

Early Danian benthic foraminiferal community structures, Geulhemmerberg, SE Netherlands

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Abstract

Benthic foraminiferal assemblages from eight clay-layers within a relatively thick section of the lowermost Paleocene (planktonic foraminifera P0 Zone) at the Geulhemmerberg, SE Netherlands, were examined for changes in abundance and species composition. The lower clay layers (A to D) are characterized by peculiar benthic foraminiferal assemblages with high numbers of small spiral forms which resemble modern epifaunal phytodetritus-feeding communities, that are well adapted to a food-limited environment in which much of the nutrient input is seasonally or erratically pulsed. Another distinct assemblage with high numbers of small, infaunal morphotypes such as *Tappanina selmensis*, *Reussella* ex gr. *europaea*, buliminids and bolivinids characterizes the upper part of the succession (clay layers E and F). This assemblage exhibits striking similarities to modern assemblages in areas with enhanced organic-matter export flux rates resulting in increased food supply for benthic organisms and slightly dysaerobic conditions at the sea floor. The occurrence of these 'high-productivity' benthic foraminiferal assemblages coincides with a marked increase in *Thoracosphaera* calcareous dinoflagellate cysts and may indicate an important phase in the recovery of the marine ecosystem after the collapse of the food web at the Cretaceous/Tertiary boundary.

Introduction

Whatever the reasons for the extinctions at the Cretaceous/Tertiary (K/T) boundary were, there is general agreement that an important decrease in primary marine production and a period of extremely oligotrophic ('Strangelove Ocean') conditions followed the K/T boundary event. These dead ocean conditions are recorded in the composition of marine plankton communities (calcareous nannoplankton, planktic foraminifera, dinoflagellates) and a major negative carbon isotope ($\delta^{13}\text{C}$) signal (Arthur et al. 1987; Zachos and Arthur 1986; Zachos et al. 1985, 1989; Kaminski and Malmgren 1989). This collapse of the marine food web had a significant impact on benthic foraminiferal communities in shallower marine environments as well as in the deep sea (Keller 1988; Thomas 1990a, b; Kuhnt and Kaminski 1993; Speijer 1994). Little is known about the timing and mechanisms of the recovery of the community structure after the cessation of the dead ocean conditions. This lack of knowledge

mainly stems from the short duration of the planktonic foraminifer P0 Zone, which in most K/T boundary sections only represents a few centimeters of sediment. Consequently the resolution of sampling for benthic foraminifera is too low to examine changes in the benthic community structure following the first blooms of primary producers when the marine ecosystem recovered. The Geulhemmerberg K/T section probably represents the most expanded sedimentary record of the earliest Paleocene P0 Zone known (Smit and Zachariasse, Smit and Brinkhuis, this issue). Eight clay layers with well-preserved autochthonous benthic foraminifera are separated by several decimeters of calcarenites, which mainly consist of transported shallow-water biogenic material, including reworked benthic foraminifers from the uppermost Maastrichtian. Changes in the composition of benthic foraminiferal assemblages within these clay layers thus offer a unique opportunity to study the reaction of benthic communities to the recovery of the marine food web after the K/T boundary event.

Table 1. Benthic foraminiferal census data of the Geulhemmerberg section. Infaunal high-productivity (HPR) forms belong to the elongate tapered morphotype of Corliss (1985) and include *Tappanina selmensis*, *Reussella* ex gr. *europaea*, *Reussella* ex gr. *paleocenica*, *Bulimina* spp., *Bolivina* ex gr. *incrassata* and *Bolivina* (elongate). Samples A-c, B-c, C-c, D1-c, and D2-c are from coarser calcarenitic material which was attached to the clay samples.

SAMPLES sample size (g)	A 6	A-c n/a	B 1,5	B-c n/a	C 3	C-c n/a	D1 10	D1-c n/a	D2 2	D2-c n/a	E-base 19	E-mid 20	E-top n/a	E-top2 12	F 1	G 2	
<i>Heterohelix globulosa</i>	46	.	46	2	20	.	17	2	30	1	349	153	28	55	25	2	planktic foraminifera
<i>Guembelitria cretacea</i>	20	.	9	.	.	.	4	.	.	1	19	7	.	6	8	.	
<i>Hedbergella</i>	4	.	5	1	.	.	4	.	2	2	39	19	1	11	5	3	
<i>Globigerinelloides</i>	3	2	2	2	1	.	agglutinates
keeled planktics	4	.	.	.	2	.	1	.	3	.	.	.	1	2	.	.	
<i>Arenobulimina</i>	3	2	2	1	4	.	3	3	4	1	10	.	2	6	.	4	
<i>Textularia</i>	7	2	3	4	7	.	.	1	2	10	.	14	
<i>Gaudryina</i> and indet. aggl.	2	1	1	.	5	.	5	.	3	1	7	.	6	2	.	6	
<i>Siderolites calcitrapoides</i>	1	7	.	18	17	14	.	1	4	small spiral morphotype
<i>Orbitoides</i>	1	3	.	1	
<i>Quinqueloculina</i>	1	
<i>Spirillina</i>	3	12	small spiral morphotype
<i>Patellina</i>	10	.	54	1	18	.	25	.	10	.	.	.	3	.	31	2	
<i>Pseudopatellina cretacea</i>	1	.	11	10	1	4	.	.	
<i>Ceratobulimina</i> (?) sp.	11	8	3	.	.	.	
Cibicides (small) and other small trochospiral forms	317	.	289	.	127	.	106	14	147	5	362	180	41	311	235	35	
<i>Cibicides</i> spp.	300	79	155	65	248	31	170	103	38	78	108	3	99	53	9	351	
<i>Cibicides</i> spp.	229	32	94	71	217	4	215	147	214	71	335	149	303	322	34	255	
indet. trochospiral forms	85	7	123	44	142	.	81	11	47	1	50	60	30	76	23	106	
<i>Mississippina binkhorsti</i>	.	1	.	2	7	1	20	3	15	
<i>Polymorphinidae</i>	63	17	14	20	45	9	24	13	14	25	10	8	20	15	4	82	
<i>Nonionella troostae</i>	35	4	12	.	47	.	21	29	9	20	4	2	19	11	4	.	
<i>Nonionella</i> (small)	11	.	15	4	1	.	10	.	7	.	5	.	1	30	10	25	
<i>Nodosariidae</i>	18	10	3	.	10	3	4	1	6	2	5	1	5	6	2	13	
<i>Stilostomella</i>	4	1	.	
<i>Pullenia</i>	3	.	2	.	4	.	6	.	5	2	2	2	10	4	.	2	
<i>Lenticulina</i>	.	.	1	.	8	2	
<i>Marginulina</i>	1	.	.	.	4	1	1	.	.	6	.	.	.	2	.	1	
<i>Lagena</i>	4	.	1	.	.	.	4	4	9	1	.	.	.	7	2	1	
<i>Gyroïdinoïdes subangulatus</i>	7	.	1	1	7	.	4	1	6	1	1	.	1	.	1	2	
<i>Fissurina</i>	1	.	1	.	1	1	.	.	
<i>Allomorphina</i>	.	.	4	1	6	.	1	3	4	2	.	.	1	2	.	8	
<i>Stensioïcina</i>	.	.	1	
<i>Bolivinoïdes draco</i>	.	.	4	.	2	.	2	2	1	.	1	.	2	4	.	.	
<i>Neoflabellina</i>	1	
<i>Tappanina selmensis</i>	34	2	52	.	25	.	9	.	11	.	228	172	8	38	68	2	infaunal "HPR"-forms
<i>Reussella</i> ex gr. <i>europaea</i>	4	.	2	.	3	.	2	.	6	.	22	8	.	2	1	.	
<i>Reussella</i> ex gr. <i>paleocenica</i>	20	.	6	.	.	.	1	.	7	.	72	40	4	5	12	.	
<i>Bulimina</i> spp.	20	.	15	.	6	.	9	.	12	.	62	39	3	24	21	2	
<i>Bolivina</i> ex gr. <i>incrassata</i>	7	.	12	.	6	.	6	1	3	1	24	1	4	3	.	3	
<i>Bolivina</i> (elongate)	6	.	3	1	1	.	.	2	.	.	1	.	5	.	3	3	
<i>Ostracoda</i>	155	17	74	8	76	7	19	6	15	9	9	.	19	122	10	105	
total benthic foraminifera	1192	167	876	242	961	63	710	336	564	217	1331	688	568	965	476	935	
faunal density (specimen/g sediment)	199	.	584	.	320	.	71	.	282	.	70	34	.	80	476	468	
% infaunal "HPR"-forms	8	1	10	0	4	0	4	1	7	1	31	39	3	8	22	1	
% plankton	6	0	6	1	3	0	4	1	6	2	23	21	5	7	8	1	
% ostracoda	12	9	8	3	7	10	3	2	3	4	1	0	3	11	2	10	

Material and methods

Eight clay layers (A, B, C, D1, D2, E, F and G) of the Geulhemmerberg section were sampled for benthic foraminifera from the main sampling point (see Brinkhuis and Smit, this issue). The thickest clay layer (E clay; about 10 cm thick) was subdivided into three subsamples (E base, E middle and E top). A duplicate of the E top sample was taken at a locality about 20 m E of the main section.

Each clay sample was carefully cleaned from attached coarser carbonate sand using a knife blade. The clay was dried, weighed, completely disintegrated just by soaking in distilled water and sieved over a 63 μm screen. The residue was again weighed and split in subsamples. One or several subsamples were completely picked for planktic and benthic foraminifera,

and ostracods; the assemblages were mounted into Plummer slides and counted. The coarser material that was scratched off the clay layers was separately processed using anionic tensides; foraminifera were picked and counted from the fraction larger than 63 μm (samples A-c, B-c... in Table 1). No attempt was made to record the faunal density of these samples since they were mainly composed of reworked carbonate material including benthic foraminifera, mixed with larger fossil (mainly bryozoan) fragments, and often did not disintegrate completely. However, the species composition of these samples is of interest since it records the composition of the 'background' fauna, that occasionally occurs as a redeposited element within the clay samples. These redeposited forms could be generally distinguished by their often corroded tests and a characteristic yellowish color. Visual examination

for minor lenses of yellowish carbonate material and cleaning of the clay samples minimized the amount of contamination in the clay layers. Carefully cleaned subsamples from the E and F layers were virtually free of redeposited tests.

Results

Biostratigraphy

Generally the species composition of the benthic foraminiferal assemblages is fairly consistent within the interval studied. No apparent first or last occurrences of more common species are observed. Only rare forms such as *Orbitoides*, *Quinqueloculina*, *Neoflabellina* and *Stensioeina* are restricted to the lower part of the section (layers A to D1), whereas *Pseudopattellinella cretacea* and *Glabratella* cf. *crassa* do not occur below layer D2.

However, a significant change in the quantitative composition of the benthic foraminiferal assemblages is observed at the base of layer E. Percentages of small opportunistic species such as *Tappanina selmensis*, small buliminids and rotaliids increase significantly. Interestingly enough, increasing numbers of *T. selmensis* are also observed in other expanded K/T boundary sections with a high-resolution record of the lowermost Paleocene. At El Kef, NW Tunisia, *T. selmensis* is first observed 95 cm above the boundary layer, within the lower part of the *G. eugubina* Zone and increases to more than 7% of the benthic assemblage in Zone P1 (Keller 1988).

Although the first appearance of *T. selmensis* is within the Upper Maastrichtian (Cushman 1933; Brotzen 1948; Hofker 1966) it is generally a rare species below the K/T boundary (Brotzen 1948; Keller 1988). The common occurrence of this species within the Geulhemmerberg samples is thus an additional indication of the Paleocene age of this interval.

Paleoecology

Significant differences in the benthic foraminiferal assemblage composition are observed between the samples from clay layers and 'background' samples from the calcarenites of the Geulhemmerberg section (Figure 1). Calcarenitic samples (including those from the top of layer E and from layer G, which do not contain significant amounts of clay) are characterized by benthic assemblages with high numbers

of Ostracoda, *Cibicides* and *Cibicidoides*, and somewhat increased numbers of agglutinated foraminifera (textulariids). Planktic foraminifera are extremely rare or absent in these samples. A rare but characteristic component of these 'calcareous' assemblages are larger foraminifera such as *Siderolites calcitrapoides* and *Orbitoides* (Table 1). Assemblages from clay layers A, B, C, E and F all have in common a higher number of planktic foraminifera (mainly heterohelicids) and higher numbers of small-sized species of two characteristic morphogroups: 1) small spiral forms which according to their test morphology lived epifaunally (Corliss 1985), and 2) small elongate tapering forms which probably lived infaunally (Figure 1). One of the most peculiar features of the clay layers are abundant occurrences of calcispheres (*Thoracosphaera*, calcareous cysts of dinoflagellates, see Willems, this issue), which are commonly observed even within the grain fraction $> 63 \mu\text{m}$ from clay layers B, D2, E and F. Samples rich in *Thoracosphaera* generally contain large numbers of small thin-walled spiral benthic foraminifera which belong to morphogroup 1 (Figure 1, Plate 1). These forms morphologically resemble modern species which feed on phytodetritus in the fluffy layer just above the seafloor (Gooday 1993). According to these modern observations, foraminifera which habitually exploit phytodetritus are opportunists able to respond to sudden food pulses with the build-up of large populations that collapse when the phytodetritus is used up (Gooday and Turley 1989; Gooday 1993). These forms are thus well adapted to a food-limited environment in which much of the nutrient input is seasonally or erratically pulsed (Gooday 1993; Smart et al. 1994). They probably were the first to take advantage of the earliest pulses of organic matter flux reaching the seafloor at shallow sites when the marine ecosystem recovered after the collapse of the food web at the K/T boundary.

The second group which characterizes mainly the benthic assemblages of the E and F layers (Figure 1) are small elongated infaunal morphotypes such as *Tappanina selmensis*, *Reussella* ex. gr. *europaea* and various bolivinids and buliminids (morphogroup 2, Plates 2, 3). These forms are probably also opportunistic species, which are closely related to the modern 'high-productivity group' (HPR) of Lutze and Coulbourne (1984) and Lutze et al. (1986). They are regarded as infaunal detritus feeders, which require a higher and more steady flux of organic matter to the seafloor (Corliss and Chen 1988). Interestingly enough these forms seem to form a significant component of the

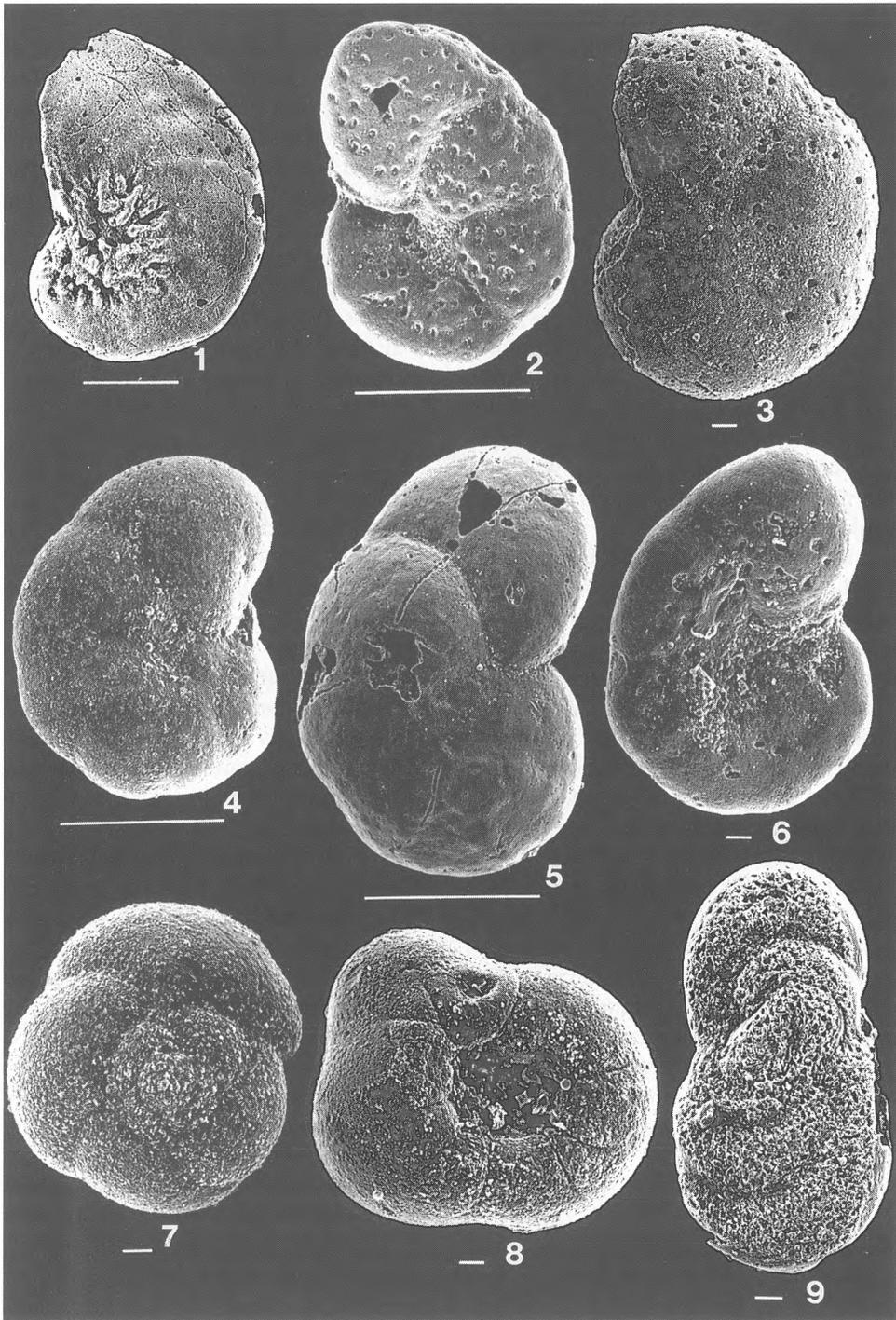


Plate 1. Small spiral morphotype (epifaunal phytodetritus-feeding opportunists, morphogroup 1). 1. *Nonionella troostae*; 2, 3. *Cibicides* sp.; 4–6. *Ceratobulimina* (?) sp.; 7, 8. *Ceratobulimina* aff. *perplexa*; 9. *Pseudopatulina cretacea*. All specimens from the base of the E clay, Geulhemmerberg. Scale bars equal 10 μm for Figures 3 and 6–9, and 100 μm for Figures 1, 2, 4 and 5.

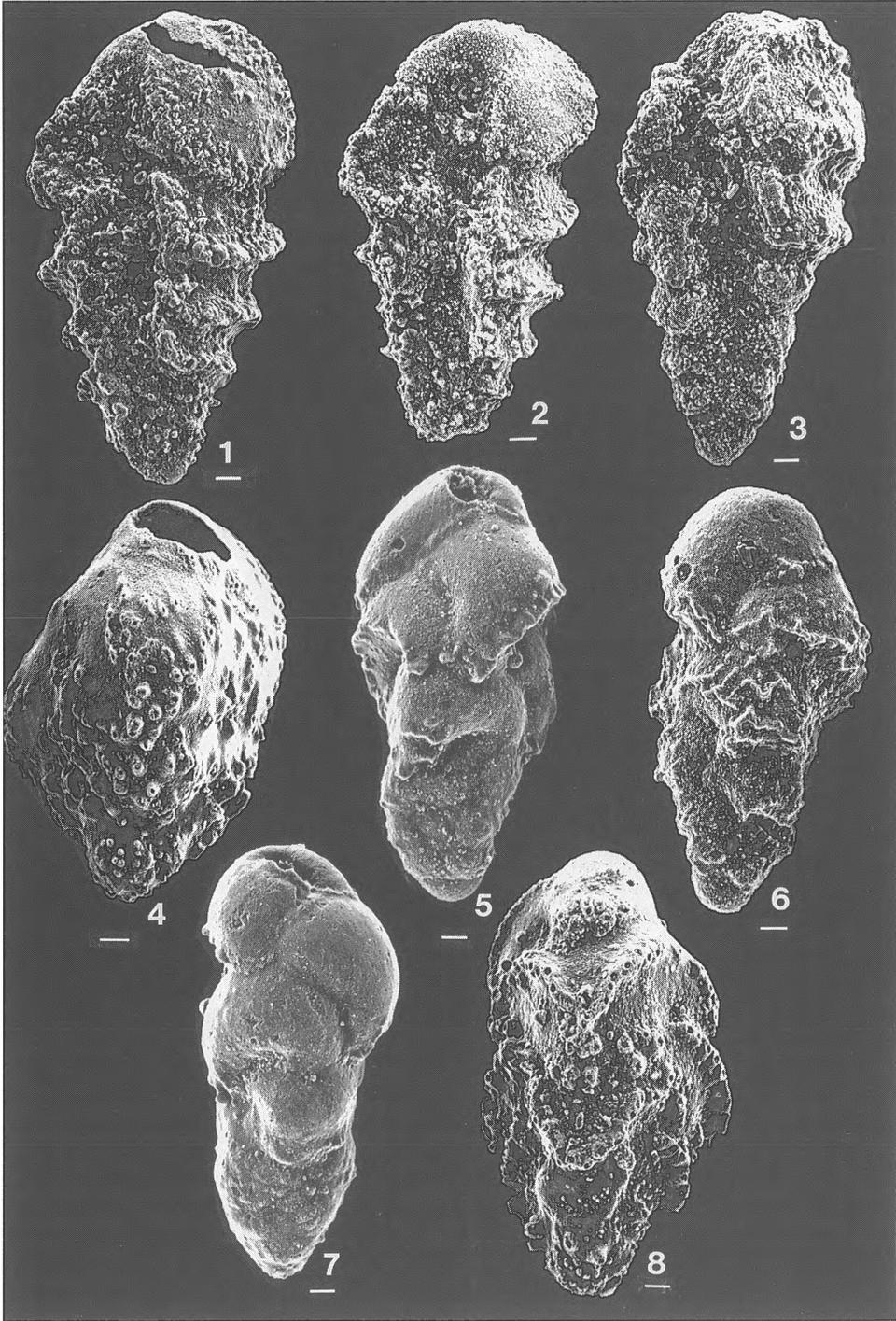


Plate 2. Elongate infaunal morphotype (morphogroup 2). 1–3. *Tappanina selmensis*; 4, 8. *Reussella europaea*; 5–7. *Reussella* sp. All specimens from the base of the E clay, Geulhemmerberg. Scale bars equal 10 μm .

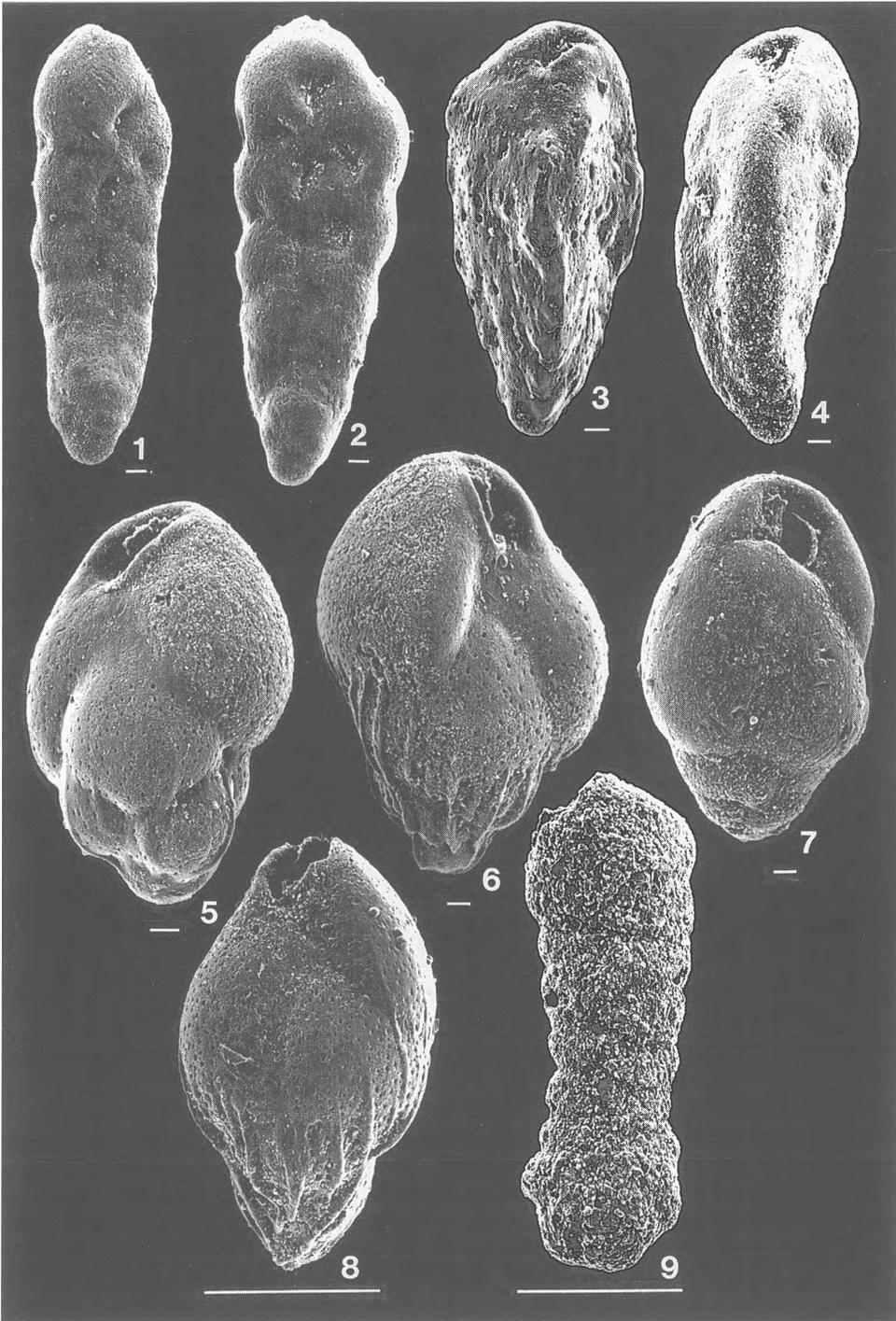


Plate 3. Elongate infaunal morphotype (morphogroup 2). 1, 2. *Bolivina* sp.; 3. *Reussella cristata*; 4. *Reussella paleocenica*; 5–8. *Bulimina* sp.; 9. *Spiroplectammina* aff. *spectabilis*. All specimens from the base of the E clay, Geulhemmerberg. Scale bars equal 10 μm for Figures 1–7, and 100 μm for Figures 8 and 9.

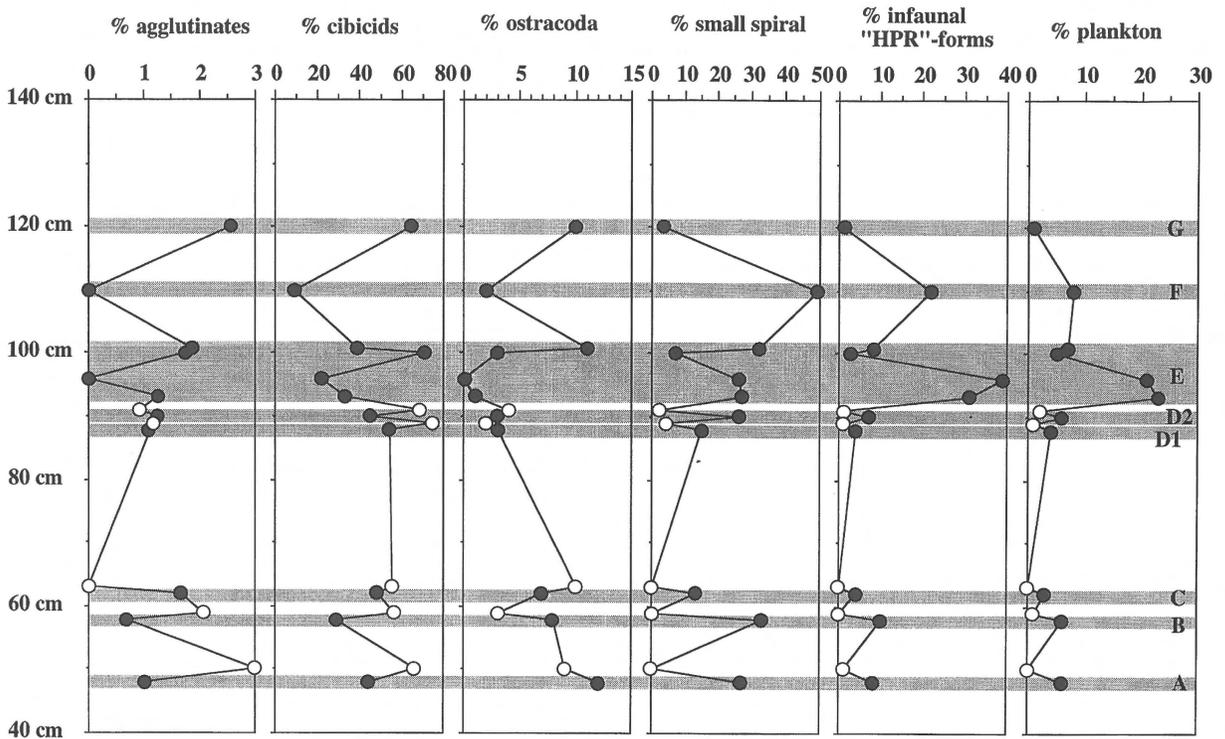


Figure 1. Relative abundance of major foraminiferal groups within clay layers (black circles) of the Geulhemmerberg section. Open circles correspond to limestone samples immediately above or below the clay layers. These samples mainly contain redeposited foraminifera.

benthic assemblages before layer E and their common occurrence within this layer may be an indication of already increased primary productivity at this time.

Stable isotopes

The unusually well-preserved benthic foraminifera in the clay layers of the Geulhemmerberg section allow reliable stable isotope measurements of individual species. Some initial data from the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ analyses are shown in Table 2. No significant trend can be observed in the $\delta^{18}\text{O}$ values, which are in the range of European Maastrichtian and Danian chalk values (Kaminski and Malmgren 1989). However, even from the few data available a difference can be depicted in $\delta^{13}\text{C}$ values of the *Cibicidoides* (1.50 to 1.88‰, average 1.67‰), the small spiral forms (1.31‰), *Tappanina selmensis* (0.84 to 0.91‰), and *Heterohelix globulosa* (1.15‰). Compared to the bulk rock data given by Kaminski and Malmgren (1989), the $\delta^{13}\text{C}$ *Cibicidoides* values fall well within the Maastrichtian values (1.52 to 2.09‰) for Stevns Klint in Denmark, whereas the values for tapaninas, small spiral forms

and heterohelicids would compare better to the Danian data (1.13 to 1.60‰, average 1.40‰ for Stevns Klint). These differences may be explained by vital effects or by reworking of the large *Cibicidoides* specimens within the clay layer. However, the data would also support the hypothesis that tapaninas and small spiral forms flourished during or immediately after phytoplankton blooms when the bottom and near-surface porewater was enriched in ^{12}C because of fluff layers, whereas the *Cibicidoides* document long-term background $\delta^{13}\text{C}$ values. This scenario fits into the 'Respiring Ocean' model after the terminal Cretaceous event which predicts a ^{12}C enrichment in near-surface waters through decay of slowly sinking phytoplankton by opportunistic bacteria (Hollander et al. 1993).

Discussion and conclusions

The most significant characteristics of the benthic foraminiferal assemblages observed in the lowermost Paleocene clay layers of the Geulhemmerberg section are:

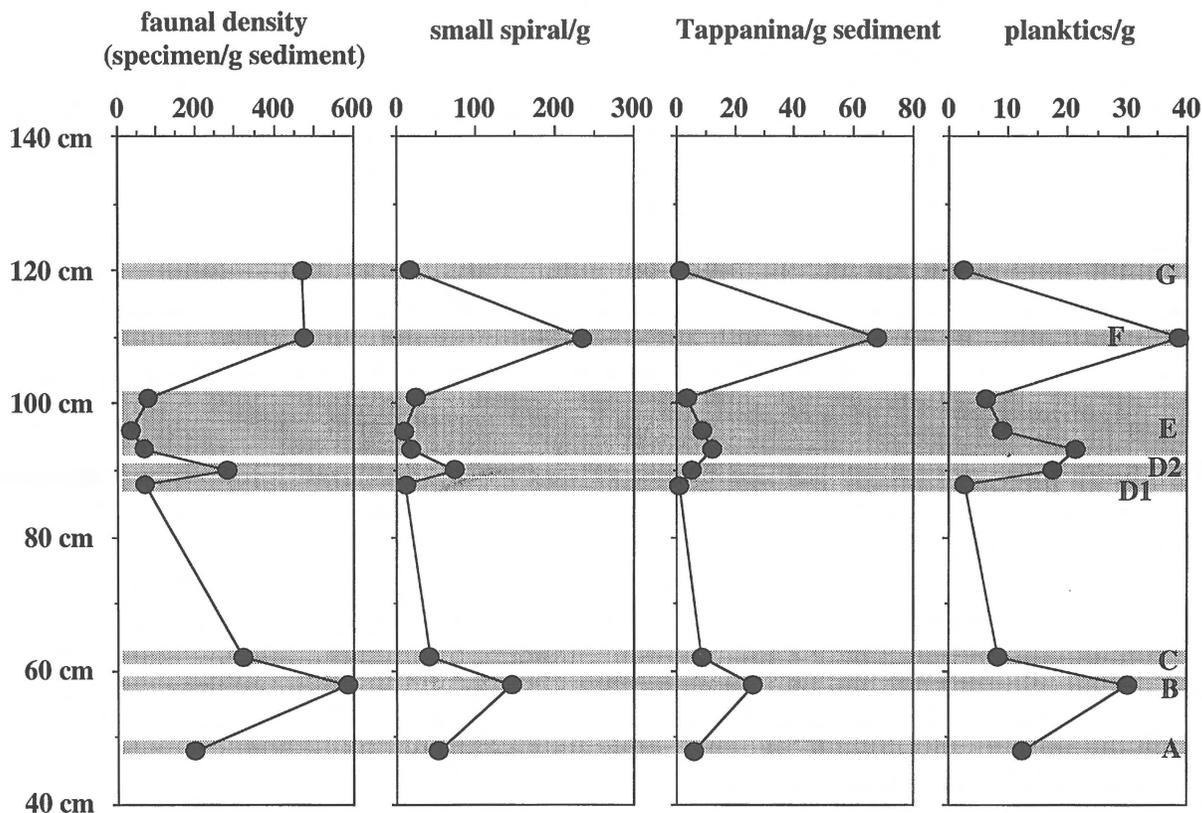


Figure 2. Faunal density of benthic and planktic foraminifera and absolute abundances of selected benthic foraminifera within the clay layers of the Geulhemmerberg section.

Table 2. Stable isotope values of individual foraminiferal species, Geulhemmerberg. Isotope values are given in δ notation versus the PDB standard.

Species, preservation	Clay	Individuals	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
<i>Heterohelix globulosa</i>	E	> 50	1.15	-1.77
Small spiral forms	E	> 50	1.31	-1.71
<i>Tappanina selmensis</i>	E	> 30	0.84	-1.89
<i>Tappanina selmensis</i>	E	> 50	0.91	-1.88
<i>Cibicidoides</i> (yellow)	E	5	1.53	-1.30
<i>Cibicidoides</i> (white)	D2	4	1.50	-1.82
<i>Cibicidoides</i> (white)	G	2	1.76	-1.47
<i>Cibicidoides</i> (yellow)	G	6	1.88	-1.75

1. absence or rare (probably reworked) occurrence of large forms with complex morphology and wall structure;
2. high numbers of small calcareous infaunal morphotypes which probably indicate enhanced organic matter fluxes;

3. high numbers of small presumably epifaunal foraminifera with spiral test morphologies, that may be associated with seasonal pulses of organic matter.

This peculiar faunal composition may be explained by a fundamental difference in selection pressure on Maastrichtian and earliest Paleocene benthic assemblages. The Maastrichtian tropical seas of southern Limburg can be ascribed largely to a stable, K-selection environment (cf. McArthur and Wilson 1967), where complex and highly specialized species, including symbiont-bearing larger foraminifera dominated the assemblages. The shallow shelf seas after the K/T boundary event most probably provided a typical r-selection environment with an extremely fluctuating pulsed food supply during occasional phytoplankton blooms (Hollander et al. 1993).

In modern marine environments, e.g. the North Atlantic, pulsed organic matter fluxes are mainly a characteristic of deep-sea environments, where outside

the spring-bloom periods the entire primary production is recycled within the water column. The benthic biofacies of the Geulhemmerberg indicate similar trophic situations in a comparatively shallow shelf setting during the earliest Paleocene (Zone P0). According to the data presented in Keller (1988) a similar succession of biofacies is observed in the deeper, outer-shelf El Kef section, with the first common occurrence of high-productivity-indicating infaunal forms (*Tappanina* assemblage) somewhat later in the Early Paleocene (Zone P1). In deep-water, bathyal K/T boundary sections, e.g. Gubbio, Caravaca, Zumaya and Sopelana, the lowermost Paleocene is dominated by agglutinated foraminiferal assemblages indicating oligotrophic conditions, that are comparable to modern abyssal environments of central oceanic gyres such as the Sargasso Sea. These fundamental differences in the succession of benthic biofacies in the modern North Atlantic Basin (Lutze et al. 1986; Sarnthein and Altenbach 1995) and in the distribution at the K/T boundary are consistent with the model of a strongly reduced primary productivity during the earliest Paleocene, wherein pulsed organic matter paleofluxes following phytoplankton blooms were limited to shallow shelf seas.

The succession of benthic communities observed in the Geulhemmerberg section indicates that the recovery of the marine ecosystem after the K/T boundary crisis may have occurred in two steps:

1. in a still oligotrophic situation, organic matter was supplied to the seafloor in erratic or seasonal pulses, favouring an opportunistic (r-selected) benthic foraminiferal community;
2. when organic matter fluxes got more steady and substantial, a high-productivity-adapted infaunal community began to thrive first at shallow-shelf sites (Geulhemmerberg) and later occupied gradually deeper outer-shelf (El Kef) and bathyal (Gubbio, Italy; Sopelana, Spain) environments.

A time-transgressive faunal turnover of benthic foraminifera across the K/T boundary, beginning in shallow-marine environments and ending in deeper (bathyal) environments, has been observed by Keller (1992) in her comparison of faunal changes in K/T boundary sections at Caravaca, Spain, Negev, Israel, El Kef, Tunisia, and Brazos River, USA. She related these changes to a global sealevel rise in the earliest Paleocene. Also in the Geulhemmerberg section, the earliest Paleocene benthic foraminiferal composition indicates somewhat deeper water conditions than the latest Maastrichtian (Witte and Schuurman, this issue). Whether or not the sea-level fluctuations at the

K/T boundary are a dominant factor in the benthic faunal change is still a matter of discussion. The Geulhemmerberg section offers the unique opportunity to examine benthic foraminiferal changes in high resolution and with unusually well-preserved material that allows reliable stable isotope measurements of single species. The initial study presented here is a starting point in an attempt to understand the earliest Paleocene changes in trophic structure and the response of the benthic foraminifera.

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Appendix

Faunal reference list

Benthic foraminifera identified in the Geulhemmerberg samples are listed below in alphabetical order. For several taxa only the generic names are given, since no attempt has been made to separate the different species in the counts. References for species which have been lumped under the generic name may be obtained from the author.

Allomorphina sp.
Arenobulimina sp.
Bolivina ex gr. *incrassata* Reuss, 1851
Bolivina sp.
Bolivinoides ex gr. *draco* (Marsson)
Bulimina sp.
Ceratobulimina (?) sp.
Cibicides sp.

Cibicidoides sp.
Fissurina sp.
Gaudryina sp.
Gyroidinoides subangulatus (Plummer, 1927)
Lagena sp.
Lenticulina sp.
Marginulina sp.
Mississippina binkhorsti (Reuss, 1862)
Neoflabellina sp.
Nonionella sp.
Orbitoides sp.
Patellinella sp.
Pseudopatellinella cretacea Takayanagi, 1960
Pullenia sp.
Quinqueloculina sp.
Reussella ex gr. *europaea* (Cushman & Ewards)
Reussella ex gr. *paleocenica* Brotzen, 1948
Siderolites calcitrapoides Lamarck, 1799
Spirillina sp.
Spiroplectamina sp.
Stensioeina sp.
Stilostomella sp.
Tappanina selmensis (Cushman, 1933)
Textularia faujasi Reuss, 1861

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