

# Recolonization of a Middle Eocene volcanic site: quantitative palynology of the initial phase of the maar lake of Messel (Germany)

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## Abstract

The research well “Messel 2001” penetrated the sediments of the Middle Eocene maar lake at Messel (near Darmstadt, Hesse, Germany) completely. The core includes 140 m of lacustrine oil-shale overlying 90 m of clastic lake sediments which are assigned to the Middle and Lower Messel Formation, respectively. Numerical techniques like TWINSPAN and correspondence analysis have been applied to a high-resolution palynological study. The Lower Messel Formation is equivalent to the Initial Lake Phase and shows a clear succession of pollen and spore associations representing a succession of plant communities colonizing and invading the area which was previously devastated by the eruption(s). On the basis of the TWINSPAN, an Early and a Late Initial Lake Phase may be distinguished. But, throughout the Initial Lake Phase, the regional climax vegetation did not change substantially and had re-occupied the area finally at a time roughly representing the boundary between the Lower and the Middle Messel Formation. © 2006 Elsevier B.V. All rights reserved.

**Keywords:** Middle Eocene; maar lake; palynology; pioneer vegetation; palaeolimnology; multivariate statistics

## 1. Introduction

The former oil-shale mine of Messel is one of the world’s best known “Fossilagerstätten” and was added to the UNESCO list of World Nature Heritage Sites “as a Window to the Past” in 1995. Because of their unique lithology and fossil assemblages the Middle Eocene lake sediments were defined as the “Messel Formation”. They consist mainly of highly bituminous shales which

were deposited in a meromictic lake about 47 million years ago.

For many years in the past the origin of the Middle Eocene Lake Messel has been the subject of an intense discussion concerning various tectonic and volcanic scenarios (Harms, 2001). In order to find unequivocal proof for one or other hypotheses, an exploratory well was drilled in 2001 to penetrate the lake sediments and to drill as deeply as possible into the underlying rocks. A total of 433 m were cored of which the lower 200 m consist of pyroclastics and collapse breccias. Thus it has been demonstrated beyond doubt that the Messel site represents a so-called maar diatreme and the filling of its crater (Harms, 2002; Schulz et al., 2002).

Since the exploratory core 2001 was drilled in the centre of the former lake where the maximum thickness of the remaining lake sediments could be expected, a

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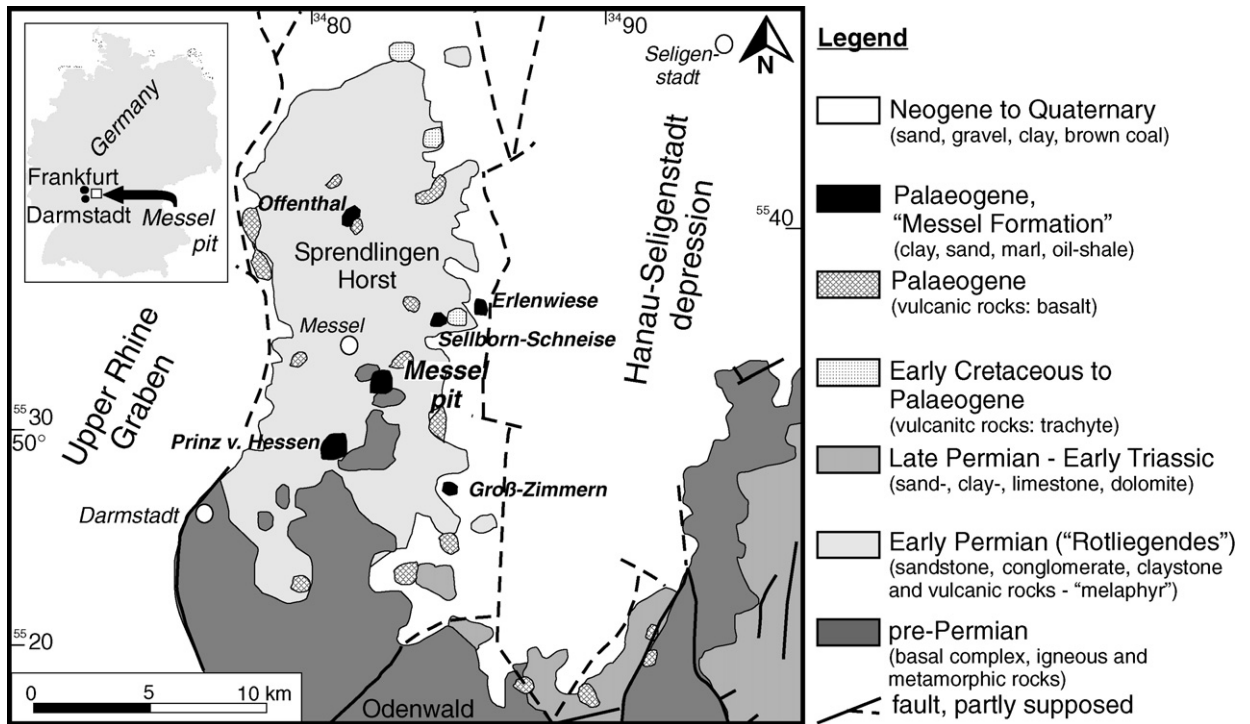


Fig. 1. Geological map showing the location of Messel pit in relation to other Palaeogene sites in the area (modified after Harms, 1999).

complete reference section was obtained (Schulz et al., 2002) including 140 m of oil-shale and 90 m of clastic lake sediments.

This provided the opportunity to conduct a detailed numerical analysis of the palynological assemblages of the entire lake deposits with the aim of trying to recognize any cyclic fluctuations and long-term trends through a time interval of several hundred thousand years during the Middle Eocene greenhouse climate at the highest possible resolution. Here we present for the first time a palynological study of the initial phase of the Messel maar lake thereby providing an insight into the successive vegetational recolonization of a volcanically disturbed site.

## 2. Geological situation

The Messel oil-shale (Fig. 1) is part of a series of isolated occurrences of Palaeogene deposits on the “Sprendlinger Horst” which forms the northern extension of the Odenwald (Felder et al., 2001). They represent individual volcanic and/or tectonic structures which are obviously of Middle Eocene age. Their origin may have been related to tectonic activity predating the later Rhine Graben system (e.g., Harms, 2001; Jacoby et al., 2005).

A generalized lithologic succession of rocks encountered in core Messel 2001 is shown on Fig. 2. The

lowermost part between 433 m and 373 m consists of a diatreme breccia which is overlain by lapilli tuffs to a depth of 228 m. The discovery of these massive volcanoclastic deposits provided final proof that the overlying lake sediments have been deposited within a maar structure which was formed by one or more phreatomagmatic eruption(s) (Lorenz, 2000; Schulz et al., 2002; Harms et al., 2003; Felder and Harms, 2004).

Soon after the eruption(s), the newly formed crater filled with water. In the initial stages great amounts of coarse debris and volcanoclastic material fell as talus or were transported by mass flows from the collapsing crater wall into the basin (Liebig, 2001; Felder and Harms, 2004). The pure mass-flow deposits and pyroclastics are overlain by the Lower Messel Formation above 228 m which is characterized by alternating breccias, tuffs, and layers of sand and clay. In its upper part, layers of oil-shale become more frequent and eventually may dominate above 139 m. The Lower Messel Formation represents the Initial Lake Phase which is terminated by an “event bed” of redeposited blocks of oil-shale, oil-shale debris and clay (Felder and Harms, 2004). The event bed occurs between 110 m and 94 m in the core and can be traced across the entire deposit. The boundary between the Lower and Middle Messel Formation was placed in the middle of the event

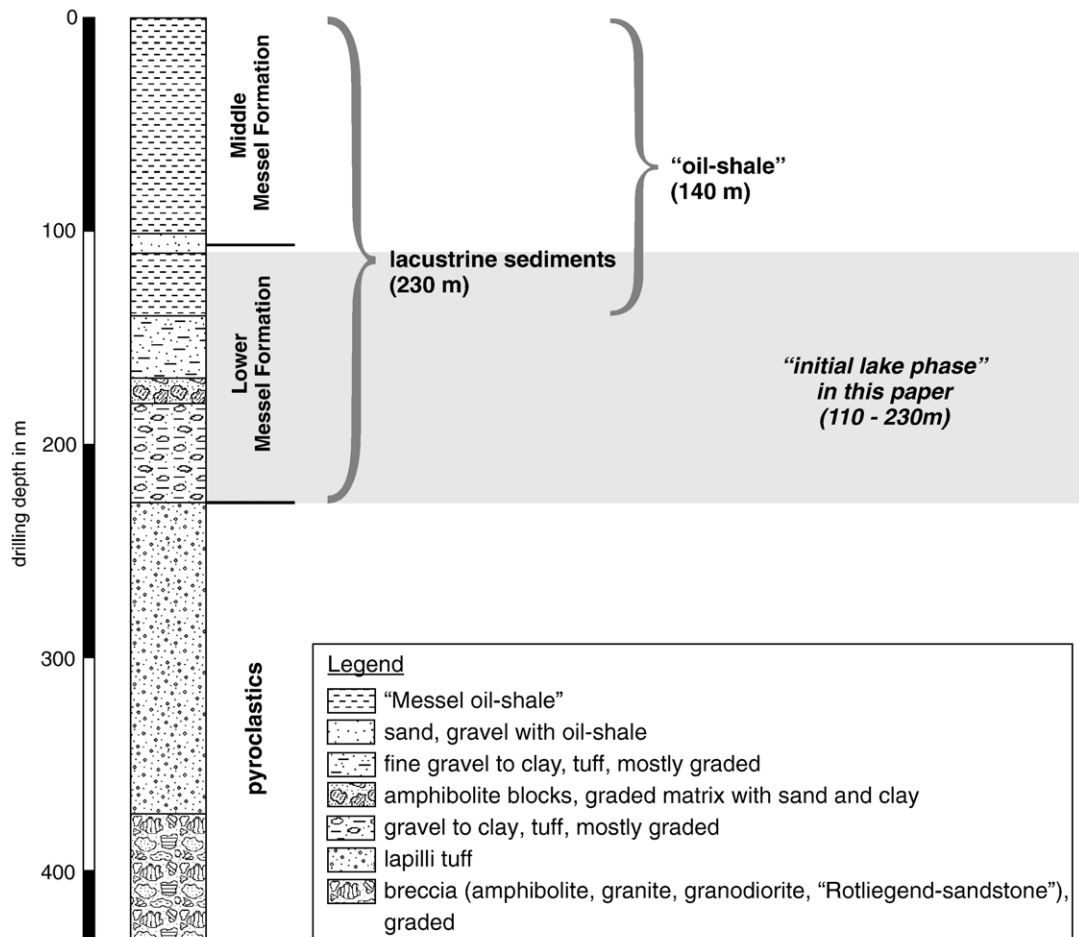


Fig. 2. Generalized section of core Messel 2001 (modified after Felder and Harms, 2004).

bed by Felder and Harms (2004), but the term "Initial Lake Phase" is used here to comprise the Lower Messel Formation only up to the base of the event bed (Fig. 2).

The Middle Messel Formation is identical with the classical "Messel Oil-shale", the finely laminated highly bituminous shale known for its unique fossil preservation and formed during the predominantly stable meromictic phase of the lake. This "oil-shale" has been the target of intense mining operations between the 1870s and 1974 (Schaal and Schneider, 1995), leaving the present "Messel pit". Part of the Middle Messel and most of the Upper Messel Formation have been removed by mining. The Upper Messel Formation is only preserved in small remnants at the margin of the Messel pit and probably represents the gradual terrestrialization of the lake (Harms et al., 2003).

For the early stages of the lake, high rates of sedimentation must be assumed suggesting that the Lower Messel Formation below 139 m was deposited in

a relatively short time. Erosion and collapse of the highly unstable and barren slopes of crater wall and tuff rim caused not only rapid sedimentation on the basin floor but also repeated mixing of the waterbody by mass flows and turbidity currents. The onset of layers of bituminous shale indicates a change towards a stabilization of the slopes and meromictic conditions in the lake. These prevailed for a long time with minimal rates of sedimentation which are estimated in the order of 0.14 mm/yr according to geophysical determinations (Schulz et al., 2002). From that, a duration of about 1.1 million years is calculated for the deposition of the 140 m of bituminous shale recorded in the core Messel 2001 (Schulz et al., 2002).

### 3. Previous work

Palynological investigations of the "Messel Oil-shale" started with Pflug (1952, 1957) who emphasized the poor

preservation and the limited stratigraphic value of the palynomorphs. On the other hand, Krutzsch in Krutzsch and Lotsch (1957), Krutzsch (1958) set up the so-called “Messel-Bild” within his succession of “Pollenbilder” (more or less equivalent to assemblage zones) as part of his palynostratigraphic subdivision of the Central European Palaeogene. He placed the “Messel-Bild” between the Lower Eocene and the Middle Eocene assemblages at Helmstedt and considered it representative for the entire Middle Messel Formation. Later, Krutzsch (1966) used the terms “Messeler Abschnitt” (subzone) respectively “Messel-Niveau” (level; Krutzsch, 1976, p. 49) equivalent to his “Pollenzone SPP 14/15” (Krutzsch, 1992, p. 177).

A number of pollen and spores from Messel was first described by Thomson and Pflug (1953) in their systematic monograph of Tertiary pollen and spores from Central Europe. Finally, Thiele-Pfeiffer (1988) published a thorough systematic and taxonomic palynological study of the oil-shale, based on a previous core from Messel (core 4/1980: Weber and Hofman, 1982; Liebig, 2001) which serves as an authoritative basis for identification in our study. However, this core did not penetrate into sediments below the Middle Messel Formation. An initial numerical analysis of Thiele-Pfeiffer’s data by Lenz et al. (2005) showed that the composition of pollen assemblages is not as homogenous

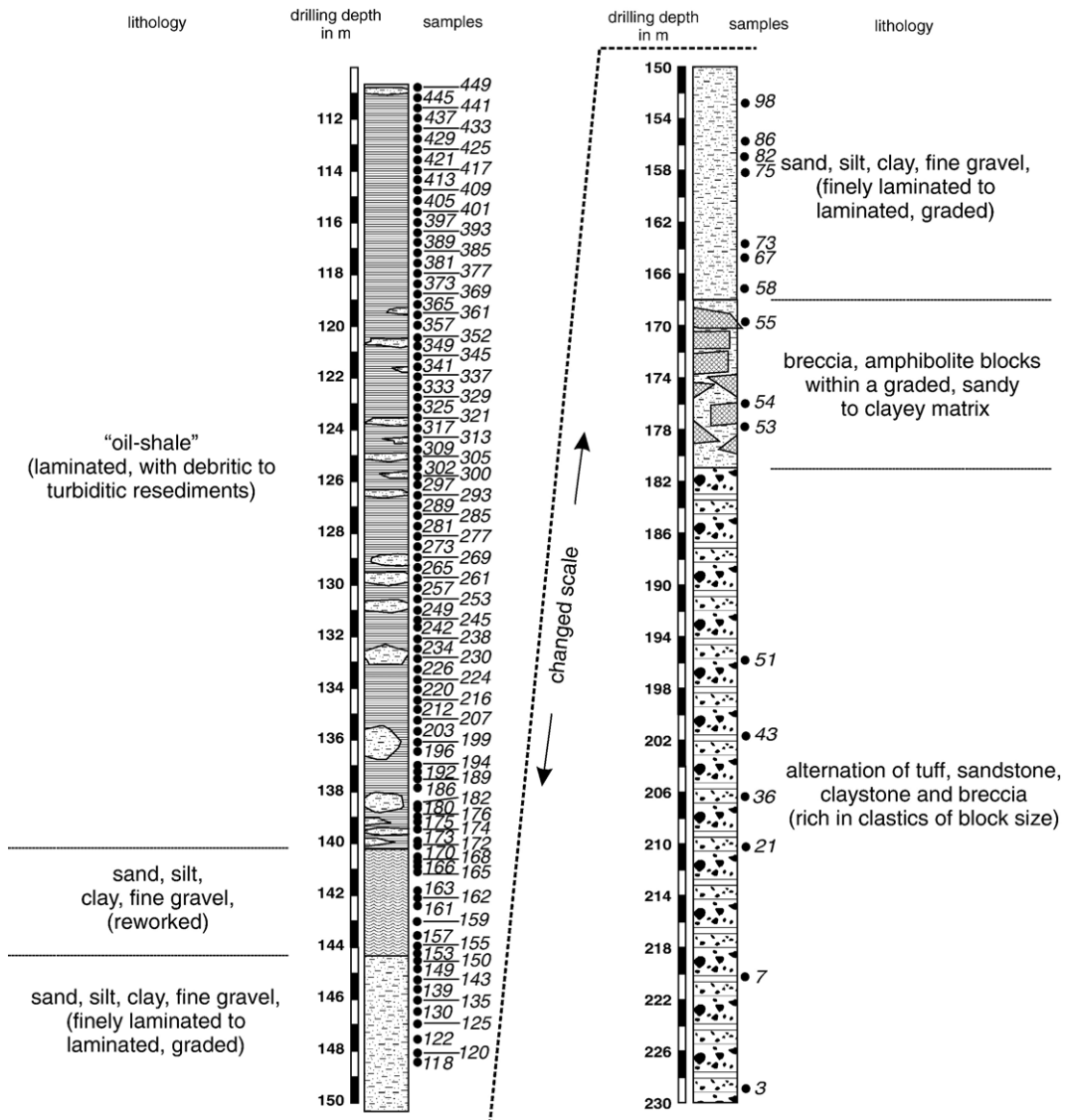


Fig. 3. Lithologic succession of the lower part of lake sediments with the position of the samples analysed in this paper.





throughout the sequence as originally stated by Thiele-Pfeiffer (1988). In addition to gaining access to the Initial Lake Phase, the new core can now be used for a higher resolution numerical study of the oil-shale and its palynological assemblages.

A detailed study of the macroflora of Messel has been carried out by Wilde (1989), thereby permitting a correlation of microfloral and macrofloral evidence (Wilde, 2004).

#### 4. Materials and methods

In order to permit a comprehensive numerical study at high resolution, a total of 1463 samples was taken from the 228 m of lacustrine sediments represented in core Messel 2001. Oil-shales within the upper part of the core were sampled by removing 1 cm increments of the laminated sediment at 10 cm intervals. In the oil-shale-free portion of the core below 140 m samples were selected on the basis of lithology, especially covering dark sediments in which a sufficiently high content of organic material could be expected. For the present analysis of the initial phase of the lake 114 samples from 110.80 m to 229.03 m were used (Fig. 3). This covers the entire Lower Messel Formation except for the event bed (100–110 m) forming the boundary between the Lower and the Middle Messel Formation. In this interval considerable redeposition took place preventing stratigraphic assignment of samples.

The specimens were treated with HCl, HF, and KOH following standard procedures described by Kaiser and Ashraf (1974). The residue was sieved with a mesh-size of 10 µm. In order to remove flocculating organic matter and to improve transparency of individual palynomorphs some of the specimens were slightly oxidised by applying diluted HNO<sub>3</sub>.

All samples, residues and slides are stored in the Forschungsinstitut Senckenberg, Frankfurt, Germany under the inventory numbers SM.B ME 6130–6249.

About 300 individual palynomorphs (spores, pollen and algae) per sample were identified and counted at 400 times magnification. Identification is based on the systematic-taxonomic study of Thiele-Pfeiffer (1988). Preservation is generally poor in the oil-shale. Thus, a relatively high proportion could not be positively identified and was recorded as “Varia” comprising between 10% and 20% of the total assemblage.

The percentage values of the most important palynomorphs are presented in the pollen diagram (Fig. 4). To derive useful ecological groups, an arrangement of pollen curves is necessary (Janssen and Birks, 1994). Therefore, the taxa are arranged

Table 1  
The 63 variables, which were used in the numerical analyses

Variables	Palynomorphs
Leiotriletes	<i>Leiotriletes maxoides</i> KRUTZSCH, 1962 <i>Leiotriletes microadriemisi</i> KRUTZSCH, 1959 <i>Leiotriletes kopeckii</i> KEDVES, 1973
Cicatricosisporites	<i>Cicatricosisporites doregensis</i> R. POTONIÉ & GELLETTICH, 1933 <i>Cicatricosisporites paradorogensis</i> KRUTZSCH, 1959
Trilites	<i>Trilites menatensis</i> KEDVES, 1982 <i>Trilites solidus</i> (R. POTONIÉ, 1934) KRUTZSCH, 1959 <i>Trilites</i> sp.
Intrapunctisporis	<i>Intrapunctisporis gracilioides</i> KRUTZSCH & VANHOORNE, 1977
Baculatisporites	<i>Baculatisporites primarius</i> (WOLF, 1934) THOMSON & PFLUG, 1953
Ischyosporites	<i>Ischyosporites tertiaris</i> KRUTZSCH, 1967 ex ROCHE, 1973
Polypodiaceoisporites/ Verrucingulatisporites	<i>Polypodiaceoisporites lusaticus</i> KRUTZSCH, 1967 <i>Polypodiaceoisporites gracillimus</i> NAGY, 1963 <i>Polypodiaceoisporites</i> sp. <i>Verrucingulatisporites undulatus</i> NAGY, 1963
Laevigatosporites	<i>Laevigatosporites haardtii</i> (R. POTONIÉ & VENITZ, 1934) THOMSON & PFLUG, 1953 <i>Laevigatosporites discordatus</i> PFLUG, 1953
Verrucatosporites	<i>Verrucatosporites favus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>Verrucatosporites microfavus</i> THIELE-PFEIFFER, 1988 <i>Verrucatosporites pseudoregulatus</i> KRUTZSCH, 1967 <i>Verrucatosporites cellarius</i> (KRUTZSCH, 1959) KRUTZSCH, 1967
Pinaceae	<i>Pityosporites labdacus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
Cupressaceae	<i>Inaperturopollenites concedipites</i> (WODEHOISE, 1933) KRUTZSCH, 1971 <i>Cupressacites insulipapillatus</i> (TREVISAN, 1967) KRUTZSCH, 1971
Restionaceae	<i>Milfordia minima</i> KRUTZSCH, 1970 <i>Milfordia incerta</i> (THOMSON & PFLUG, 1953) KRUTZSCH, 1961
Chloranthaceae	<i>Emmapollis pseudoemmaensis</i> KRUTZSCH, 1970
M. tranquillus	<i>Monocolpopollenites tranquillus</i> (R. POTONIÉ, 1934) THOMSON & PFLUG, 1953
D. kockelii	<i>Dicolpopollis kockelii</i> PFLANZL, 1956
Hydrocharitaceae	<i>Punctilongisulcites microechinatus</i> THIELE-PFEIFFER, 1988
Nudopollis	<i>Nudopollis terminalis</i> (THOMSON & PFLUG, 1953) <i>hastiformis</i> THOMSON & PFLUG, 1953
P. pseudoexcelsus	<i>Plicapollis pseudoexcelsus</i> (KRUTZSCH, 1957) KRUTZSCH, 1961 <i>Plicapollis pseudoexcelsus</i> (KRUTZSCH, 1957) KRUTZSCH, 1961 <i>microturgidus</i> PFLUG, 1953

(continued on next page)

Table 1 (continued)

Variables	Palynomorphs
T. excelsus	<i>Triatriopollenites excelsus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
T. excelsus minor	<i>Triatriopollenites excelsus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>minor</i> PFLUG, 1953
T. rurensis	<i>Triatriopollenites rurensis</i> THOMSON & PFLUG, 1953 <i>Triatriopollenites bituitus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
L. menatensis	<i>Labraferoidaepollenites menatensis</i> KEDVES, 1982
Plicatopollis	<i>Plicatopollis plicatus</i> (R. POTONIÉ, 1934) KRUTZSCH, 1962 <i>Plicatopollis hungaricus</i> KEDVES, 1974 <i>Plicatopollis lunatus</i> KEDVES, 1974
Momipites	<i>Momipites punctatus</i> (R. POTONIÉ, 1931) NAGY, 1969 <i>Momipites quietus</i> (R. POTONIÉ, 1931) NICHOLS, 1973
Platycarya	<i>Platycaryapollenites platycaryoides</i> (ROCHE, 1969) KEDVES, 1982 <i>Platycaryapollenites miocaenicus</i> NAGY, 1969 <i>Platycaryapollenites semicyclus</i> (KRUTZSCH & VANHOORNE, 1977) THIELE-PFEIFFER, 1988
Pterocarya	<i>Pterocaryapollenites stellatus</i> (R. POTONIÉ, 1931) THIERGART, 1937
Carya	<i>Caryapollenites triangulus</i> (PFLUG, 1953) KRUTZSCH, 1961 <i>Caryapollenites circulus</i> (PFLUG, 1953) KRUTZSCH, 1961
Subtriporopollenites	<i>Subtriporopollenites anulatus</i> THOMSON & PFLUG, 1953 <i>nanus</i> THOMSON & PFLUG, 1953 <i>Subtriporopollenites constans</i> PFLUG, 1953
T. rhenanus	<i>Tripoporopollenites rhenanus</i> (THOMS. in R. POT., THOMS. & THIERG. 1950) TH. & PF. 1953 <i>Tripoporopollenites robustus</i> PFLUG, 1953
Ulmaceae	<i>Polyporopollenites eoulmoides</i> KRUTZSCH & VANHOORNE, 1977 <i>Polyporopollenites undolosus</i> (WOLF, 1934) THOMSON & PFLUG, 1953 <i>Polyporopollenites verrucatus</i> THIELE-PFEIFFER, 1980
Celtis	<i>Celtipollenites intrastructurus</i> (KRUTZSCH & VANHOORNE, 1977) THIELE-PFEIFFER, 1980 <i>Celtipollenites laevigatus</i> THIELE-PFEIFFER, 1988
Tiliaceae	Div. species of the genus <i>Intratripoporopollenites</i> THOMSON & PFLUG, 1953
Bombacaceae	<i>Bombacidites eckfeldensis</i> KRUTZSCH, 2004 <i>Bombacidites messelensis</i> KRUTZSCH, 2004
P. rarobaculatus	<i>Porocolpopollenites rarobaculatus</i> THIELE-PFEIFFER, 1980
L. labraferus	<i>Labrapollis labraferus</i> (R. POTONIÉ, 1931) KRUTZSCH, 1968

Table 1 (continued)

Variables	Palynomorphs
Icacinaceae	<i>Compositoipollenites rhizophorus</i> (R. POT 1934) R. POT. 1960 ssp. <i>burghasungensis</i> (MÜRRIGER & PFLUG 1952) THOMSON & PFLUG, 1953 <i>Compositoipollenites minimus</i> KRUTZSCH & VANHOORNE, 1977
Pentapollenites spp.	<i>Pentapollenites pentangulus</i> (PFLUG, 1953) KRUTZSCH, 1957 <i>pentangulus</i> KRUTZSCH, 1962 <i>Pentapollenites pentangulus</i> (PFLUG, 1953) KRUTZSCH, 1957 <i>foveostriatus</i> KRUTZSCH, 1962
T. liblarensis	<i>Tricolpopollenites liblarensis</i> (THOMS. in R. POT., THOMS. & THIERG. 1950) TH. & PF. 1953 <i>liblarensis</i> (THOMS. in R. POT., THOMS. & THIERG. 1950) TH. & PF. 1953 <i>Tricolpopollenites liblarensis</i> (THOMS. in R. POT., THOMS. & THIERG. 1950) TH. & PF. 1953 <i>fallax</i> (R. POTONIÉ, 1934) THOMSON & PFLUG, 1953
T. asper	<i>Tricolpopollenites asper</i> THOMSON & PFLUG, 1953
T. retiformis	<i>Tricolpopollenites retiformis</i> THOMSON & PFLUG, 1953
T. vegetus	<i>Tricolpopollenites vegetus</i> (R. POTONIÉ, 1934) KRUTZSCH, 1959
T. cingulum	<i>Tricolporopollenites cingulum</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>fuscus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>Tricolporopollenites cingulum</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>pusillus</i> (R. POTONIÉ, 1934) THOMSON & PFLUG, 1953 <i>Tricolporopollenites cingulum</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953 <i>oviformis</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
T. satzveyensis	<i>Tricolporopollenites satzveyensis</i> PFLUG, 1953
T. edmundii	<i>Tricolporopollenites edmundii</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
T. marcodurensis	<i>Tricolporopollenites marcodurensis</i> THOMSON & PFLUG, 1953
T. microreticulatus	<i>Tricolporopollenites microreticulatus</i> THOMSON & PFLUG, 1953
T. parmularius	<i>Tricolporopollenites parmularius</i> (R. POTONIÉ, 1934) KR. IN KR., PCH. & SPIEG. 1960
T. microporitus	<i>Tricolporopollenites microporitus</i> THOMSON & PFLUG, 1953
T. solé de portai	<i>Tricolporopollenites solé de portai</i> KEDVES, 1965
T. mansfeldensis	<i>Tricolporopollenites mansfeldensis</i> KRUTZSCH, 1969
T. messelensis	<i>Tricolporopollenites messelensis</i> THIELE-PFEIFFER, 1988
T. belgicus	<i>Tricolporopollenites belgicus</i> KRUTZSCH & VANHOORNE, 1977
T. eocaenicus	<i>Tricolporopollenites eocaenicus</i> KRUTZSCH & VANHOORNE, 1977
T. abbreviatus	<i>Tricolporopollenites abbreviatus</i> (R. POT. 1934) KRUTZSCH, 1961



Table 1 (continued)

Variables	Palynomorphs
Rhamnaceae	<i>Tricolporopollenites</i> sp.
Nyssaceae	<i>Nyssapollenites kruschii</i> (R. POT. 1931) NAGY, 1969 <i>analepticus</i> (R. POT. 1934) NAGY, 1969 <i>Nyssapollenites kruschii</i> (R. POT. 1931) R. POT., TH. & THIERG. 1950 <i>accessorius</i> (R. POT. 1934) R. POT., TH. & THIERG. 1950 ex SIMONCSICS, 1969
Ilex	<i>Ilexpollenites iliacus</i> (R. POTONIÉ, 1931) THIERGART 1937 ex R. POTONIÉ, 1960 <i>Ilexpollenites margaritatus</i> (R. POTONIÉ, 1931) THIERGART, 1937 ex R. POTONIÉ, 1960
Araliaceae	<i>Araliaceipollenites euphorii</i> (R. POTONIÉ, 1931) R. POTONIÉ, 1951 <i>Araliaceipollenites reticuloides</i> THIELE- PFEIFFER, 1980
Sapotaceae	<i>Tetracolporopollenites sapotoides</i> THOMSON & PFLUG, 1953 <i>Tetracolporopollenites manifestus</i> (R. POTONIÉ, 1931) THOMSON & PFLUG, 1953
Ericaceae	<i>Ericipites callidus</i> (R. POTONIÉ, 1931) KRUTZSCH, 1970 <i>Ericipites ericius</i> (R. POTONIÉ, 1931) R. POTONIÉ, 1960
Dinoflagellates	<i>Geiselodinium</i> sp.
Botryococcus	<i>Botryococcus</i> sp.
Ovoidites	<i>Ovoidites</i> sp.

Detailed taxonomic information on the listed species: Thomson and Pflug (1953), Krutzsch and Vanhoorne (1977), Thiele-Pfeiffer (1980, 1988), Krutzsch (2004).

according to their weighted average value (WA regression, ter Braak and Looman, 1995) in relation to depth by means of TRAN 1.81 (S. Juggins, University of Newcastle). The pollen diagrams were produced by PanPlot 10.16 (Alfred Wegener Institut für Polare und Marine Forschung, PANGEA). Pollen and spores were calculated to 100% while the values for algae (dinoflagellates, *Botryococcus*, *Ovoidites*) are plotted as additional percentages (% of the total pollen sum). In order to facilitate a condensed synoptical view of the diagram the samples are arranged at equal intervals. This seemed to be appropriate since in this part of the section sample distances hardly reflect time intervals due to considerable differences in rates of sedimentation between various lithologic units. The true sample positions along the core are shown in Fig. 3.

For the numerical treatment of palynological data TWINSpan (two way indicator species analysis) was implemented using the TWINSpan program (Hill, 1979 with modifications by Oksanen and Minchin, 1997). The nine pseudospecies cut levels 0–0.5–1–2–5–10–20–50–70 were defined for the sporomorph percentages (sensu Hjelle, 1999; Rull, 2003). Corre-

spondence analyses (CA: Hill, 1973, 1974; ter Braak, 1985) were carried out using the software PAST 1.31 (Hammer et al., 2001).

Because of the great diversity including more than 200 “species” of pollen and spores (Thiele-Pfeiffer, 1988) and the limited quality of preservation it seemed appropriate to reduce the data set for numerical analysis. For that purpose the number of variables, i.e. families, genera or individual species, has been limited to 63 as shown in Table 1. Thereby, taxa were omitted which are very rare (average frequency <1%) and do not show any significant pattern of distribution throughout the section. Other taxa such as various species of *Plicatopollis* were lumped in order to minimize errors in identification of individual “species”. By taking these measures a minimal loss of information can be expected.

## 5. Results

In the pollen diagram of the Lower Messel Formation below the event bed (Fig. 4) taxa are arranged on the basis of weighted average regression with depth as the predictor variable (Janssen and Birks, 1994; ter Braak and Looman, 1995). It shows that several palynomorph taxa vary significantly in their distribution throughout the Initial Lake Phase.

In order to detect similarities between samples independent of depth a TWINSpan analysis was run on the 114 samples selected from samples #3 to #449 (Fig. 5). Thus the samples clustered into individual TWINSpan groups and subgroups, group two and three on the first, subgroups four to seven on the second, and eight to fifteen on the third level. The groups and subgroups were then arranged according to depth (Fig. 6).

The division at the first level clearly shows a separation of samples from an Early Initial Lake Phase up to sample #257 (TWINSpan group 3) from those representing a Late Initial Lake Phase (samples #261 to #449, TWINSpan group 2). This closely corresponds to the oil-shale-free and the oil-shale-bearing part of the section, respectively, and thus to the change from a completely holomictic to a partly meromictic phase of the lake. The main difference between TWINSpan groups 2 and 3 after the first subdivision (Fig. 5) is based on the occurrence of algal cysts and pteridophyte spores, both of which increase in importance in the third group. TWINSpan group 2 on the other hand is characterized by the dominance of various forest elements.

Even subdivisions at the second level reveal a definite relationship with the stratigraphic sequence (Fig. 6a). In the lower part of the core, only sample #51 which is clustered with subgroup 6 deviates from this

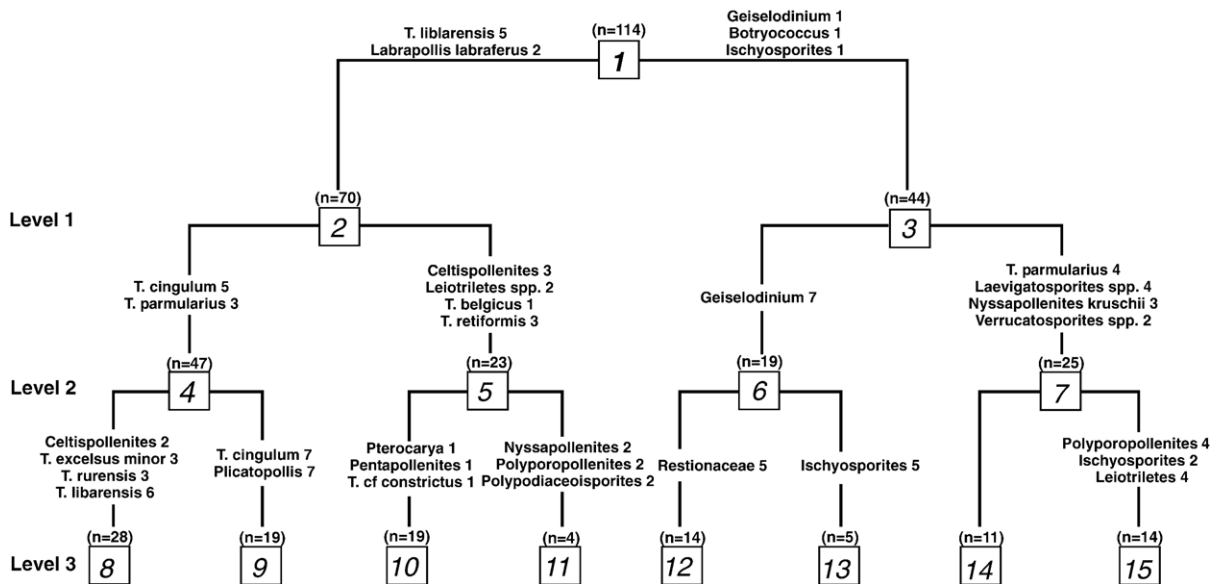


Fig. 5. Dendrogram showing TWINSpan results obtained for the total data set. Numbers in squares refer to the groups which are mentioned in text. The TWINSpan indicator species and their pseudospecies cut-levels for each division are indicated.

pattern. Other fluctuations between TWINSpan subgroups characterize transitional stages.

No significant trends are shown by subdivisions at the third level (Fig. 5, TWINSpan groups 8 to 15) except for subgroups 12 and 13 (Fig. 6b).

### 5.1. TWINSpan group 3 and its subdivisions

This group includes 44 samples (#3 to #182) from the lowermost part of the lake sediments (230 m to 138.25 m). This interval is characterized by an alternation of tuffites, sands, clays and breccias including clasts up to boulder size of Permian red beds (Rotliegend), amphibolites and granites (Felder and Harms, 2004; Fig. 7b). A breccia between 181 m and 167 m consists of blocks of amphibolite up to 4 m in diameter which are embedded in a clay matrix. Laminated to well-bedded, often graded gravels, sands and clays are confined to the upper part of the section above 168 m. A mass flow with chaotic bedding above 144.25 m (Fig. 8) is of particular interest since it is associated with significant palynological changes (Fig. 9).

Oil-shale layers begin to occur in a transitional zone between 143 m and 139 m where they alternate with thin bedded to laminated sands and silts (Felder and Harms, 2004). Above 139 m this alternation is more intimate within a generally oil-shale dominated sequence (Fig. 8). The transition from frequently holomictic to

dominantly meromictic conditions with a stable stratification in the water column is recorded at this point.

The most characteristic taxa of TWINSpan group 3 are various taxa of freshwater plankton which occur regularly (TWINSpan subgroup 7) and often in masses (TWINSpan subgroup 6). They may be considered as indicator elements. This is particularly true for dinoflagellate cysts. Their massive occurrence below 140 m (Fig. 9) is due to the single genus *Geiselodinium*, a type of peridinioid freshwater dinoflagellate cyst widely distributed throughout the Tertiary of central Europe (Kruttsch and Pacltová, 1990). The *Geiselodinium* specimens of Messel (Plate II, 1–4) are very similar to those from the type locality in the Middle Eocene lignite of the Geiseltal near Halle, Germany (Kruttsch, 1962). They have first been recorded at Messel as “freshwater phytoplankton” by Thiele-Pfeiffer (1988) and recognized as “dinoflagellates” in thin sections of fish coprolites and background sediment by Richter and Clausen (2004) and Richter and Wedmann (2005). Dinoflagellate cysts occur massively in TWINSpan subgroup 6. More than 10,000 specimens of these cysts have been counted in single slide preparations from samples immediately below the first oil-shale layers (Fig. 4).

Since the presence of dinoflagellates has first been suggested by means of geochemical evidence (Michaelis et al., 1988) the present study now allows tracing the frequency distribution of dinoflagellate cysts throughout the Messel Lake sediments.

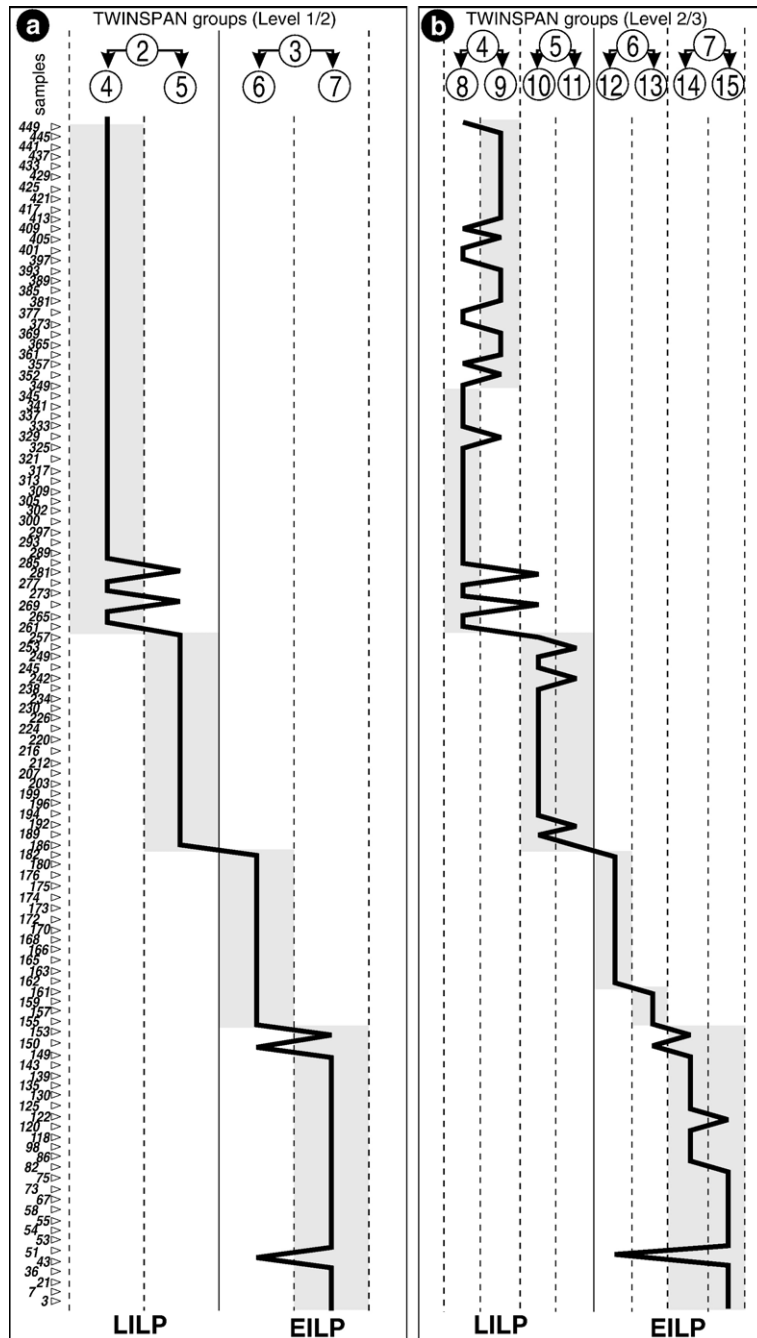


Fig. 6. Stratigraphic succession of TWINSPAN groups; (a) level 1/2, (b) level 2/3 (see Fig. 5); EILP: Early Initial Lake Phase, LILP: Late Initial Lake Phase).

*Botryococcus*, a coccal green alga, is occasionally frequent in the succession, while other algal cysts such as *Ovoidites* and *Tetraporina* (both cysts of Zygnemataceae) occur regularly but only in small numbers.

Previous studies of the lacustrine primary production have demonstrated that the organic content of the oil-

shale is largely derived from the coccal green alga *Tetraedron minimum* (Goth, 1990) which also contributed to the fine laminations by producing seasonal algal blooms. Due to the small size and the screening employed during preparation, however, *Tetraedron* cannot be detected in our preparations. Additional

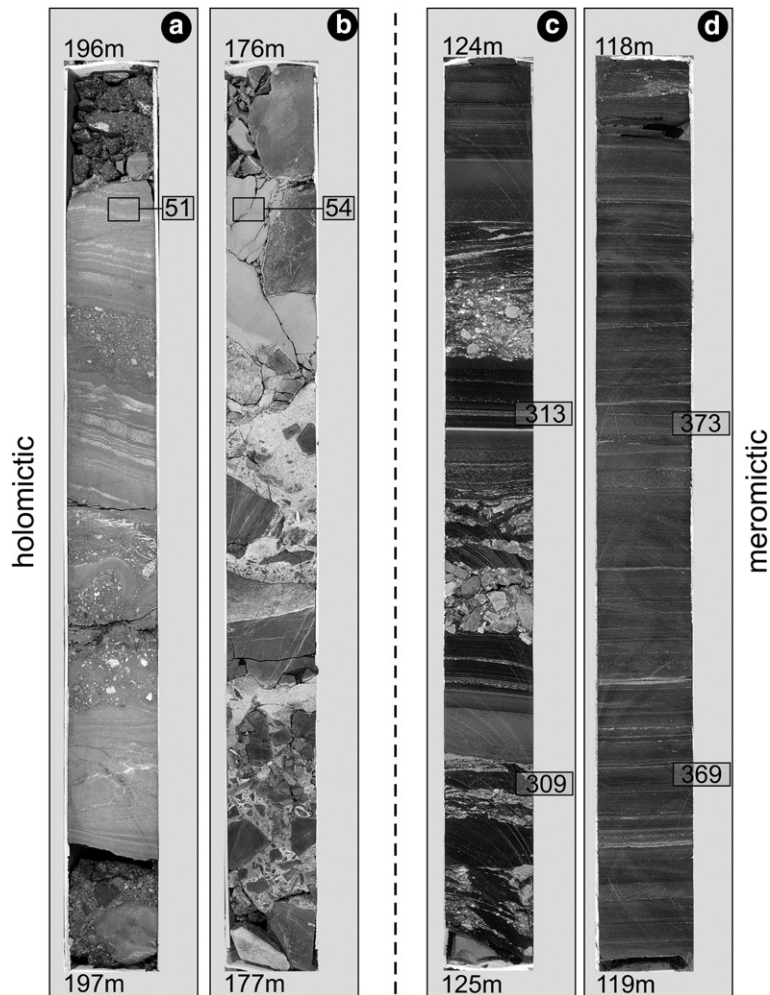


Fig. 7. Photographs of selected core sections showing examples from the holomictic and the meromictic phase of Lake Messel and position of samples; (a) fine to coarse laminated silt, sand and clay, (b) amphibolite breccia with calcitic matrix, (c) oil-shale with debritic resediments, (d) oil-shale of the Lower Messel Formation. The pictures are based on photographs of FIS/HLUG 2001: (a) 12425.pcd–12427.pcd, (b) 12365.pcd–12367.pcd, (c) 12209.pcd–12211.pcd, (d) 12191.pcd–12193.pcd.

lacustrine primary producers which are lost in palynological HF preparations have been reported by Goth (1990) such as central planktonic diatoms (*Melosira*) and cysts of Chrysophyceae.

Next to the planktonic *Botryococcus* and *Geiselodinium*, an important additional characteristic of TWINSPAN subgroup 7 (samples #3 to #153, Fig. 4) is a specific association of pollen and spores. A number of pteridophyte spores are well represented and show their maximum distribution here. These are, in particular, monolete spores of the genera *Laevigatosporites* (Plate I, 3) and *Verrucatosporites* (Plate I, 4) as well as trilete spores belonging to the genera *Cicatricosisporites* (Schizaeaceae, Plate I, 2) and *Baculatisporites* (Osmundaceae, Plate I, 1) which appear with relatively

high quantities almost exclusively in TWINSPAN subgroup 7 (Fig. 4).

Some elements (Plate I, 6–11) showing their peak abundance in the Early Initial Lake Phase are palm pollen such as *Monocolpopollenites tranquillus* and *Dicolpopollis kockelii* and pollen of Nyssaceae (*Nyssapollenites kruschii* ssp.), Aquifoliaceae (*Ilexpollenites iliacus*, *I. margaritatus*) and Ericaceae (*Ericipites callidus*, *E. ericius*). Among the pollen of Fagaceae, *Tricolpopollenites liblarensis* is only poorly represented, while *Tricolpopollenites cingulum* is dominant.

Additional spore taxa such as *Ischyosporites tertiaris* and *Intrapunctisporis* sp. (Plate I, 12, 13), probably belonging to the Schizaeaceae, begin to appear in TWINSPAN subgroup 7 but reach peak abundances in

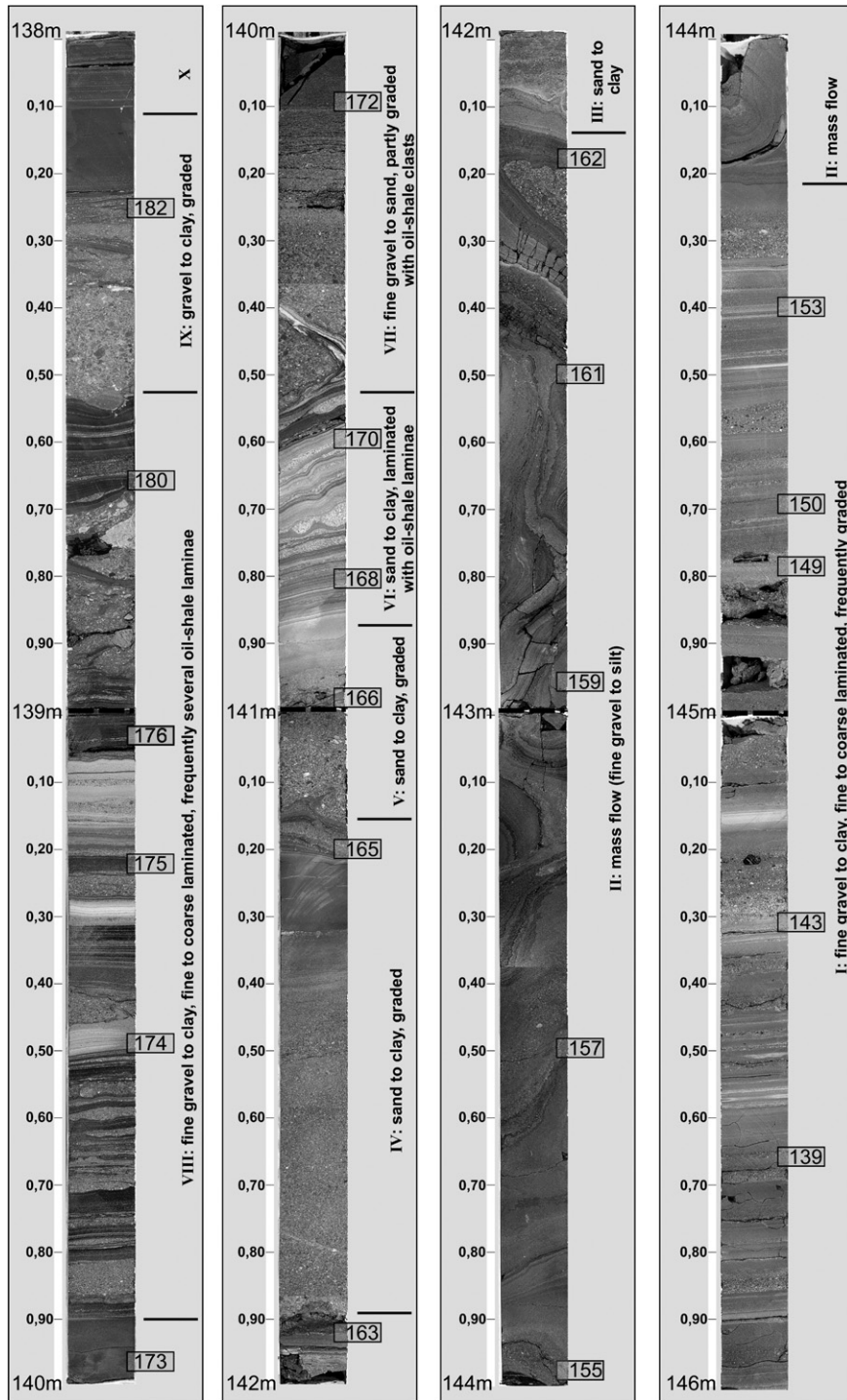


Fig. 8. Photographs of core sections between 138 m and 146 m depth showing the major sedimentological units (I–X) and position of samples. The pictures are based on photographs of FIS/HLUG 2001: 12251.pcd–12274.pcd.

subgroup 6. Especially *I. tertarius* occurs in masses in TWINSPAN subgroup 6 prior to the mass occurrence of Restionaceae pollen (Plate I, 14). Restionaceae with

their reed-like habit may have been growing within the shoreline vegetation. Their pollen is recorded in small numbers in the entire section. They occur, however, in

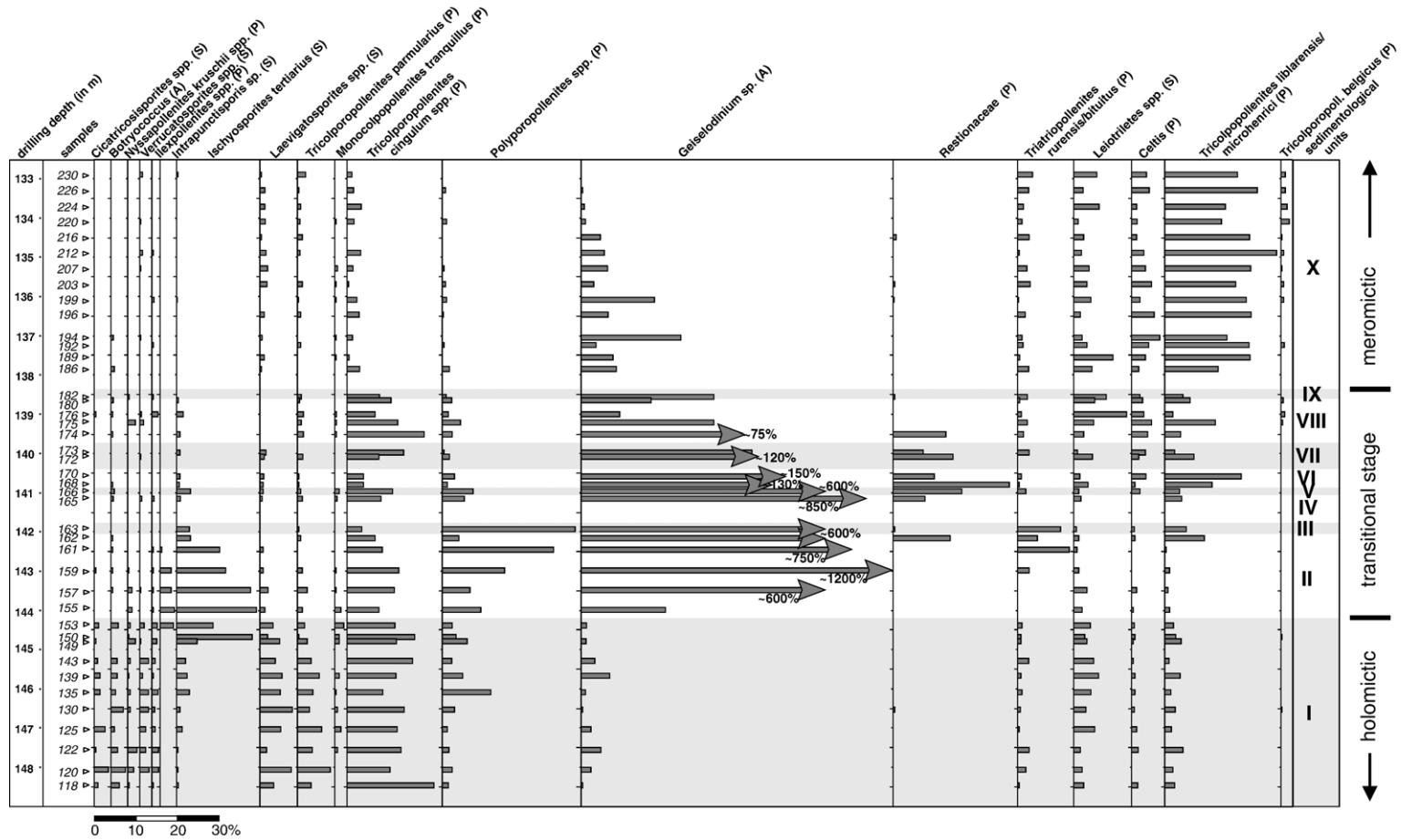


Fig. 9. Pollen diagram of the most important palynomorphs occurring between 183 m and 148 m core depth. Abbreviations behind the species names: (A) alga, (P) pollen, (S) spore. For sedimentological units I to X see Fig. 8.

large numbers only in the mass flow and in a few succeeding samples up to 139.5 m (Fig. 9). Thus, similar to dinoflagellates, pollen and spores of plants growing at the lake margin appear to be concentrated in the mass-flow deposit.

Palynologically the mass flow below 140 m can be subdivided into two parts on the basis of the occurrence of *Intrapunctisporis* sp. and *I. tertarius* on one side and pollen of Restionaceae on the other (TWINSPAN subgroups 12 and 13). There is no overlap between the two groups (Fig. 9).

Similar relationships exist in sample #51 (Fig. 4) which deviates from the samples of subgroup 7 by being assigned to TWINSPAN subgroup 6. Very high values are recorded in this sample for Polypodiaceae spores (*Polypodiaceoisporites* spp., *Verrucingulatisporites undulatus*), *Ischyosporites tertarius* and the pollen taxon *Tricolporopollenites solé de portai*.

Another characteristic of TWINSPAN subgroup 6 is the abundance of *Polyporopollenites* spp. (Ulmaceae) and *Triatriopollenites rurensis/bituitus* (Myricaceae complex) (Plate I, 15, 16). In contrast, the monoete spore species *Laevigatosporites haardtii* and *Verrucatosporites favus* occur only sporadically and *Cicatricosisporites dorogensis/paradorogensis* disappears entirely. *Tricolporopollenites liblarensis* now clearly increases in abundance and even predominates over *Tricolporopollenites cingulum* in some samples. The strong predominance of some sporomorphs in this group may lead to a statistical masking effect of other forms not necessarily reflecting a reduction of their parent plant in the original vegetation.

At Messel, various species may be distinguished within the genus *Polyporopollenites* (e.g. *P. eoulmoides*, *P. verrucatus* and *P. undulosus*; Thiele-Pfeiffer, 1988). However, due to insufficient preservation, a reliable botanical assignment to extant genera of the Ulmaceae on the basis of light microscopy is limited since the number of pores and the structure and sculpture of the exine are highly variable at the genus level (Zavada, 1983; Stafford, 1995). The genera *Ulmus*, *Zelkova* (both extant) and *Cedrelospermum* (extinct) have been identified at Messel on the basis of leaves and fruits (Wilde, 1989; Wilde and Manchester, 2003). Among the species of *Polyporopollenites* known to occur at Messel *P. eoulmoides* as described by Thiele-Pfeiffer (1988) seems to be most similar to pollen of the extinct genus *Cedrelospermum* as illustrated by Manchester (1989) and represents the majority of specimens within the mass occurrence of the genus in samples of TWINSPAN subgroup 6.

Higher up in the section *Polyporopollenites* nearly disappears. The genus returns soon thereafter beginning

with sample #273 (Fig. 4) but seems to be represented mainly by the species *P. undulosus* and *P. verrucatus* which are generally assigned to the extant genera *Ulmus*, *Zelkova* and *Hemiptelea* (Thiele-Pfeiffer, 1980, 1988).

Like *Polyporopollenites* spp. the Myricaceae which are represented by *Triatriopollenites rurensis* and *T. bituitus* reach their maximum abundance at the beginning of this stage. Their assignment to the extant genus *Myrica* (Thiele-Pfeiffer, 1980) is somewhat ambiguous here due to the poor preservation in the Messel samples and the great morphological similarity among pollen in the Myricaceae (Sundberg, 1985).

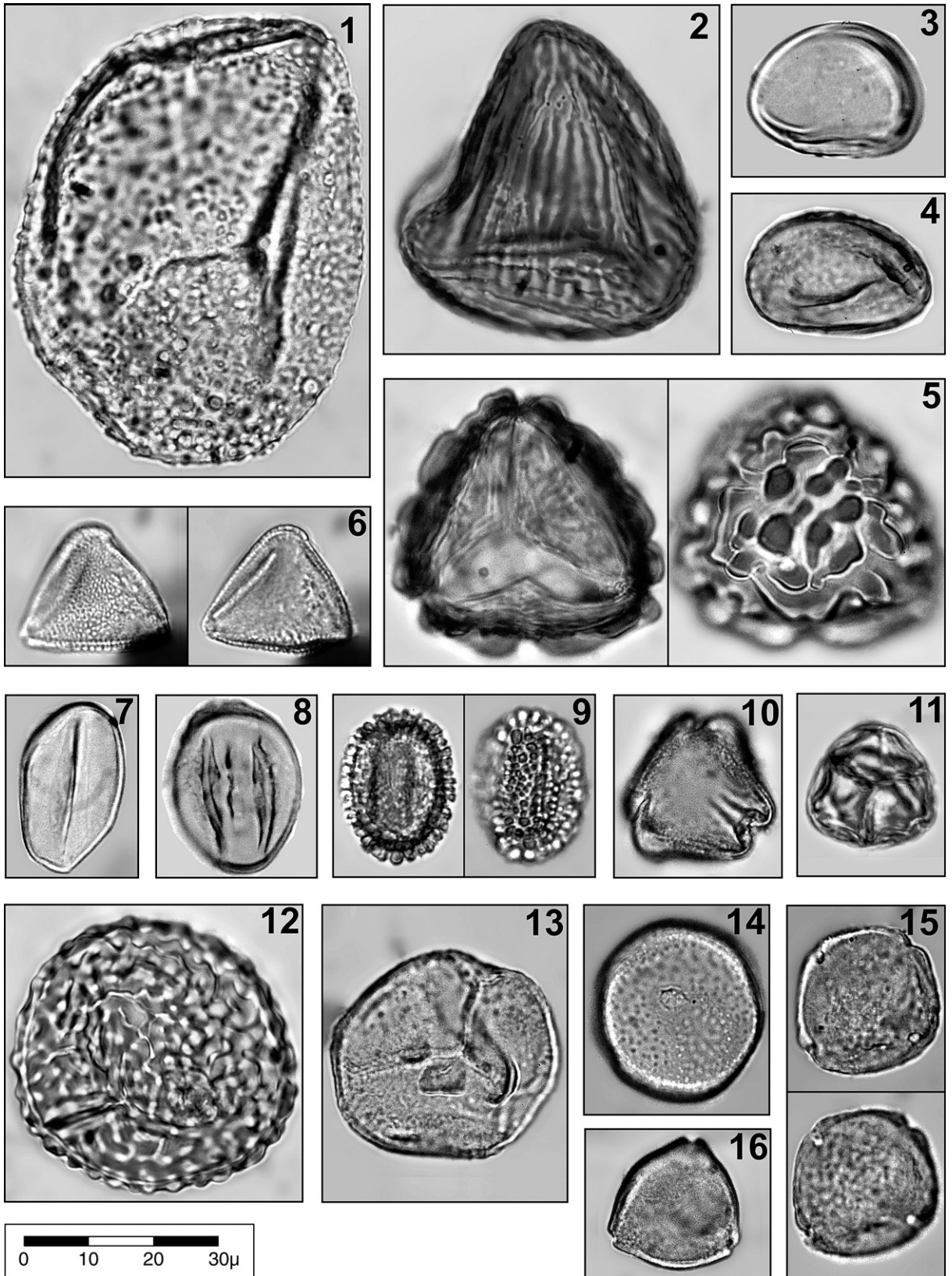
## 5.2. TWINSPAN group 2 and its subdivisions

The composition of palynomorph assemblages changes significantly between samples #182 and #186 at a depth of 138.5 m (see Figs. 4, 6 and 9). This coincides with the distinction of TWINSPAN groups 2 and 3 separating an Early from a Late Initial Lake Phase.

Sedimentologically, the Late Initial Lake Phase is characterized by laminated oil-shales formed under meromictic conditions. In the lower part, oil-shales are still frequently interrupted by breccias and turbidites (Fig. 7c) while the upper 120 m consist of pure oil-shale (Fig. 7d).

TWINSPAN group 2 can be subdivided into subgroup 4 (samples #187 to #257 between about 138 m to 130 m) and subgroup 5 (samples #261 to #449 between about 130 m to 110 m). TWINSPAN subgroup 5 succeeds subgroup 4 without a sharp break (Fig. 6). The forest vegetation as represented by TWINSPAN group 2 appears to develop in two steps. Some elements of subgroup 5 first become more prominent to be replaced later by elements of subgroup 4. This is repeated once (Fig. 6) before stable conditions were finally established in the crater area towards the end of the Initial Lake Phase.

Particularly marked is the disappearance or the strong decline of palynomorphs which were widely distributed in the Early Initial Lake Phase such as pollen of Restionaceae and dinocysts. Also some woody elements such as Nyssaceae (*Nyssapollenites kruschii*), Aquifoliaceae (*Ilexpollenites* spp.) and Ericaceae (*Ericipites* spp.) are absent or greatly reduced in abundance. Furthermore, pollen of palms (*Monocolpopollenites tranquillus*, *Dicolpopollis kockelii*) and Ulmaceae (*Polyporopollenites* spp.) are rarely recorded in the percentage counts. Somewhat unexpected is the decrease in the fagaceous pollen *Tricolporopollenites cingulum* which is generally considered to be an element of the zonal vegetation.





Dominant anemophilous plants within TWINSPAN group 2 are the Juglandaceae which are represented among others by a number of species of the *Plicatopollis* group assignable to *Engelhardia*, *Platycarya* (Plate II, 14, 15), *Carya* (Plate II, 6) and *Pterocarya* (Plate II, 7) and by *Labraferoidaepollenites menatensis* and *Subtriporopollenites* spp. Juglandaceae are also frequently recorded among macrofossils from Messel (Wilde, 1989, 2004). Myricaceae pollen of the *Triatriopollenites excelsus* type occur regularly. The Ulmaceae are still well represented by pollen assignable to the genera *Celtis*, *Ulmus*, *Hemiptelea* and *Zelkova*.

In addition to the Juglandaceae, Fagaceae are dominant and represented by the two common Palaeogene species *Tricolpopollenites liblarensis* and *Tricolporopollenites cingulum* (Plate II, 21, 22). However, it should be pointed out that the frequency of these two species is negatively correlated and usually shows a distinct dominance of one species over the other. Since Pflug (1952) and Thomson and Pflug (1953), *T. liblarensis* has generally been considered as an allochthonous element derived from the extratelmatic high forest. However, our studies of the Middle Eocene lignite deposits at Helmstedt indicate that the parent plant(s) of *T. liblarensis* can be considered as a mire or forest-swamp element, preferring rather wet conditions and mineral substrates (Lenz, 2005). It should be noted that the dominance of *T. liblarensis* coincides with the beginning of the meromictic phase of the Messel lake while *T. cingulum* dominates in the Early Initial and towards the end of the Late Initial Lake Phase.

The subdivision of TWINSPAN group 2 into the two successive subgroups 4 and 5 is based on a number of forms widely distributed at the beginning of this phase but becoming rare later on, e.g. pollen of *Celtis* and *Carya* (Plate II, 6, 8). Other forms such as *Plicatopollis plicatus* and Ulmaceae pollen of the genus *Polyporopollenites* spp. become more abundant towards the end of this phase. Accordingly, the early forest vegetation is characterized by elements common in TWINSPAN subgroup 5 such as Ulmaceae with the genus *Celtis* and Juglandaceae with the genus *Carya* as well as the parent plant of *Labraferoidaepollenites menatensis*.

Additional characteristic forms of this subgroup are *Tricolporopollenites belgicus* (Plate II, 11) and *T. eocaenicus*, the parent plants of which are not yet known (Krutzsch and Vanhoorne, 1977). These two species are absent from TWINSPAN subgroup 4 which, on the other hand, includes other members of the Juglandaceae such as *Platycarya* and parent plants of the various species of *Plicatopollis*. The latter become more common later on during oil-shale deposition. Other typical forms are *T. cingulum* and *T. parmularius* which were already regularly present but reach their maximum abundance only towards the end of the Initial Lake Phase.

## 6. Interpretation

After the devastating eruption(s) ceased, the newly formed barren surface of the crater wall and surrounding areas was gradually colonized by vegetation. During this process a pioneering succession developed according to

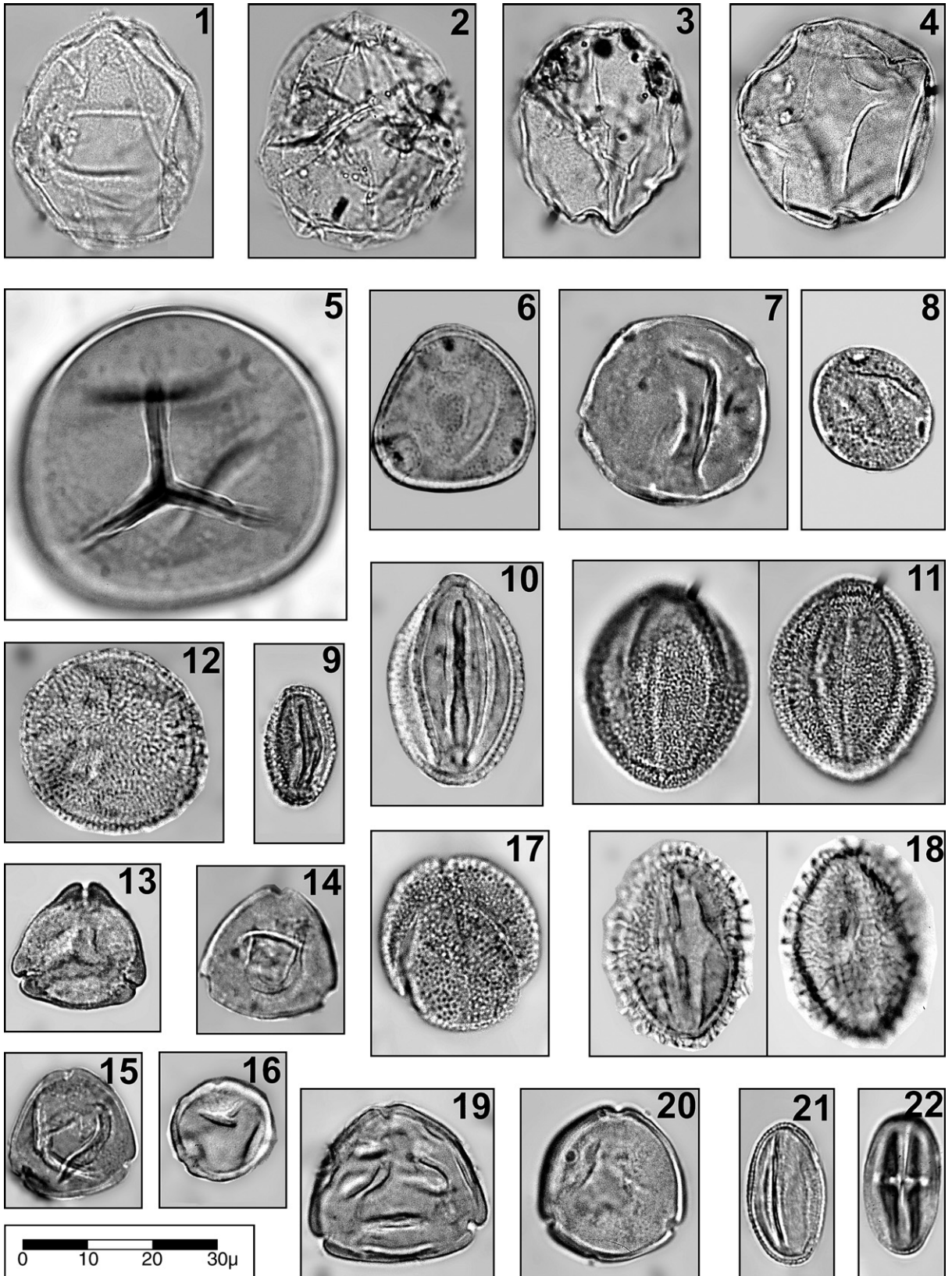
Plate I. (magnification: 1000×)

### Major elements of TWINSPAN subgroup 7.

1. *Baculatisporites primarius* (sample 189-3, Inv.Nr. SM.B Me 6181/3-I).
2. *Cicatricosisporites dorogensis* (sample 157-3, Inv.Nr. SM.B Me 6163/1-I).
3. *Laevigatosporites hardtii* (sample 98-1, Inv.Nr. SM.B Me 6147/1-I).
4. *Verrucatosporites microfusus* (sample 98-1, Inv.Nr. SM.B Me 6147/1-II).
5. *Verrucingulatisporites undulatus* (sample 51-1, Inv.Nr. SM.B Me 6135/1-I).
6. *Dicolpopollis kockeli* (sample 86-2, Inv.Nr. SM.B Me 6145/2-I).
7. *Monocolpopollenites tranquilus* (sample 98-1, Inv.Nr. SM.B Me 6147/1-III).
8. *Tricolporopollenites parmularius* (sample 139-1, Inv.Nr. SM.B Me 6157/1-I).
9. *Ilexpollenites iliacus* (sample 130-1, Inv.Nr. SM.B Me 6155/1-I).
10. *Nyssapollenites kruschii accessories* (sample 51-2, Inv.Nr. SM.B Me 6135/2-I).
11. *Ericipites callidus* (sample 67-1, Inv.Nr. SM.B Me 6141/1-I).

### Major elements of TWINSPAN subgroup 6.

12. *Ischyosporites tertiaris* (sample 176-2, Inv.Nr. SM.B Me 6177/2-I).
13. *Intrapunctisporis* cf. *graciloides* (sample 153-2, Inv.Nr. SM.B Me 6161/2-I).
14. *Milfordia minima* (sample 172-1, Inv.Nr. SM.B Me 6173/1-I).
15. *Polyporopollenites verrucatus/eoulmoides* (sample 174-1, Inv.Nr. SM.B Me 6175/1-I).
16. *Triatriopollenites bituitus* (sample 163-1, Inv.Nr. SM.B Me 6167/1-I).



the different dispersal and growth strategies of the various plant species involved. As the crater filled with water, this recolonization was documented by pollen and spores trapped and preserved in the lake sediments. Quality and resolution of this record improved with time as conditions within the lake became more stable and continuous sedimentation occurred.

General trends of this recolonization including specific perturbations as detectable from the palynomorph record have been described in the previous section and graphically summarized in Fig. 4. The pollen and spore record is complemented by the record of dinoflagellate cysts indicative of hydrologic conditions within the lake. The following is an attempt to interpret the palynological record and the concurrent lithologic succession in terms of the recolonization of a devastated volcanic site.

In a very general way the pollen diagram (Fig. 4) shows that a considerable number of palynomorph taxa have their peak abundance in the lower part of the Lower Messel Formation; only a few have their maximum distribution in the upper part. This suggests that some plant species were widespread in the catchment area of the lake during the Early Initial Lake Phase and retreated or lost dominance during the Late Initial Lake Phase. During the latter, only a few

species gained peak importance. Nevertheless, the overall diversity of the vegetation as reflected in pollen and spores at Messel did not change significantly.

### 6.1. Early Initial Lake Phase

Pollen and spores of land plants in the Early Initial Lake Phase may in part be attributed to a herbaceous and shrubby pioneer vegetation invading the immediate vicinity of the lake and an initial reforestation starting from the margin of the disturbed area. Within the initial herbaceous communities ferns like Polypodiaceae (*Laevigatosporites* spp., *Verrucatosporites* spp.), Schizaeaceae (*Cicatricosisporites* spp.) and Osmundaceae (*Baculatisporites* spp.) apparently played an important role in various combinations and may have been initial colonizers of the crater walls and the shoreline (Fig. 9, unit 1). Low and rapidly growing trees and shrubs including palms and Aquifoliaceae may soon have followed and invaded the herbaceous cover since their pollen (*Monocolpopollenites tranquillus* and *Ilexpollenites* spp.) have their main distribution in the lower part of the Early Initial Lake Phase (TWINSPAN group 7).

Later during the Early Initial Lake Phase some palynomorphs show mass occurrences in successive

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#### Plate II. (magnification: 1000×)

##### Major elements of TWINSPAN subgroups 6/7.

- 1–4. *Geiselodinium* sp. (sample 172-1, Inv.Nr. SM.B Me 6173/1-II; sample 58-1, Inv.Nr. SM.B Me 6193/1-I; sample 82-2, Inv.Nr. SM.B Me 6144/1-I; sample 163-1, Inv.Nr. SM.B Me 6167/1-II).

##### Major elements of TWINSPAN subgroup 5.

5. *Leiotriletes microadriennis* (sample 176-2, Inv.Nr. SM.B Me 6177/2-II).  
 6. *Caryapollenites triangulus* (sample 176-1, Inv.Nr. SM.B Me 6177/1-I).  
 7. *Pterocaryapollenites stellatus* (sample 245-3, Inv.Nr. SM.B Me 6197/3-I).  
 8. *Celtipollenites intrastructurus* (sample 189-1, Inv.Nr. SM.B Me 6181/1-I).  
 9. *Tricolpopollenites retiformis* (sample 345-1, Inv.Nr. SM.B Me 6223/1-I).  
 10. *Tricolpopollenites asper* (sample 220-1, Inv.Nr. SM.B Me 6190/1-I).  
 11. *Tricolporopollenites belgicus* (sample 220-1, Inv.Nr. SM.B Me 6190/1-II).

##### Major elements of TWINSPAN subgroup 4.

12. *Emmapollis pseudoemmaensis* (sample 261-1, Inv.Nr. SM.B Me 6201/1-I).  
 13. *Plicatopollis pseudoexcelsus* (sample 437-1, Inv.Nr. SM.B Me 6246/1-I).  
 14. *Platycaryapollenites semicyclus* (sample 277-1, Inv.Nr. SM.B Me 6137/1-II).  
 15. *Platycaryapollenites platycaryoides* (sample 365-1, Inv.Nr. SM.B Me 6137/1-I).  
 16. *Labrapollis labraferus* (sample 220-3, Inv.Nr. SM.B Me 6190/3-I).  
 17. *Tricolporopollenites microporitus* (sample 345-1, Inv.Nr. SM.B Me 6223/1-I).  
 18. *Tricolpopollenites messelensis* (sample 437-1, Inv.Nr. SM.B Me 6246/1-II).

##### Important persistent elements.

19. *Plicatopollis hungaricus* (sample 352-1, Inv.Nr. SM.B Me 6225/1-I).  
 20. *Plicatopollis lunatus* (sample 53-2, Inv.Nr. SM.B Me 6136/2-I).  
 21. *Tricolpopollenites liblarensis liblarensis* (sample 130-1, Inv.Nr. SM.B Me 6155/1-III).  
 22. *Tricolporopollenites cingulum fusus* (sample 130-1, Inv.Nr. SM.B Me 6155/1-IV).

order. At first *Ischyosporites tertiaris* forms a peak together with *Intrapunctisporis* sp. with the latter confined to the middle of the *I. tertiaris* peak (Fig. 9, units II–III). This is followed by a sudden mass occurrence of Restionaceae pollen (*Milfordia* spp.; Fig. 9, units IV–VII). The parent plants of these palynomorphs may have dominated the early vegetation adjacent to the shoreline which was at that time still frequently disturbed. Thus, palynomorphs which normally reach the basin centre only in small numbers such as Restionaceae pollen may have been inwashed in greater concentrations from the lake margin by means of turbidites. Their general sporadic occurrence, however, documents the continued presence of these plants throughout the duration of oil-shale deposition. This is supported by the fact that similar to dinocysts these mass occurrences are largely restricted to the mass-flow deposit (Fig. 8, units II–VI).

Palynologically, the mass-flow deposit is clearly divided into a lower part containing peaks of the two fern spore taxa *Ischyosporites tertiaris* and *Intrapunctisporis* sp. and an upper part with the mass occurrence of Restionaceae pollen. There is only a little overlap between the two units. This suggests that the palynological data do not reflect a chronological succession of vegetation units but that the mass flow as a whole (144.2 m to 140 m) is composed of at least two separate flows (see Fig. 8). Most of the sediment was transported by slumping during the first phase (Fig. 8, units II–III), while graded sediments indicate later transport, in part, by turbidity currents (Fig. 8, units IV–VII). Rapid sedimentation diminished and the Late Initial Lake Phase started with the onset of oil-shale deposition (Fig. 8, unit VIII).

The exceptional palynological assemblage of sample #51 (Fig. 4) can also be interpreted as reflecting a shoreline vegetation which was transported into the basin by mass flow. The sample has been taken from redeposited material immediately overlain by a megabreccia of 6 m thickness which probably resulted from a major collapse of the crater wall (Felder and Harms, 2004). Since it includes some elements commonly occurring in later phases the pollen and spore assemblage sample #51 may represent the beginning of an expansion of a predominantly herbaceous pioneer vegetation. This was, however, disrupted by the collapse of the crater wall.

Among the pioneer elements of the Early Initial Lake Phase there are also members of the Ulmaceae and Myricaceae as represented by various species of the pollen genera *Polyporopollenites* and *Triatriopollenites*. Though these pollen occur throughout the oil-shale,

often in significant numbers, their mass occurrence, however, is restricted to TWINSPAN group 6 (Fig. 9, units II–III) and represented there mainly by *P. eoulmoides* which may be referred to the genus *Cedrelospermum* (see Section 5). *Cedrelospermum* has previously been envisaged as a fast-growing pioneer plant colonizing volcanic substrates under different climatic conditions (Manchester, 1989). Thus, the mass occurrence of *P. eoulmoides* in the Early Initial Lake Phase at Messel supports the pioneer character of the *Cedrelospermum* plants which may have grown on the tuff rim. However, since they have not inhabited the immediate lake-shore the concentration effect is not as pronounced as, for instance, in the Restionaceae. The role of Ulmaceae as pioneer elements following a major disaster has also been discussed for the Cretaceous–Tertiary boundary event by Sweet and Braman (1992).

As with the Ulmaceae a botanical assignment of *Triatriopollenites* species to known Myricaceae is difficult due to the poor preservation. However, the genus *Comptonia* considered to be a pioneer element by Mai (1995) has been identified at Messel on the basis of leaves (Wilde, 1989; Wilde and Frankenhäuser, 1999) and may therefore be a likely member of the pioneer succession at Messel.

The proportion of allochthonous pollen and spores derived from the regional vegetation is difficult to assess. This is the case, in particular, for pollen of Fagaceae represented by *Tricolpopollenites liblarensis* and *Tricolporopollenites cingulum* which make up a large proportion of the pollen spectra. Since the Fagaceae are not documented by macrofossils (Wilde, 1989, 2004), their habitat must have been located outside the catchment area of the lake.

The initial phase not only includes the recolonization of the area surrounding the crater but also the establishment of an algal flora within the lake. Green algae (*Botryococcus*) and Zygnemataceae (*Ovoidites*) are consistently present without any significant changes in abundance. In contrast, freshwater dinoflagellates show marked mass occurrences, particularly towards the end of the Early Initial Lake Phase. Such massive proliferation of dinoflagellates may have been caused by changes in water chemistry associated with enhanced nutrient availability. Clausing et al. (2000) consider volcanoclastic input as a source for nutrients followed by the mass occurrence of freshwater dinoflagellates in the Oligocene Enspel Lake. However, the close association of mass occurrences of dinocysts and volcanic tuffs as observed at Enspel does not exist at Messel. On the other hand, the “bloom” of dinocysts at Messel is restricted to the mass-flow deposit below 140 m while dinocysts gradually disappear with the

onset of meromictic conditions (see also Thiele-Pfeiffer, 1988). The mass flow consists of marginal sediments which slumped from the lake margin to the basin centre (Figs. 8 and 9). The palynology of these sediments, therefore, reflects a source at or near the shoreline of the lake and may represent a concentration of cysts along the shore by wave and wind drift. Similar phenomena have been described for concentrations of *Botryococcus* colonies at the Eckfeld maar lake (Nickel, 1996).

The relative frequency of dinocysts with more than 25% in the two basal samples (samples #3 and #7), however, may be due mainly to the scarcity of pollen and spores which causes an overrepresentation of algae there.

### 6.2. Late Initial Lake Phase

Palynomorphs of the initial pioneer vegetation disappear almost entirely towards the end of the Early Initial Lake Phase. Botanically this reflects the change from a strictly pioneer vegetation to a forest vegetation succes-

sively invading the area around the crater and reaching a climax state towards the end of the initial phase.

With the beginning of TWINSPAN group 2 at sample #186 a distinct change in palynological assemblage composition takes place. Now, pollen of the Juglandaceae become dominant in addition to those of the Fagaceae, but Myricaceae and Ulmaceae are still well represented. Since all these elements are already recorded to some extent in the pioneer vegetation of TWINSPAN group 3 the change to TWINSPAN group 2 documents that the crater area has been gradually colonized by a diverse thermophilic forest. Within the Late Initial Lake Phase a major change among fagaceous pollen is observed. The dominance in the lower part of *T. liblarensis* is replaced by a dominance of *T. cingulum* in the upper part. Some other elements (*Platycarya*, *Labrapollis labraferus*) show limited peaks in the Late Initial Lake Phase without showing any distinct pattern. Finally the pollen spectra indicate that the climax vegetation has reoccupied the surroundings of the lake.

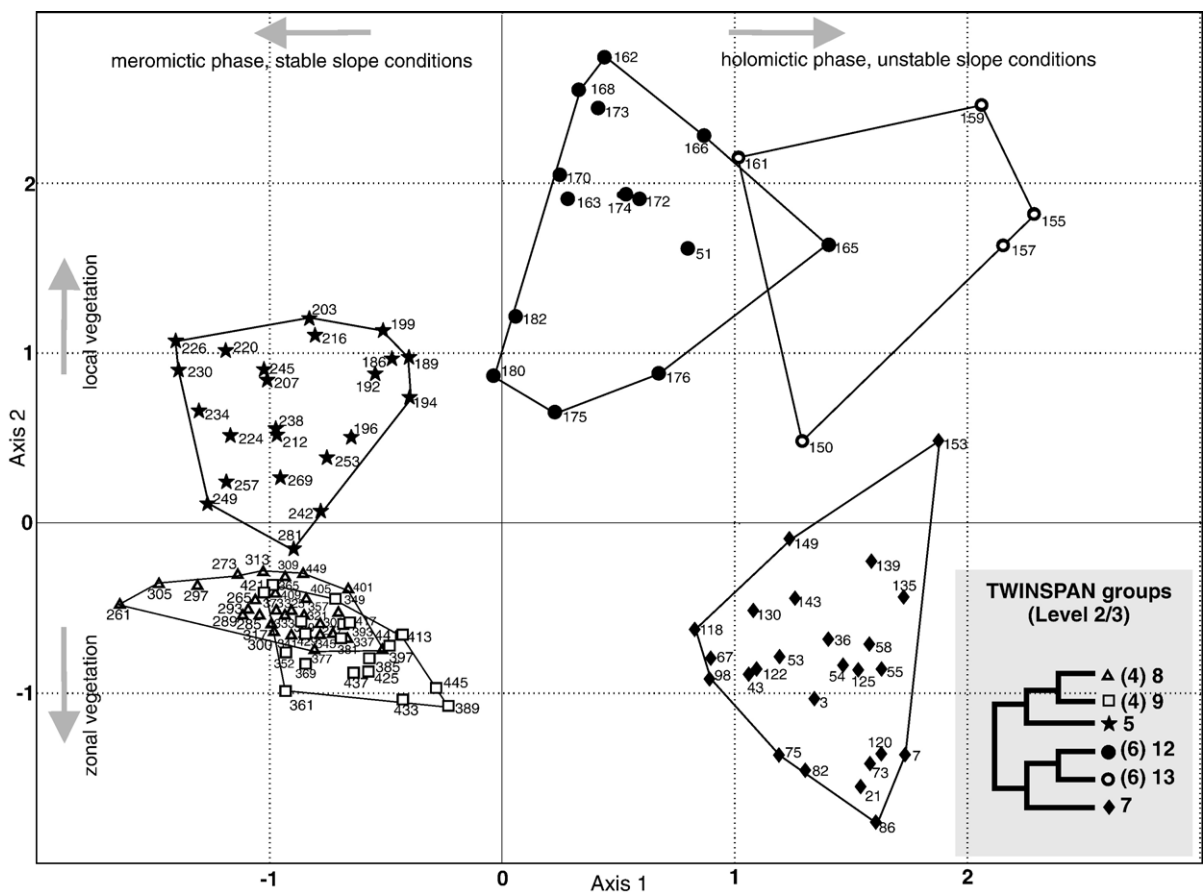


Fig. 10. Scatter plot of the first two axes from a correspondence analysis, showing the arrangement of samples. The different symbols represent TWINSPAN subgroups 4, 5, 7, 12, 13 (see text).



are clearly separated from one another. Only the two TWINSpan subgroups 12 and 13 overlap each other somewhat.

### 6.3.1. CA 1

There is a clear separation between samples from the lower part of the core (samples #3 to #182) on the positive side of the first axis and samples from the succeeding part (samples #186 to #449) on the negative side (Fig. 10). This is in general identical with a separation of samples from oil-shale-free sediments and from the oil-shale. Though the first oil-shale layers begin to occur with sample #173 at 140 m, continuous oil-shale deposition marking the onset of stable meromictic conditions begins at 138.20 m above sample #182 (Fig. 8). Thus, the first axis clearly separates the holomictic from the meromictic phase of Lake Messel

reflecting the distribution of algae (*Geiselodinium*, *Botryococcus* and *Ovoidites*) and response to changes within the water column. Correspondingly, the plot of taxa in Fig. 11 shows the algae on the positive side of axis 1 since the algae were only abundant during the holomictic phase of the lake.

While only fast-growing pioneer plants such as ferns were able to colonize the unstable slopes at the beginning of lake sedimentation, conditions within the lake became more stable with the progressive colonization of the crater slope and rim by deeply rooting trees and shrubs. Thus, it can be concluded that the onset of meromictic conditions within the lake is correlated with the degree of stability of the crater slopes. The first axis, therefore, represents the influence of vegetation on slope stability. Correspondingly, pollen and spores of fast-growing pioneer plants such as various fern spores, palm

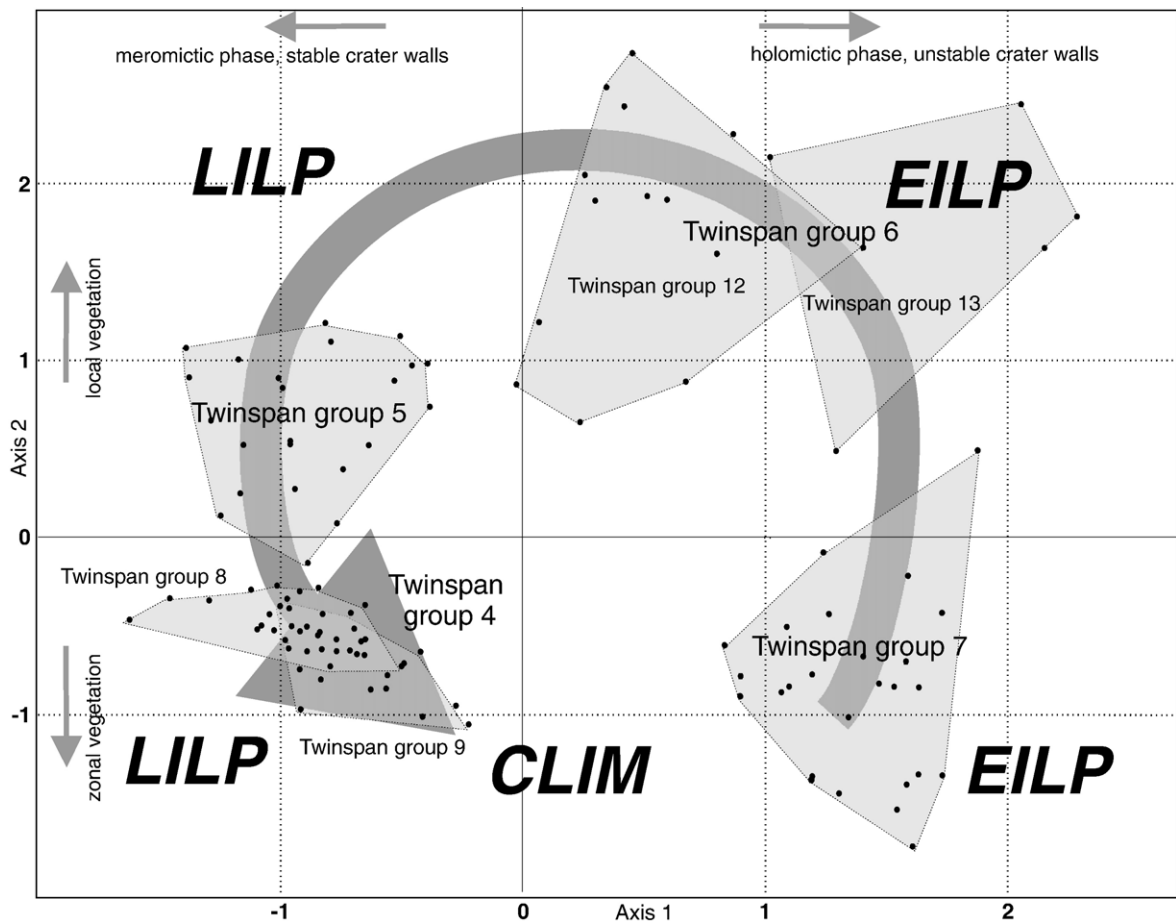


Fig. 12. Scatter plot of the first two axes from a correspondence analysis, showing the arrangement of TWINSpan groups and subgroups 4, 5, 6, 7, 8, 9, 12, 13 and samples (black dots). The arrow traces the temporal succession of TWINSpan groups. This demonstrates that there is no significant change in the general composition of the vegetation between samples of the earliest stages of the lake (Early Initial Lake Phase, EILP) and the climax stage (Late Initial Lake Phase, LILP; climax stage, CLIM).

pollen, *Ilexpollenites* spp., *Nyssapollenites* spp. etc. appear on the positive side of axis 1 (Fig. 11).

### 6.3.2. CA 2

In axis 2 the positive sample values are correlated with pollen of Restionaceae, with *Intrapunctisporis* sp. and *Ischyosporites* sp., i.e. pollen and spores of plants growing near the shoreline, but also with dinoflagellates (Fig. 11). In accordance with the sedimentology, the samples from the mass flow between 140 and 144 m (#155 to #170) show high positive values on axis 2.

Obviously, samples are grouped on opposite sides of axis 2 which are either strongly (positive values) or weakly (negative values) influenced by the local vegetation. This may be due to a concentration of pollen and spores by sedimentological processes rather than reflecting the representation of the respective parent plants in the original vegetation. In particular, the mass flow transported from the shoreline into the basin centre shows high values for Restionaceae but also for *Ischyosporites tertiaris*. In addition, there are the mass occurrences of dinoflagellates which may have been concentrated along the shoreline.

Samples with negative values along axis 2 show no concentration of sporomorphs of plants from the lake margin, but reflect primarily the zonal vegetation. It is interesting to note in this context that samples from the basal lake sediments as well as samples from the later phase of oil-shale formation (TWINSPAN subgroups 4 and 7) both have negative scores. Thus, there is no fundamental difference in composition of assemblages between these two subgroups. This shows that the zonal vegetation did not change in general composition from the earliest stages of the lake during its re-advance into the crater area (Fig. 12). The differentiation between TWINSPAN subgroups 4 and 7 is merely based on the pioneer vegetation during the early stages of the lake.

TWINSPAN subgroups 4 and 5 are likewise juxtaposed since samples of subgroup 5 include some pollen of plants which may have advanced into the crater area somewhat earlier, e.g. *Celtis* and the parent plant of *T. belgicus*. Thus, TWINSPAN subgroup 5 still reflects some local influence.

## 7. Conclusions and outlook

The eruption(s) at Messel not only led to the formation of a maar crater structure but also to a destruction and disturbance of considerable areal extent within the Middle Eocene paratropical vegetation. The recolonization of the volcanically disturbed site can now be traced by the pollen and spore record preserved in the

maar lake sediments. The evaluation of our results has to consider both the simultaneous colonization of widely differing habitats such as the lake margin, the crater wall, and the tuff rim, and the chronological succession of various plant communities.

The composition of the palynological assemblages during the initial phase of Lake Messel is primarily governed by the progressive recolonization of a completely disturbed habitat. It is evident that the majority of plant species represented in the pollen (and spore) spectra was present at least within the general vicinity of the disturbed area and contributed to the regional pollen rain during the Early Initial Lake Phase. Thus, allochthonous pollen input may be responsible for the relatively high proportion of zonal elements, especially during the earliest phase. On the other hand, taxa which are abundant mainly during the Early Initial Lake Phase may be attributed to a pioneer vegetation in successional stages developing on the disturbed areas around the maar lake. Due to a rapid dispersal of spores by wind and reproduction via gametophytes, ferns flourished at the beginning almost without competitors. Ferns have repeatedly been recorded as early colonizers of volcanic sites in the tropics (e. g. Krakatao: Richards, 1996, Motmot: Harrison et al., 2001). The fern-spore spike at the Cretaceous/Tertiary boundary is a well known example of initial recolonization of deeply disrupted habitats by ferns (Tschudy et al., 1984, Fleming and Nichols, 1990). Grasses followed the early fern colonizers on Krakatao and apparently were the first to settle on crater walls of volcanoes on Papua New Guinea (Taylor, 1957). Since grasses were rare during the Eocene their ecological role in the succession at Messel was probably taken by the Restionaceae. The fact that Restionaceae were preferentially found in the major mass flow between 140 and 142 m may reflect a habitat on the crater wall at Messel. Other opportunistic herbaceous, shrubby, and later also woody plants, especially angiosperms (e.g. Ulmaceae), followed in a distinct succession that was repeatedly disturbed by partly collapsing slopes. With increased stability of the rim and slopes, the zonal climax vegetation was finally re-established around the lake. This is reflected sedimentologically by the change from holomictic to meromictic conditions within the lake. This is finally reached at the base of the event bed marking the boundary between the Lower and the Middle Messel Formation. Palynologically, the boundary proper should be placed at the base of the event bed and not in the middle as defined before by Felder and Harms (2004).

Main factors controlling the composition of the palynomorph assemblages during the initial phase of Lake Messel are the condition and stability of the crater



slopes and the relative influence of local (mostly pioneering) and zonal vegetation. The quantitative distribution of the organic-walled remains of algae, e.g. cysts of dinoflagellates, *Botryococcus* and *Tetraedron*, is related to changes in the water chemistry within the lake. A mass occurrence of dinoflagellate cysts is obviously coupled with a major mass-flow event.

The Middle Eocene plant taphocoenoses of Messel and Eckfeld were previously interpreted as representing the zonal paratropical “inland” vegetation of the Western/Central European area. Such a concept is supported by the present study where the respective association of pollen and spores can definitely be identified as representing the climax state. It is the aim of ongoing statistical studies including time series analyses (Lenz et al., 2005) to detect any subordinate changes in the climax vegetation of the Middle Messel Formation which may reflect changes in climatic conditions. Time series analyses will be applied to check for Milankovitch and even sub-Milankovitch frequency bands.

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