marine regression (Mollusca)	95.20	
E4/E5 boundary	97.05	3000
Onset of lower energy deposition	97.60	
E3/E4 boundary	97.70	750
Earliest E3	98.80	ca. 300
Appearance of marine Mollusca	100.50	
Appearance of marine Dinoflagellata	101.00	
Onset of marine conditions	101.50	
E1 or E2	101.63–99.40	<300
Saalian/Eemian Stage boundary	123.70	0

| *Sedimentation rates* Pollen zone	Duration (yr)	Thickness (m)	Sedimentation rate (cm/yr)
E5	4000	>2.5	>0.063
E4	2250	0.65	0.029
E3	450	ca. 1.1	ca. 0.245

Regional pollen (bio-)zones (RPAZ; Mamakowa, 1988, 1989) are as follows: E1 = *Pinus–Betula*, E2 = *Pinus–Betula–Ulmus*, E3 = *Quercus–Fraxinus–Ulmus*, E4 = *Corylus–Quercus–Tilia*, E5 = *Carpinus–Corylus–Alnus*, E6 = *Picea–Abies–Alnus* (not represented in pollen diagram in Fig. 4), and E7 = *Pinus*. The age of zonal boundaries is in years from the Saalian/Eemian Stage boundary (Zagwijn, 1996; Fig. 5). Sample depths are mean values for each sampling interval (see text for explanation).

8. Age model

Recognition that the local pollen zones (LPAZs) in the Licze sequence (Figs. 4 and 5) can be directly correlated with the regional pollen zones of northern Poland (Mamakowa, 1988, 1989), and through them with those from northern Germany (Menke and Tynni, 1984) and Denmark (Andersen, 1961, 1965, 1975), allows the sequence to be assigned a chronology by comparison with that from Bispingen in northern Germany (Müller, 1974; Field et al., 1994; Zagwijn, 1996). Using Müller's (1974) timescale, which is based partly on counts of laminae in varved lacustrine sediment, tentative ages have been allocated to the local pollen zone boundaries (Fig. 5, Table 1). These ages are given as years after the Saalian/Eemian-Stage boundary, and provide estimated sedimentation rates for each pollen zone. The calibrated pollen zonation allows hydrographic events within the Licze sequence to be approximately dated (Table 1), and thereby compared with events recorded elsewhere in the Baltic region. The temporal correlation is necessarily tentative since Licze is about 600 km east of Bispingen, although these two sites are at similar latitudes (Fig. 1). Major pollen zones

Fig. 11. Dinoflagellate cysts from the marine Eemian of Licze. Various magnifications. (a–c) *Echinidinium zonneveldiae* Head 2003, upper, mid and lower foci; arrow in (c) indicates theropylic archeopyle; central body max. dia. 48 μm; sample 37(2)H20/3; depth 96.30–96.40 m. (d) *Quinquecuspis* sp. cf. *Q. concreta* (Reid 1977) Harland 1977, mid focus; note rounded outline and very reduced horns; length 54 μm; sample 19(2)G7/0; depth 94.50–94.60 m. (e, f) *Quinquecuspis* sp. cf. *Q. concreta*, upper and mid foci; length 67 μm; sample 46(2)V9/0; depth 97.20–97.30 m. (g, h) *Quinquecuspis* sp. cf. *Q. concreta*, upper and lower foci; length 76 μm; sample 34(1)P30/0; depth 96.00–96.10 m. (i–l) *Lejeunecysta* sp. 1, upper though lower foci; note ridges and spinules on both epi- and hypocyst, and (l) irregularly denticulate crests on both margins of cingulum; length 66 μm; sample 37(2)T38/1; depth 96.30–96.40 m. (m–o) Cyst of *Protoperidinium oblongum* sensu Dale (1983, figs. 11 and 12), ventral view at upper, mid, and lower foci; operculum in place representing a broad 2a plate that includes apex, and whose ventral margin is shown by arrow in (m); length 80 μm; sample 47(3)R49/2; depth 97.30–97.40 m. (p, q) *Selenopemphix quanta* (Bradford, 1975) Matsuoka, 1985, upper and lower foci, principal archeopyle suture visible in (q); breadth excluding processes 74 μm; sample 30(4)N16/0; depth 95.60–95.70 m. (r, s) *Selenopemphix?* sp. 1, upper and slightly lower foci; note pronounced apical horn and discontinuous reticulum of low crests on epicyst; breadth, including cingular crests, 64 μm; sample 46(2)U24/1; depth 97.20–97.30 m.
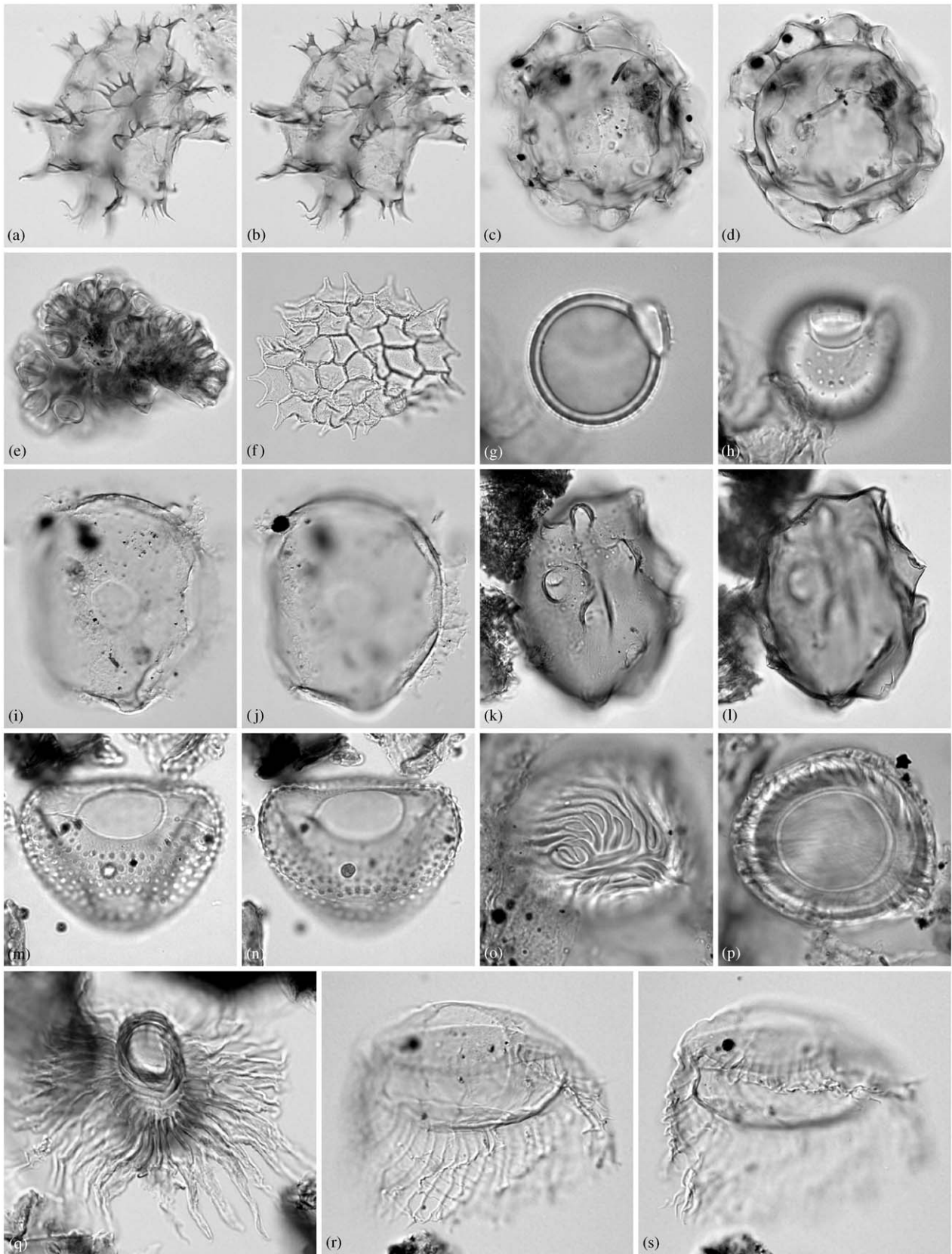
for the Eemian are nonetheless considered broadly synchronous from western France to Poland, with differences in the general succession representing no more than a few centuries (Cheddadi et al., 1998; Turner, 2002).

9. Results of dinoflagellate cyst analysis

Of 28 samples processed for marine palynology (Fig. 7), fifteen contained sufficiently numerous dinoflagellate cysts to count 200 or more specimens (Appendix A). The distribution of individual dinoflagellate taxa in these samples is given in Fig. 6. At least 25 marine dinoflagellate cyst species were recorded, with estimated cyst concentrations ranging from 180 to 94,601 cysts per gram dry weight. The concentrations of all non-pollen aquatic palynomorph groups encountered are shown in Fig. 7, and most taxa are illustrated (Figs. 8–13). Raw data are given in Appendix A.

9.1. Local dinoflagellate cyst zonation

Beginning at 101.00 m depth, four local marine dinoflagellate cyst zones have been recognised (Figs. 6 and 7).

9.1.1. Zone LDf 1 (samples from 101.00 to 99.20 m)
This zone is characterised by low cyst concentrations and low species richness comprising *Lingulodinium machaerophorum* (Fig. 8c and d) including forms with reduced processes (Fig. 8e and f), *Spiniferites bentorii* (Fig. 9h–l) including forms with reduced processes, *Spiniferites* indet. including cysts of *Gonyaulax baltica*, *Operculodinium centrocarpum* (Fig. 8g–i), and *Tuberculodinium vancampoae* (Fig. 12c and d). This zone occurs within RPAZ E1 or E2.

9.1.2. Zone LDf 2 (samples from 98.80 to 97.65 m)
An increasing species richness (12 taxa or more), *Lingulodinium machaerophorum* exceeding 20%, and low total dinoflagellate cyst concentrations (180–2207 cysts

per g) characterise this zone. A marked increase in species richness occurs towards the top of the zone. A pollen spectrum in the lowest sample of Zone LDf 2 (98.80 m), counted from the same slide as that used for dinoflagellate cyst analysis, shows that this level belongs to the earliest part of RPAZ E3.

9.1.3. Zone LDf 3 (samples from 97.45 to 96.35 m)
An abrupt decrease in *L. machaerophorum* (up to 15% or less) and an increase in *Spiniferites bentorii* (mostly 30% or more) characterise this zone. The zone is also marked by high total dinoflagellate cyst concentrations (31,156–94,601 cysts/g) and high species richness. The base of LDf 3 coincides with the change from sand- to silt-dominated sedimentation, and occurs within RPAZ E4. Zone LDf 3 extends into RPAZ E5.

9.1.4. Zone LDf 4 (samples from 96.05 to 94.55 m)
Continued low abundance of *L. machaerophorum* and abruptly reduced numbers of *Spiniferites bentorii* characterise this zone. Dinoflagellate cyst concentrations (5028–27,682 cysts/g) are considerably lower than for the subjacent zone. The base of Zone LDf 4 lies within RPAZ E5. The top of Zone LDf 4 is undefined but presumably occurs within an overlying 2.5-m thick, unrecovered interval. The highest sample (at 94.55 m) is still within RPAZ E5.

9.2. Reworked dinoflagellate cysts

Reworked dinoflagellate cysts are present throughout, and generally represent between 5% and 20% of the total dinoflagellate cysts, although this proportion increases greatly in the lower part of the section (below about 97.60 m) probably due to an increased rate of clastic input and the higher preservational potential of reworked cysts. Reworked specimens were recognised by differential preservation (including their propensity to take up stain) and stratigraphic range and include the typically Palaeogene taxa: *Areosphaeridium diktyoplokum*, *Cordosphaeridium funiculatum*, *Dapsilidinium pseudocolligerum*, *Distatodinium paradoxum*, *Enneadocysta*

Fig. 12. Dinoflagellate cysts (a–d) and other aquatic palynomorphs (e–s) from the Eemian of Licze. Various magnifications. (a, b) *Xandarodinium xanthum* Reid 1977, upper and slightly lower foci; length, including processes, 63 μm; sample 46(2)X42/3; depth 97.20–97.30 m. (c, d) *Tuberculodinium vancampoae* Rossignol (1962) Wall 1967, upper focus on archeopyle and mid focus; maximum diameter 80 μm; sample 60(1)G45/3; depth 98.70–98.90 m. (e) *Botryococcus* sp., upper focus; maximum diameter 72 μm; sample 47(3)F49/4; depth 97.30–97.40 m. (f) *Pediastrum* sp., mid focus; maximum diameter 91 μm; sample 30(4)C7/2; depth 95.60–95.70 m. (g, h) *Sigmopollis* sp., mid and lower foci; central body max. dia. 22 μm; sample 27(2)K18/2; depth 95.30–95.40 m. (i, j) *Halodinium majus* Bujak 1984, antapertural view at mid focus on apertural surface (apertural plug in place), and lower focus; central body max. dia. 67 μm; sample 50(1)G7/2; depth 97.60–97.70 m. (k, l) Incertae sedis 1, upper and slightly lower foci; length 101 μm; sample 21(1)R33/3; depth 94.70–94.80 m. (m, n) Incertae sedis 2, upper and slightly lower foci; maximum diameter, including ornament, 60 μm; sample 73(2)W47/4; depth 101.40 m. (o, p) Incertae sedis 3, upper and mid foci; maximum diameter 38 μm; sample 60(1)U10/1; depth 98.70–98.90 m. (q) Incertae sedis 4, mid focus; maximum diameter of inner coil 19 μm; sample 24(2)V42/0; depth 95.00–95.10 m. (r, s) *Radiosperma corbiferum* Meunier 1910 (= Sternhaarstatoplast of Hensen, 1887), equatorial view at upper focus showing circular pylome, and lower focus; width of central body 52 μm; sample 46(2)V34/0; depth 97.20–97.30 m.
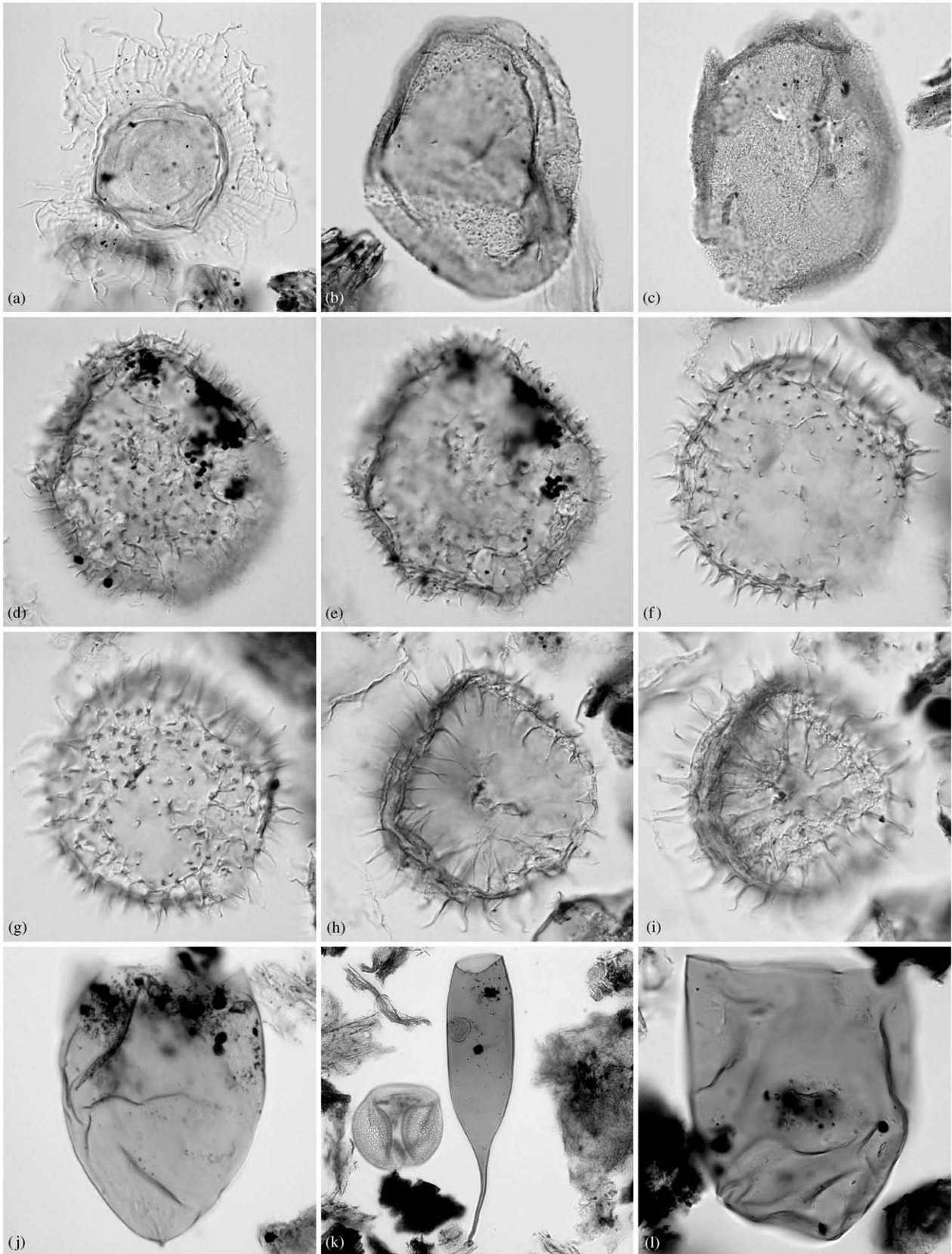
arcuata, *Heteraulacacysta porosa*, *Membranophoridium aspinatum*, *Reticulatosphaera actinocoronata*, *Tityrosphaeridium cantharellus*, and *Wetzeliella symmetrica*; and the Cretaceous taxa: *Odontochitina* sp. and *Palaeohystrichophora infusorioides*. Palaeogene deposits underlie the Quaternary in the Licze area (see Fig. 3), so many of the reworked dinoflagellate cysts may have been sourced locally. No dinoflagellates having exclusively Neogene ranges were found.

9.3. Palaeoenvironmental interpretation of dinoflagellate cyst record

Two samples, within the intervals 101.75–101.50 m (101.63 m mean depth) and 101.50–101.30 m (101.40 m mean depth), do not contain dinoflagellate cysts or foraminiferal linings in spite of their well preserved state and so may represent non-marine deposition (Fig. 7). The sample at 101.50–101.30 m is a brown silty sand, and the palynological preparation contains abundant invertebrate remains as well as pollen. The sample is presumably from the lower part of the sampled interval because the earliest marine sediments are logged at 101.50 m (Makowska et al., 2001).

Dinoflagellate cysts within the interval 101.00–94.55 m (Zones LDf 1–4) comprise a diverse record indicating the presence of warmer and considerably more saline summer sea-surface conditions than today. However, an absence of *Impagidinium* species indicates that unmixed oceanic watermasses, characterised by high-salinity (usually in excess of 30 psu), oligotrophic conditions, were not present at Licze.

9.3.1. Zone LDf 1 (samples from 101.00 to 99.20 m)

Only one sample, at 101.00 m, contained dinoflagellate cysts sufficiently numerous (concentration, 120 cysts per gram) to count (see Appendix A). This sample comprises *Lingulodinium machaerophorum* (33%), *L. machaerophorum* with <3 μm-long processes (10%), *Spiniferites* indet. including cysts of *Gonyaulax baltica* (38%), *Tuberculodinium vancampoae* (9.6%), *Operculodinium centrocarpum* (6.8%), and *Spiniferites bentorii* (4.1%). Two of the three specimens of *S. bentorii* have

stunted processes. These taxa occur sporadically throughout this zone.

The assemblage at 101.00 m indicates a salinity of ca. 10–15 psu, based on the presence of *Lingulodinium machaerophorum* which requires at least ca. 10 psu or more (see below), and low species richness compared to modern assemblages in the Belt Sea (e.g., Nehring, 1994) where salinities are ca. 15 psu or more (Stockholm University, 2002). Salinity might have been at the lower end of this range judging from the high percentage of *Lingulodinium machaerophorum* cysts bearing short processes (10%) (Dale, 1996), the presence of *Spiniferites bentorii* specimens with stunted processes, and the dominance of *Gonyaulax baltica* cysts among the *Spiniferites* indet. category. Culturing studies of *Gonyaulax baltica* show it to endure salinities as low as 5 psu, although cyst formation requires salinities of 10 psu or more (Ellegaard et al., 2002).

At 100.40 m, four specimens of *Spiniferites bentorii*, from a total of just six specimens, suggest that salinity was increasing slightly through Zone LDf 1, although the low species richness nonetheless places all of this zone within the ca. 10–15 psu salinity range. A mesohaline (5–25 psu) molluscan assemblage found at 100.50 m (Makowska, 2001; see Section 5; interpreted from Funder et al., 2002, table 1) is consistent with this salinity estimate based on dinoflagellates.

Summer sea-surface temperatures were probably higher than those of today, judging from significant numbers of the thermophilic species *Tuberculodinium vancampoae* (see below).

The sediments are interpreted as beach sands, and the high sedimentation rates, winnowing of sediments, and adverse preservational environment all probably account for the low cyst and overall palynological concentrations in Zone LDf 1.

9.3.2. Zone LDf 2 (samples from 98.80 to 97.65 m)

Several species are present whose (palaeo-)environmental parameters are well known. *Lingulodinium machaerophorum* (the cyst name for *Lingulodinium polyedrum*) occurs with frequencies of up to 30%. Culturing experiments have shown that in the laboratory *Lingulodinium polyedrum* requires salinities of at

Fig. 13. Aquatic palynomorphs from the Eemian of Licze. Various magnifications. (a) *Radiosperma corbiferum* Meunier 1910 (= Sternhaarstatoplast of Hensen, 1887), polar view at mid focus; maximum diameter of central body 45 μm; sample 47(2)T28/4; depth 97.30–97.40 m. (b) Invertebrate egg (spinules), mid focus showing scattered spinules; length 89 μm; sample 40(2)K41/0; depth 96.60–96.70 m. (c) Invertebrate egg (spongy), upper focus showing thick spongy outer wall; length 95 μm; sample 48(1)U47/4; depth 97.40–97.50 m. (d, e) Invertebrate egg (long processes), upper and mid foci showing long, hollow, tapering processes; length of central body 72 μm; sample 19(1)P8/3; depth 94.50–94.60 m. (f, g) Invertebrate egg (long processes), upper and slightly lower foci; morphology as for specimen in (d, e); length of central body 69 μm; sample 30(4)V46/3; depth 95.60–95.70 m. (h, i) Invertebrate egg (long processes), upper and mid foci showing long, hollow, tapering processes of which some are bifurcate; length of central body 70 μm; sample 34(2)T9/4; depth 96.00–96.10 m. (j) Tintiniid lorica type 1, upper focus showing fine striations radiating from holdfast; length 151 μm; sample 43(1)V8/2; depth 96.90–97.00 m. (k) Tintiniid lorica type 2, mid focus; length 283 μm; sample 40(2)Q27/2; depth 96.60–96.70 m. (l) Tintiniid lorica type 3, upper focus; note fine, parallel wrinkles running in various directions, and absence of aboral horn or holdfast; length 94 μm; sample 27(1)T9/0; depth 95.30–95.40 m.

least 15 psu to sustain growth and to reproduce (Lewis and Hallett, 1997; Hallett, 1999). Cultures of motile cells have occasionally been sustained in salinities as low as 10 psu in the laboratory, but these cultures soon failed to thrive (Hallett, 1999). *Lingulodinium polyedrum* occurs presently in the plankton of the Kattegat and Belt Seas (e.g., Edler et al., 1984; Nehring, 1994) but not in the Baltic Sea proper, where surface water salinities are about 8 psu or less. Cyst studies of modern Baltic sediments confirm that *Lingulodinium machaerophorum* is presently rare or absent from the Baltic Sea proper (Gundersen, 1988; Dale, 1996). The abundance of *Lingulodinium machaerophorum* therefore indicates salinities of about 15 psu or more. Species richness is an important criterion for distinguishing low from high-salinity environments (Dale, 1996). The high numbers of species recorded in the upper part of Zone LDf 2 (at least 17 species at 97.85 m; Appendix A) are comparable to the Belt Seas and Kattegat today (e.g. Gundersen, 1988; Ellegaard et al., 1994; Nehring, 1994; Persson et al., 2000), where summer surface salinities range between about 15 and 25 psu (Persson et al., 2000; Stockholm University, 2002). Indeed, most neritic species today are found between 20 and 35 psu (Dale, 1996), suggesting that the upper part of Zone LDf 2 represents salinities closer to about 20 psu or more. Hence, salinities might have slightly increased through Zone LDf 2 judging by the species richness which is lowest (ca. 12 species) in the basal sample at 98.80 m.

Elevated summer sea-surface temperatures throughout Zone LDf 2 are indicated by relatively high frequencies (7–9%) of *Tuberculodinium vancampoae* (Figs. 12c and d). This is the cyst of *Pyrophacus steinii* whose motile cell occurs in warm-temperate to tropical environments today (Faust, 1998). A survey of cyst distributions in modern sediments of the North Atlantic shows highest abundances (above 2%) where summer sea-surface temperatures are above 27°C and water depths are less than 60 m (Edwards and Andrle, 1992). This species presently does not occur in the Baltic Sea, North Sea, or offshore UK. Its abundance suggests that summer sea-surface temperatures were more than about 3°C warmer than today in the Gulf of Gdansk. *Tectatodinium pellitum* (Fig. 10c–e), which occurs in the upper part of Zone LDf 2, is another thermophilic species indicating warmer-than-present summer sea-surface temperatures (Head, 1994). This species is not reported in the region today.

Of additional significance is the absence or near absence of cool-water taxa, such as *Bitectatodinium tepikiense*, *Pentapharsodinium dalei* cysts (Fig. 10f), and *Spiniferites elongatus* (Fig. 9m–p) (Dale, 1996, 2001; Rochon et al., 1999). *Pentapharsodinium dalei* is a spring-blooming species (Dale, 2001) and the low representation of its cysts is best explained by relatively warm spring surface-water temperatures, implying mild winters.

9.3.3. Zone LDf 3 (samples from 97.45 to 96.35 m)

An abrupt decrease in *L. machaerophorum* and reciprocal increase in *Spiniferites bentorii* (Fig. 9h–l) at the beginning of this zone co-occurs with the change from sand-dominated to silt-dominated sedimentation, and signals a rise in sea level. *Lingulodinium machaerophorum* and *Spiniferites bentorii* are most common in estuaries and embayments of the North Atlantic, France, the British Isles, and Mediterranean today (Morzadec-Kerfourn, 1992); and *Lingulodinium machaerophorum* is also a known indicator of elevated nutrient levels (Dale, 1996). A record of Holocene sea-level fluctuations from the Vilaine estuary in Brittany, France has shown that *S. bentorii* characterises transgressive phases, whereas *L. machaerophorum* dominates during regressive phases (Morzadec-Kerfourn, 1992). In an estuary, a transgressive phase will be characterised by increasing salinity and hydrographic stability, and by a general decrease in nutrient levels. A comparable situation is apparent at Licze.

Spiniferites bentorii has not been reported from modern sediments of the Baltic Sea proper, where salinities are too low, but is known from the Kattegat (Persson et al., 2000). It has also been reported in a late Holocene sediment core from Limfjord, Denmark, where it co-dominates (ca. 17–47%) the cyst assemblages with *L. machaerophorum* at two intervals of changing or intermediate salinity (Ellegaard, 2000). These intervals (90–102 and 9 cm) have estimated salinities at between 22 and 30 psu (M. Ellegaard, personal communication, 2002). This response of *Spiniferites bentorii* to salinity suggests a similar range, of about 22 psu or more, for Zone LDf 3.

Zone LDf 3 also contains the highest dinoflagellate cyst concentrations in the Licze core (31,156–94,601 cysts per gram). This appears to represent a peak in biological productivity, although concentrations will have been enhanced by low sedimentation rates at least in the lower part of this zone (0.029 cm/yr for RPAZ E4; Table 1). It should be noted that species richness is highest in the upper part of Zone LDf 2 and in the lower part of Zone LDf 3, suggesting salinities reached highest levels during this interval. Species richness drops from 16 or 17 species per sample in the lower part of Zone LDf 3, to 14 or 15 species at the top of this zone (Appendix A), suggesting a slight reduction in salinity. The thermophilic species *Tuberculodinium vancampoae* has its highest relative abundance in the lower part of Zone LDf 3 (13% at 97.35 m), indicating high summer temperatures at this time.

A notable increase in *Pediastrum* (Fig. 12f) occurs within Zone LDf 3. *Pediastrum* is a common alga of lakes or slow-moving rivers and streams (Parra Barrientos, 1979; Bold and Wynne, 1985), although some species are known from coastal brackish waters of the present Baltic Sea where salinities are below about 5 or

10 psu (see discussion in Brenner, 2001). Given the much higher salinities determined from the dinoflagellate cysts of Zone LDf 3 and LDf 4 at Licze, increasing abundance of *Pediastrum* indicates elevated levels of river inflow at this site.

9.3.4. Zone LDf 4 (samples from 96.05 to 94.55 m)

An abrupt decline in *Spiniferites bentorii* at the beginning of this zone suggests a small reduction in salinity (see above), although salinity did not change substantially from zone LDf 3 into LDf 4 as species richness remains high, at between about 14 and 16 species per sample throughout Zone LDf 4 (Appendix A). The highest sample at 94.55 m reflects salinities of about 15 psu or more and contains the strongly thermophilic species *Tuberculodinium vancampoae*, showing that warmer and much more saline waters than present continued to occupy the area well into RPAZ E5. A similar decline in salinity by the end of RPAZ E5 was similarly noted from molluscan evidence for the Nowiny boring nearby (Funder et al., 2002).

Pediastrum frequency increases considerably in this zone, along with elevated values of reworked dinoflagellate cysts. The abundance of these groups indicates a substantial increase in river inflow, although a brief reduction in river inflow near the top of the zone (at 95.05 and 94.75 m) is evidenced by lower values of *Pediastrum* and reworked dinoflagellates and by an increase in *Spiniferites bentorii*. The coexistence of high river-input and maintenance of high salinity throughout this zone requires comment. The increasing influence of river discharge presumably originates from the palaeo-Vistula whose mouth was nearby. In an embayment, this will have created strongly stratified conditions, with low-salinity water restricted to a thin surface layer. Dinoflagellates, being motile organisms, would have adjusted their depth to more saline waters below the shallow halocline. This interpretation is corroborated by the diatom record for the Licze borehole, where a substantial uphole increase in freshwater diatoms has been observed (Hui Jiang, personal commun. to M.-S.S.). The increased freshwater input in Zone LDf 4 is interpreted to reflect shallowing conditions during this interval.

10. Licze and other Baltic dinoflagellate cyst floras compared

The Eemian dinoflagellate cyst flora at Licze has no direct analogue in the Baltic region today because key thermophilic elements at Licze (e.g., *Tuberculodinium vancampoae*, *Tectatodinium pellitum*) are absent from the Baltic, as apparently are *Spiniferites* sp. 1, *Echinidinium zonneveldiae*, and *Lejeunecysta* sp. 2. Moreover, *Spiniferites bentorii* has not been reported in high numbers from the Baltic region. In addition, cool-water species such as *Bitectatodinium tepikiense*, which occurs in the Belt Sea and Kattegat today (e.g., Persson et al., 2000), are absent from Licze. In all these respects, the dinoflagellate cyst flora at Licze has a Lusitanian/Mediterranean aspect, not a Baltic one.

The low number of dinoflagellate cyst species in the present Baltic Sea proper (about seven species recorded; Gundersen, 1988) reflects low salinities of about 8 psu or below. The dinoflagellate cyst flora at Licze comprises at least 25 species in total, and certainly in Zones LDf 2–4 is more similar to the diversity of the Belt Sea and Kattegat today (Gundersen, 1988; Ellegaard et al., 1994; Nehring, 1994; Ellegaard, 2000; Persson et al., 2000), where salinities are in the range of 15–25 psu.

The Licze dinoflagellate cyst flora shows strongest similarity with those from the Eemian eastern Danish sites at Ristinge Klint and Mommark (Head et al., 2001; Fig. 1); although species richness is somewhat greater at these sites, presumably owing to slightly increased salinities brought about by their closer proximity to North Sea inflow. The Licze flora is also similar to a record from the Eemian of the Amsterdam-terminal borehole in The Netherlands, of which notable shared features are persistent *Tuberculodinium vancampoae* and the poor representation of *Bitectatodinium tepikiense* (van Leeuwen et al., 2000). At Mertuanoja, in Ostrobothnia (Fig. 1), Eemian dinoflagellate cyst assemblages are notably less diverse than at Licze (Eriksson et al., 1999), and probably reflect cooler and less saline surface-water conditions.

11. Hydrographic history

Eemian sedimentation at Licze began with deltaic sands that overlie glaciolacustrine varved clays of Wartanian (late Saalian) age. Within this deltaic environment, peat bogs and shallow lakes developed during the first hundred years or so of the Eemian (RPAZ E1 or E2). A sample from within the interval 101.50–101.30 m (101.40 m mean depth) has a non-marine palynological aspect. Beach deposits at 101.50 m are the first indication of a marine transgression, followed by marine dinoflagellate cysts and foraminiferal linings at 101.00 m, and then by marine molluscs at 100.50 m. This transgression occurred within the first 300 years of the interglacial (RPAZ E1 or E2). Dinoflagellate cysts at 101.00 m (Zone LDf 1) indicate salinities of about 10–15 psu, and summer sea-surface temperatures probably higher than today. These warm, saline waters were evidently sourced from the North Sea.

At 98.80 m, pollen assignable to the early part of RPAZ E3 (probably close to the E2/3 boundary) are accompanied by a diverse dinoflagellate cyst assemblage

(Zone LDf 2). This assemblage indicates that already by about 300 years into the interglacial, surface water salinities were about 15 psu or more, while summer temperatures may have exceeded 27°C.

At about 750 years into the interglacial (lowest RPAZ E4; depth 97.60 m), sediments abruptly became finer grained and silty, and the sedimentation rate fell, indicating the establishment of quieter waters within this protected embayment. The dinoflagellate cyst record signals a transgressive phase beginning at this time. High dinoflagellate cyst concentrations during the later part of RPAZ E4 and earlier part of E5 (corresponding to Zone LDf 3; Fig. 7) apparently reflect an episode of maximum marine productivity. Salinity was probably highest within the upper part of RPAZ E3 and E4 (upper part of Zone LDf 2 and lower part of Zone LDf 3) judging from high species richness, with salinities probably about 22 psu or more. This compares favourably with salinity estimates based on molluscs from the Nowiny boring, which are generally about 25 psu, but reaching a maximum within RPAZ E3 and periodically rising above 30 psu (Funder et al., 2002).

Later within RPAZ E5, rising frequencies of *Pediastrum* and reworked dinoflagellate cysts (Zone LDf 4) indicate an increasing influence of river discharge, presumably from the proto-Vistula whose mouth was nearby. This is interpreted to have resulted in seasonal, strongly stratified conditions within the embayment, with low-salinity water restricted to a thin surface layer. Below this brackish surface layer, salinities of about 15 psu or more, as well as very warm temperatures, are reflected by a diverse dinoflagellate cyst flora throughout Zone LDf 4. Shallowing conditions are nonetheless indicated by more sandy deposition, a reduced diversity of marine molluscs above 95.20 m, and probabaly reflected also by a decline in *Spiniferites bentorii*. Progradation of the river estuary as well as isostatic rebound are responsible for this shallowing trend.

Non-marine deltaic sediments occur between 91.00 and 89.75 m. They were assigned an Early Vistulian age on sedimentological evidence (Makowska, 2001), but pollen analysis dates them as Eemian (RPAZ E7). The timing of emergence cannot be determined precisely, because sediment was not recovered between 94.55 and 91.00 m, but it occurred after the beginning of RPAZ E5 which is more than 3000 years into the interglacial. At the Nowiny boring, just 25 km north of Licze, marine conditions continued until some time into RPAZ E6 (Makowska, 1986).

12. Discussion and conclusions

The interglacial deposits at Licze are unambiguously assigned to the Eemian Stage because they overlie tills of Wartanian (late Saalian) age, and yield a detailed pollen record that can be directly compared to Mamakowa's (1988, 1989) regional pollen assemblage zonation for the Eemian of Poland. It has not been possible to distinguish between RPAZ E1 and E2 at Licze, but otherwise all of Mamakowa's Eemian zones are recognised, with the exception of RPAZ E6 which appears to fall within an unsampled interval. Although the top of RPAZ E5 was not identified, this zone represents the main part of the marine silt-dominated sequence at Licze and reflects an apparently stable late-temperate *Carpinus–Picea–Corylus* forest that colonised the region during this time. This observation is consistent with other studies that have found no evidence of substantial climate fluctuation in RPAZ E5 (e.g., Boettger et al., 2000; Binka and Nitychoruk, 2003, and references therein), despite earlier claims to the contrary (e.g., Field et al., 1994; Cheddadi et al., 1998).

The marine transgression at Licze in RPAZ E1 or E2 predates the reported onset of marine conditions at the start of RPAZ E3 in the Nowiny boring just 25 km to the north (Makowska, 1986). However, at Plasumi in Latvia (Fig. 1), glaciomarine conditions became established during the latest Saalian, with true interglacial marine conditions occurring in the early Eemian (correlative with RPAZ E1) (Kalnina, 2001). An early marine transgression is also known from the Estonian island of Prangli (Fig. 1), where sea water invaded a glacial lake during RPAZ E1 times (Cheremisinova, 1961; Liivrand, 1984, 1987, 1991). A somewhat later transgression at Licze would imply a higher site elevation. Nevertheless, very warm, saline conditions were established at Licze within RPAZ E1 or E2, the timing of which is consistent with a warm-water incursion into the Wadden Sea (eastern North Sea) during the earliest Eemian (Funder et al., 2002). These events imply that the English Channel was by now open (Funder et al., 2002, and references therein), and accord with the rapid increase in summer temperatures that characterises the early Eemian (Zagwijn, 1996). At the eastern Danish sites of Ristinge Klint and Mommark (Fig. 1), a marine ingression does not occur until the rise in *Quercus* (about 300 years into the Eemian; Head and Gibbard, 2000; Head et al., 2001). Higher site elevations at Ristinge Klint and Mommark must account for this discrepancy.

At Licze, sedimentological and dinoflagellate cyst evidence point to a rise in relative sea level at about the start of RPAZ E4 (ca. 750 years into the interglacial). The timing of this event suggests that it relates to an abrupt increase in salinity recorded at Ristinge Klint and Mommark (Head and Gibbard, 2000; Kristensen et al., 2000; Head et al., 2001) that coincides with the *Corylus* increase at the end of RPAZ E3. Kristensen et al. (2000) attributed this rise in salinity at the Danish sites to a presumed opening of the Danish Belts. This

same event appears to have influenced the hydrography of the southeastern Baltic Sea, implying a basinwide extent.

There is no evidence of arctic water influence in the Licze dinoflagellate cyst record. The absence of *Islandinium minutum* and *Islandinium? cezare* is particularly significant as these species dominate Eemian assemblages from the White Sea region, where conditions were not much warmer than today (Grøsfjeld et al., 2000). This is consistent with the view that the Karelian seaway did not effect a significant exchange of waters between the Baltic and White seas during its existence in the early Eemian (Funder et al., 2002).

Marine dinoflagellate cysts and other aquatic palynomorphs, notably the freshwater to brackish alga *Pediastrum*, have been used collectively to reconstruct hydrographic conditions at Licze. The co-occurrence of relatively high-salinity dinoflagellates with abundant *Pediastrum* highlights the complex interplay of marine and freshwater influences near a large river mouth.

Eemian dinoflagellate cyst assemblages at Licze belong to a distinctive flora of Lusitanian/Mediterranean affinities that extended fully along the southern margin of the Baltic Sea and into the Belt Seas, with similar assemblages occurring at Ristinge Klint and Mommark in eastern Denmark (Head and Gibbard, 2000; Head et al., 2001). Comparable dinoflagellate cyst assemblages unsurprisingly occur in the Eemian of the North Sea (van Leeuwen et al., 2000). This distribution appears to mirror that of the molluscs, which have a strong Lusitanian element (Funder et al., 2002). Upper water-column summer temperatures possibly exceeded 27°C and were clearly warmer than today. The low representation of cool-water species including the spring-blooming species *Pentapharsodinium dalei* cysts suggests warm spring temperatures. This accordingly implies mild winter sea-surface temperatures, which agrees with estimates of winter sea-surface temperatures about 9°C (i.e., 6°C higher than today) based on molluscs from northern Poland (Funder et al., 2002). These observations point to a strong North Atlantic current during the Eemian. Summer salinities, in excess of about 15–20 psu, persisted throughout RPAZ E3 and

into E5, and were more than about twice present values for the southeastern Baltic Sea. Fully oceanic conditions did not reach Licze, but the dinoflagellate cyst flora is consistent with salinity estimates generally of up to 25 psu based on molluscs for the Nowiny boring nearby (Funder et al., 2002). Dinoflagellate cyst and molluscan evidence therefore demonstrate the deep penetration of warm, saline North Sea waters into the southeastern Baltic Sea. This supports the view of Funder et al. (2002) that the Danish Belts were wider and deeper than today, facilitating much greater exchange with the North Sea than presently occurs. The wide distribution and distinctiveness of this Eemian dinoflagellate flora might also prove helpful in recognising marine Eemian deposits whose stratigraphic position is currently in question.

Appendix A

Counts of dinoflagellate cysts and other non-pollen palynomorphs for samples within the interval 101.00–94.55 m, and associated sample data.

Dinoflagellate cyst zones	LDf 1	LDf 2					LDf 3						LDf 4					
Sample depth (m)	101.00	98.80	98.05	97.95	97.85	97.65	97.45	97.35	97.25	96.95	96.65	96.35	96.05	95.65	95.35	95.05	94.75	94.55
Sample number	71	60	54	53	52	50	48	47	46	43	40	37	34	30	27	24	21	19
Dinoflagellate cysts																		
Spiniferites spp. indet	27	43	1	1	51	55	71	65	35	43	66	52	82	97	79	74	53	78
L. machaerophorum (>3 μm processes)	24	67	3	3	55	54	16	11	10	32	10	19	20	13	15	13	12	21
L. machaerophorum (<3 μm processes)	7	11			6	5	+	3	1	+	1	+	3	+			+	2
O. centrocarpum (>2 μm processes)	5	18		4	30	22	22	25	19	19	34	16	36	29	52	30	40	38
O. centrocarpum (<2 μm processes)		+			3	+	+	1	1	1			+	1	1	1		1
Spiniferites bentorii	3	49		2	31	50	51	92	120	80	71	102	45	38	44	64	68	34
Tuberculodinium vancampoae	7	19		+	15	19	12	31	11	24	7	5	3	11	6	17	20	9
Spiniferites sp. 1		?2			2	1				1		+			2	1		
Spiniferites elongatus		+			1	+											+	
Spiniferites mirabilis		2			+		+										+	
Polykrikos schwartzii		4			2	+	6	2	7	4	6	9	+	2	7	3	11	+
Brigantedinium spp. indet.		2			3	1	8	3	6	1	6	3	3	6	6	+	3	6
Selenopemphix quanta		2			3	1	3	+	2	3	6	2	2	5	3	5	3	2
Pentapharsodinium dalei		2			1	2					1					+	1	2
Tectatodinium pellitum					1	+	+	+	+	1	+	1	2	+	1	2	1	+
Dubridinium caperatum					1				+	3	+	1			2		1	
Dubridinium sp. 1					+	2	5	1	3	1	1	+	10	15		1		9
Lejeunecysta sp. 1					1		+		1		+							
Echinidinium zonneveldiae					+		2	+	2	1	1	2	2	1	3	+		+
Ataxiodinium choane						+		+	1								1	+
Quinquecuspis cf. *concreta*						2	+	+										
Protoperidinium spp. indet.						1	4	2		4				1	2			6
P. oblongum sensu Dale (1983, figs. 11, 12)						+	2	+	+									
Brigantedinium cariacoense							+						+					
Xandarodinium xanthum							2	+		2	+	2	+	1	4	2	1	+
Capisocysta? sp.							1											
Selenopemphix? sp. 1									1?									
Brigantedinium simplex													+					
Total heterotrophs		8			10	7	32	8	20	20	20	19	17	32	27	11	19	25
Total dinoflagellate cysts	73	219	4	10	206	215	205	236	218	221	210	214	208	221	227	213	215	210
Minimum number of species		12			17	17	16	17	16	16	14	15	14	14	14	14	14	16
Other groups																		
Pediastrum	18	21	1	1	13	11	16	9	11	25	71	29	135	139	99	36	37	77
Reworked dinoflagellate cysts	103	109	193	32	36	41	30	6	4	22	15	19	50	68	74	33	52	73
Botryococcus	16	90	43		2	6	7	5	1	3	3	4	4	7	5	3	9	4
Tintiniid loricae	5	2	1		10	1	1	1	1	4	4	4	+	9	12	1	20	7
Foraminiferal linings	5	64		3	39	59	4	13	+	3	3	2	3		3	12	56	5
Incertae sedis 3	5	1			+													
Sigmopollis sp.	3	3			1	+		2		+	1		1	1	3		1	1
Invertebrate mouthparts/appendages	10	9		1	9	4	3	3	3	10	11	12	10	37	29	15	21	34
Halodinium majus		+			2	+	+	+	+	+	+		+		1	+	1	
Invertebrate egg (long processes)				1			6	3	9	17	83	42	28	172	79	68	113	45
Invertebrate egg (scattered spinules)					1		15	5	6	5	15	8	2	2	7	4	5	8
Invertebrate egg (spongy wall)					+		5	+		1		1			3	+	1	
Invertebrate egg (fibroreticulate wall)							4	+	+	2	+	1		4	2	2		1
Radiosperma corbiferum							+	+	+		+		1	2	1			3
Incertae sedis 4										+			+	+		+	+	
Incertae sedis 1														+		1		2
Sample data																		
Spike	576	3364	258	772	875	1125	68	43	26	48	61	41	84	234	454	98	162	96
Grams dry weight	11.1	11.6	3.1	3.1	3.5	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.2	3.4	3.1	3.1
No. *Lycopodium* tablets	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3

Only samples in which dinoflagellates were sufficiently numerous to count are included. Dinoflagellate cyst zones LDf 1–4 are from the present study. Sample depths are mean values for each sampling interval (see text for explanation). A cross (+) indicates the presence of a taxon recorded outside of the main count.

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