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Palynology of the Geulhemmerberg Cretaceous/Tertiary boundary section (Limburg, SE Netherlands)

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Abstract

The newly found, relatively complete section across the Cretaceous/Tertiary (K/T) boundary in the Geulhemmerberg caves contains rich and well-preserved palynological assemblages. Stratigraphically diagnostic dinoflagellate cysts indicate that the lower part of the Geulhemmerberg succession represents the latest Maastrichtian and that an early Danian age may be assigned to sediments overlying the Berg en Terblijt Horizon, notably on the basis of the appearance of *Senoniasphaera inornata*. On the basis of quantitative palynological analysis, the sediments are interpreted to represent relatively marginal marine, inner neritic conditions, with nearby landmasses providing important terrestrial input.

Almost all terrestrial palynological elements are most probably derived from Bryophyta (mosses). Their sudden proliferation at the K/T boundary may be associated with increased transport from the coastal plain, and/or it may reflect a major change in the terrestrial ecosystem at K/T time. Changes in the palynomorph distribution are probably mainly caused by differing hydrodynamical conditions, possibly combined with slightly varying waterdepths and/or the introduction of restricted marine conditions.

Introduction

Several palynological studies focus on parts of the upper Cretaceous and lower Paleocene succession in the southern Netherlands and its immediate surroundings (e.g. Wilson 1971, 1974; Schumacher-Lambry 1977; Robaszynski et al. 1985; Herngreen et al. 1986; Batten et al. 1988; Bless and Streel 1988). Although these studies indicate the presence of rich and well-diversified palynomorph assemblages, none of them report on the Cretaceous/Tertiary (K/T) transition in detail. In effect, the K/T boundary was thought to represent a considerable hiatus in the area (Jagt et al., this issue). Recently, however, a presumably relatively complete K/T boundary section was discovered in this area within the Geulhemmerberg caves.

As part of the multidisciplinary analysis of this section, the present paper reports on its palynology, emphasizing dinoflagellate cysts. It aims to present a biostratigraphical analysis, complemented by palaeoenvironmental interpretations.

Material and methods

Two sets of samples were used. The first set is derived from the so-called 'main section' within the caves of the Geulhemmerberg (for location and other details, see Brinkhuis and Smit this issue). This set involves 24 closely spaced samples covering the entire succession of 125 cm, and labelled G1A to G7B (Figure 1). The set is also used by other disciplines involved in the project. An additional set of samples was taken from the A, D and E clays for more detailed investigation. The D clay was split into two samples D1 and D2, while the well-developed E clay was divided into 16 samples with an average thickness of 0.5 cm each (E1–E16; see Figure 1).

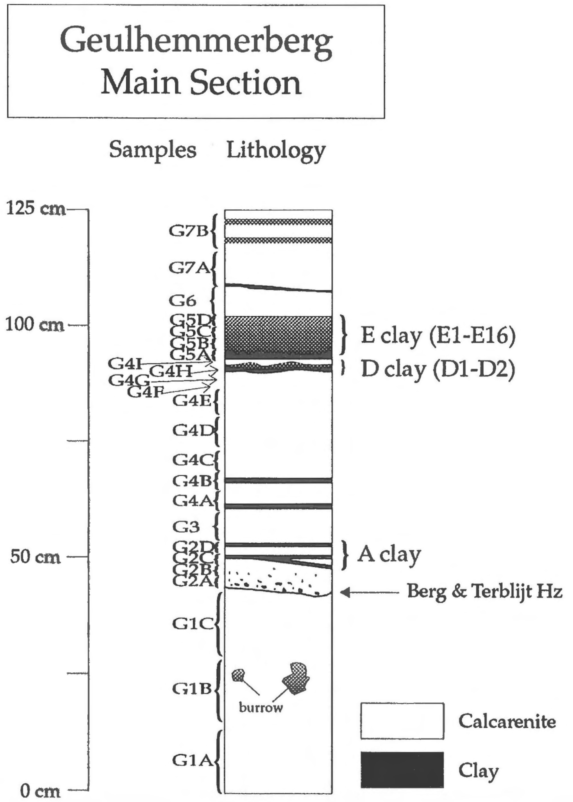


Figure 1. Schematic lithological column and sample positions at the Geulhemmerberg main sample site.

Approximately 10 to 15 g of sample was processed following standard palynological techniques, with the exception of samples from the main section (see below). Heavy-liquid separation ($ZnCl_2$) was applied in all cases. Residues were sieved using a 10 μm precision sieve. After extensive mixing to obtain homogeneity, two to eight slides were prepared using glycerine jelly as mounting medium. Where possible, approx. 250 palynomorphs were counted per sample. Dinoflagellate cysts were counted on species level while other palynomorphs were counted in broad categories, e.g. bisaccate pollen, other pollen, spores, different groups of prasinophyte algae, acritarchs, and inner walls of foraminifera. Remaining material was scanned for additional dinoflagellate cyst taxa.

The set of 24 samples from the main section was primarily used to document the concentration variations of the various groups of palynomorphs through the succession. This was carried out by preparing two slides per sample using 1) standard techniques, combined with 2) a full count of one slide representing a known fraction of the sample. Only a relatively small amount of material could be analysed of these samples, leading to apparently less diversified dinoflagellate cyst associations relative to those derived from the additional (clay) sample set.

The taxonomy of dinoflagellate cysts follows that given in Lentin and Williams (1993). Previously undescribed taxa and those not included in Lentin and Williams (1993) are briefly treated in the Appendix which also includes a list of recorded taxa. Characteristic taxa are illustrated on Plates 1–4.

Light-photomicrographs were taken from permanent scatter mounts, using a Leitz Orthoplan/Orthomat combination and interference-contrast illumination. England Finder coordinates are provided for photographed specimens. All material is stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands.

Results

Palynomorph distribution

The relative distribution of the recorded categories of palynomorphs within the main section is plotted in Figure 2. The aquatic component mainly consists of dinoflagellate cysts and representatives of the acritarch genus *Paralecaniella*. The terrestrial component is dominated by well-preserved, simple, spherical spores (Plate 3, Figure 8; Plate 4, Figures 2–6). In addition, other, relatively small, equally well-preserved spherical spiny palynomorphs (Plate 4, Figure 1) occur in relatively large numbers. The morphologies of both these groups of palynomorphs bear a great similarity to spores of extant Pottiaceae species (Bryophyta; B.O. van Zanten, personal communication 1994). They are therefore tentatively considered to be derived from this category of lower landplants. Some extant representatives of the Pottiaceae are well-known for their pioneering character. They occur for instance in coastal areas, and along episodically flooded river banks, specifically on calcareous and/or clayey substrates, and they are cosmopolitan in nature (B.O. van Zanten, personal communication 1994). Other spores and pollen (of vascular plants) are poorly preserved and only occur in trace amounts. The encountered palynodebris is mainly composed of relatively small, blocky opaque elements.

The distribution of the various categories clearly seems to be related to the lithology. The clays consistently contain abundant bryophyte spores and

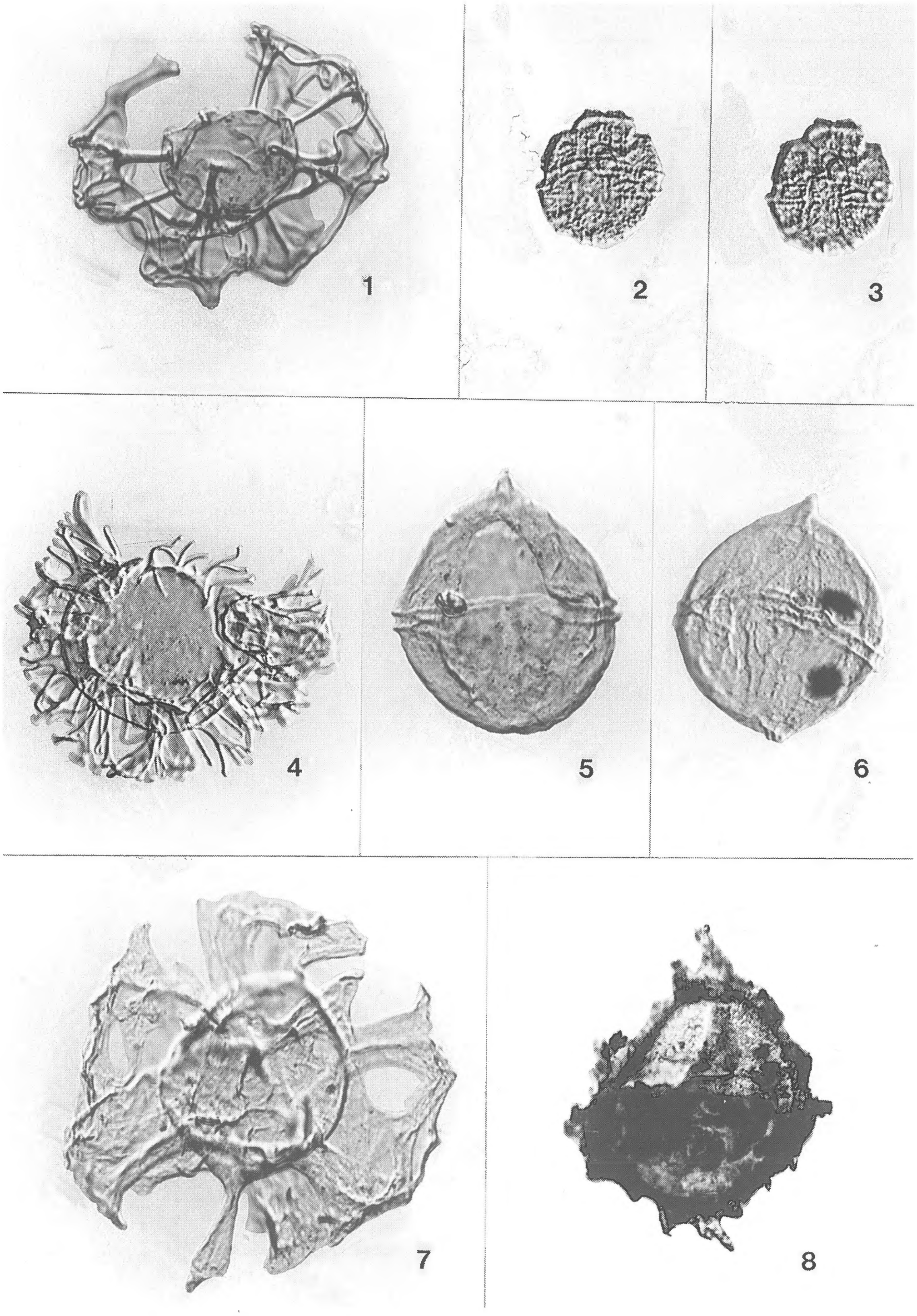


Plate 1. Dinoflagellate cysts, Geulhemmerberg. All magnifications 250 ×; England Finder coordinates provided. Figure 1. *Adnatosphaeridium buccinum* Hultberg, 1985; sample/slide E16/02, O39/2. Figures 2. 3. *Alisocysta* sp. cf. *A. reticulata* Damassa, 1979; sample/slide E8/02, L48/4. Figure 4. *Areoligera senonensis* Lejeune-Carpentier, 1938; sample/slide E14/02, G39/4. Figures 5, 6. *Cribroperidinium* sp. A. Figure 5. sample/slide D2/05, J34/3. Figure 6. sample/slide D2/01, F33/1. Figure 7. *Disphaerogena carposphaeropsis* O. Wetzel, 1933; sample/slide E7/01, H41. Note development of apical/antapical horns. Figure 8. *Fibrocysta* sp. A; sample/slide E11/01, S41.

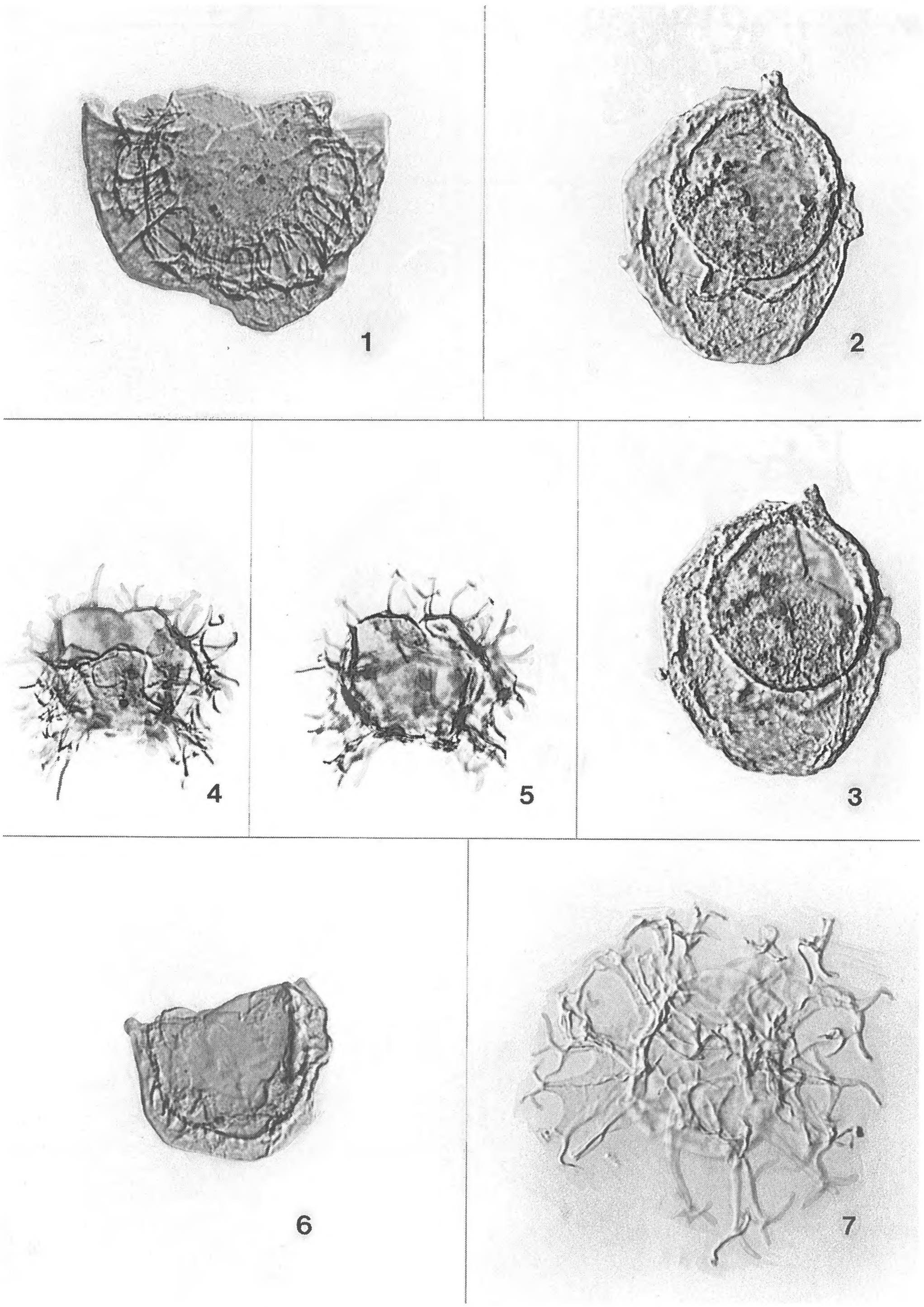
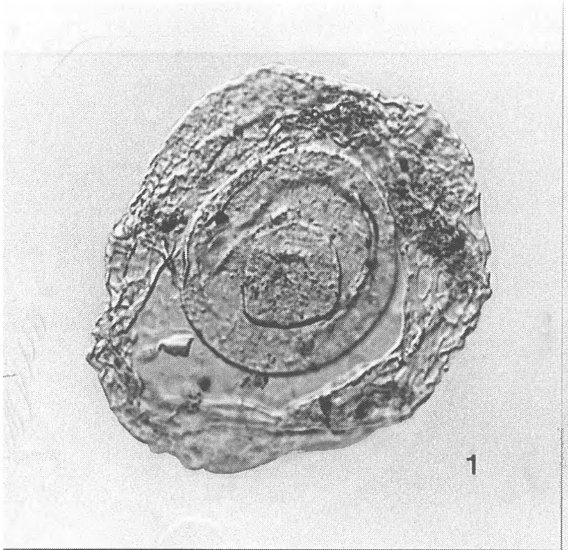


Plate 2. Dinoflagellate cysts, Geulhemmerberg. All magnifications 250 ×; England Finder coordinates provided. Figure 1. *Glaphyrocysta perforata* Hultberg and Malmgren, 1985; sample/slide E16/02, W31. Figures 2, 3. *Lanternosphaeridium reinhardtii* Moshkovitz and Habib, 1993; sample/slide E14/02, X42. Figures 4, 5. *Palynodinium grallator* Gocht, 1970; sample/slide E9/01, U43. Figure 6. *Senoniasphaera inornata* (Drugg) Stover and Evitt, 1978; sample/slide A/03, U31. Figure 7. *Spiniferites ramosus* ssp. A; sample/slide E14/02, U42.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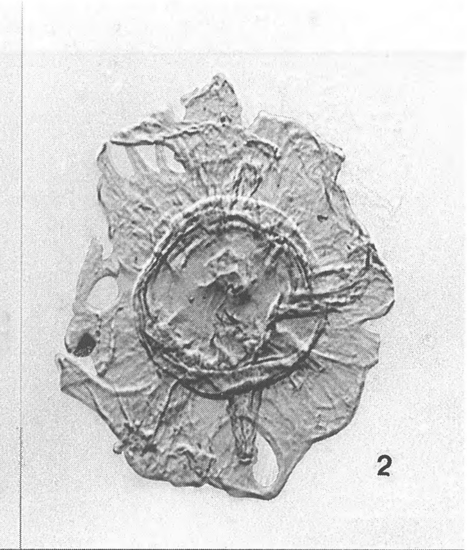
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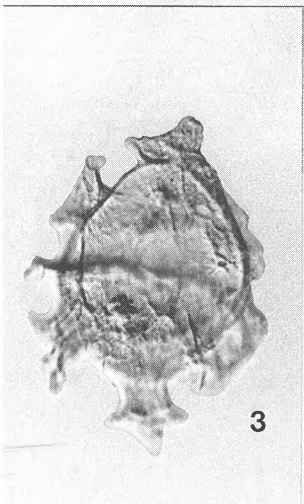
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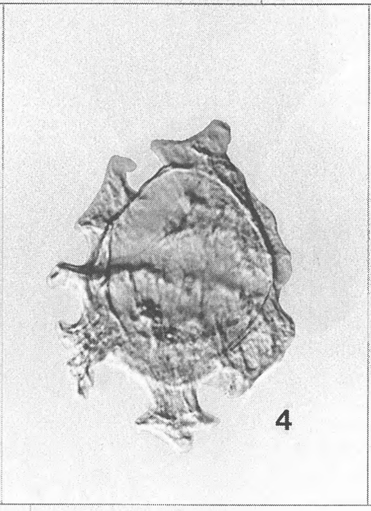
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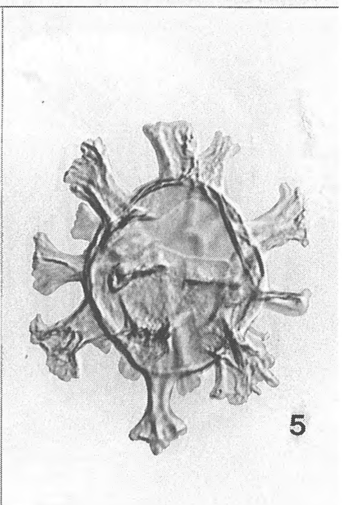
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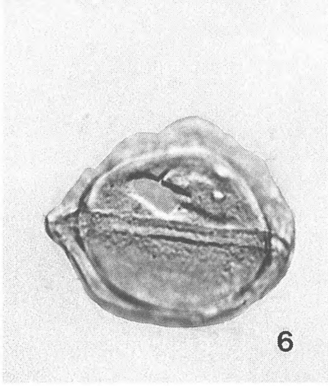
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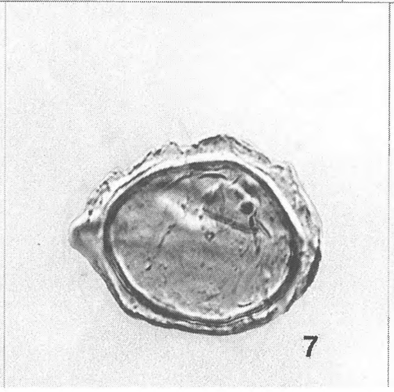
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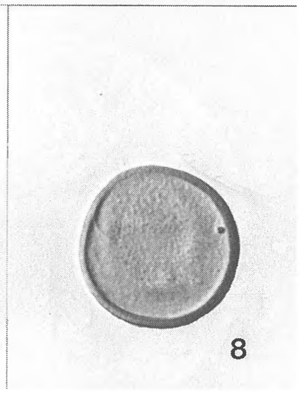
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Plate 3. Dinoflagellate cysts (Figures 1–5), acritarchs (Figures 6, 7) and bryophyte spores (Figure 8), Geulhemmerberg. All magnifications 250 × except Figure 8; England Finder coordinates provided. Figure 1. *Thalassiphora bononiensis* Corradini, 1973; sample/slide E1/02, V32. Figure 2. *Thalassiphora patula* (Williams and Downie) Stover and Evitt, 1978; sample/slide A/01, K39/2. Figures 3, 4. *Turbiosphaera* sp. A; sample/slide A/03, R31/1. Figure 5. *Cordosphaeridium fibrospinosum* Davey and Williams, 1966b; sample/slide A/03, R45/1. Figures 6, 7. *Paralecaniella indentata* (Deflandre and Cookson) Cookson and Eisenack, 1970; sample/slide G4B/01, P40/3. Figure 8. Spherical, smooth bryophyte spore; × 400; sample/slide A/01, H42.

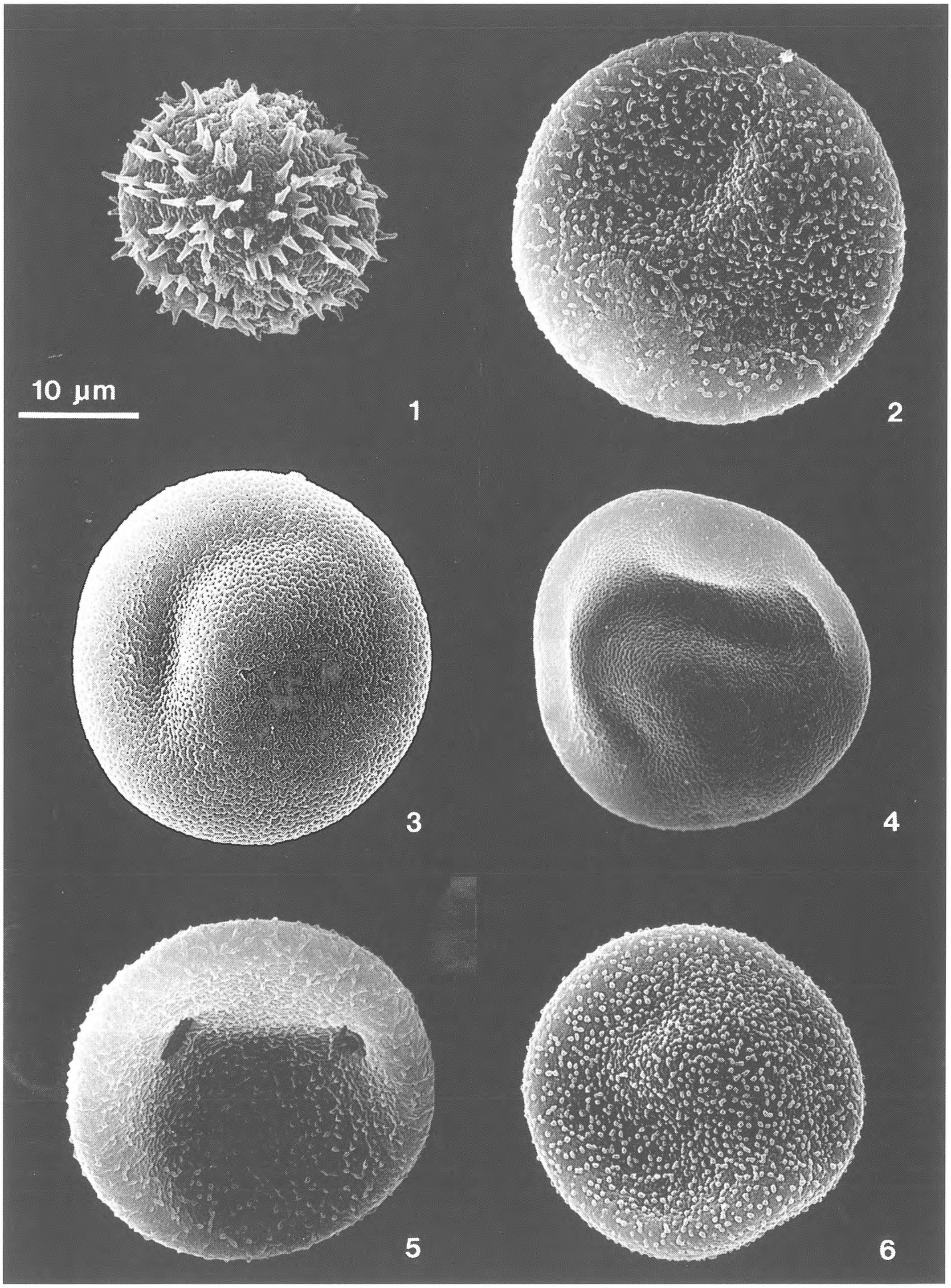

Plate 4. Bryophyte spores, Geulhemmerberg. SEM-photography. Figure 1. Spherical spiny bryophyte spore, gen. and sp. indet.; sample E5. Figures 2–6. Spherical, smooth or ornamented bryophyte spores, gen. and sp. indet.; sample E5.

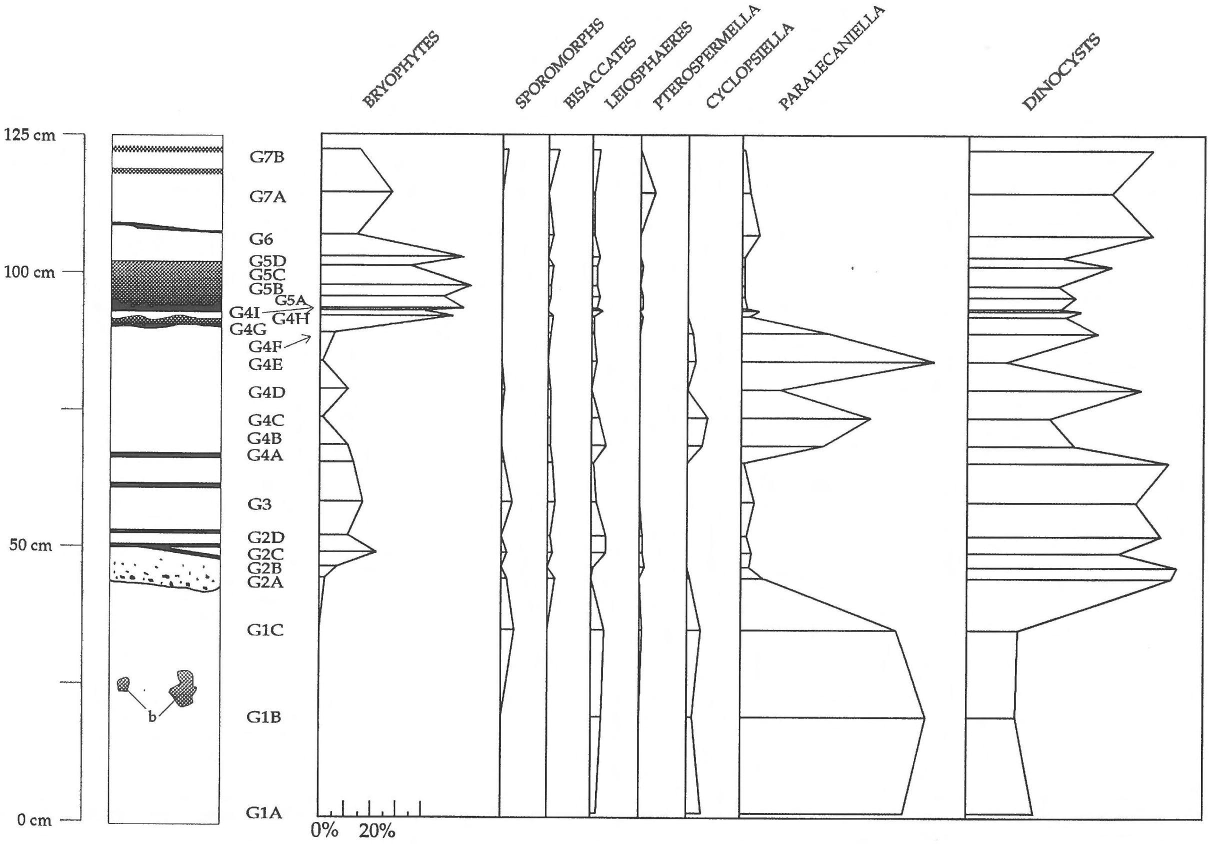

Figure 2. Relative quantitative distribution of palynomorph categories in the Geulhemmerberg main section.

dinoflagellate cysts, while *Paralecaniella* spp. dominate assemblages in the calcarenitic parts of the section (Figure 2). This is confirmed by the detailed study of the clay layers A, D and E. Relative percentages of the various groups of palynomorphs remain virtually identical throughout these layers. Only in the lowermost clay, bryophyte spores are less abundant; the sample is dominated by dinoflagellate cysts (Figure 3).

The absolute concentrations of selected groups of palynormorphs in the main section are plotted in Figure 4. As may be expected, concentrations are highest at and near the clay layers, and may go up to approx. 20 000 palynomorphs/g. The calcarenitic layers do not contain significant amounts of palynomorphs. Importantly, although on a relative basis *Paralecaniella* spp. dominate in this layers, it becomes clear from Figure 4 that their absolute abundance is relatively low, and remains more or less constant throughout the section. Hence, their proliferation at some horizons seems to be due to the absence of other palynomorphs.

Dinoflagellate cysts

The dinoflagellate cyst distribution is tabulated in Table 1 for the main section and in Table 2 for the additional samples from the A, D and E clays.

In general, rich and diverse dinoflagellate cyst associations are recovered from nearly all samples, notably from the clay layers. Typically, however, a few taxa and/or groups of morphologically related taxa consistently make up approx. 80% of the associations. These are 1) *Cribroperidinium* sp. A, 2) *Areoligera* spp., 3) *Glaphyrocysta* spp. (mainly *G. perforata*, but also including the morphologically similar *Senoniasphaera inornata* and *G. pastielsii*), 4) *Hystrichosphaeridium* spp., here combined with the few occurring *Oligosphaeridium* spp., 5) *Disphaerogena carposphaeropsis* and morphologically related forms such as *Cordosphaeridium* spp., and finally 6) the *Spiniferites* complex (mainly consisting of subspecies

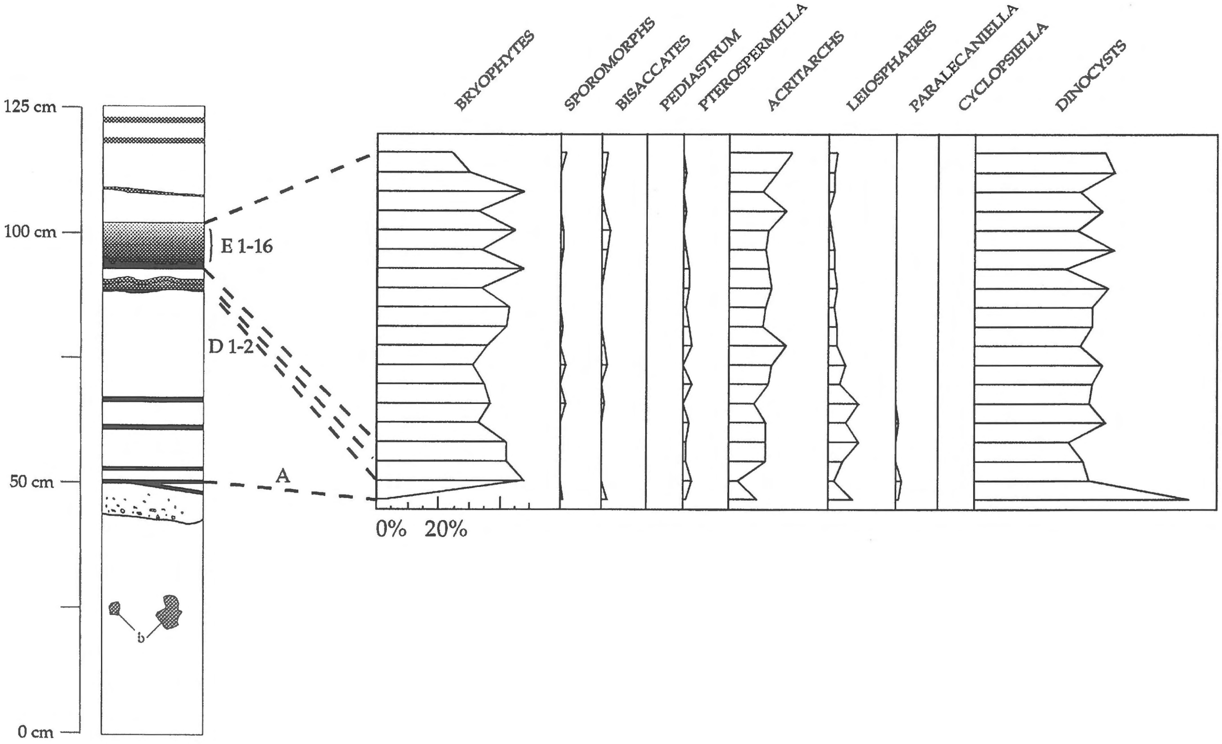

Figure 3. Relative quantitative distribution of palynomorph categories in selected clay layers at the Geulhemmerberg (additional sampling).

of *S. ramosus*), here grouped together with species of the morphologically similar genus *Achomosphaera*.

The relative distributions of these groups are plotted in Figure 5 for the main section, and in Figure 6 for the individual clay layers A, D and E. All other taxa, except for all peridinioid species in Figure 6, have been grouped together in the category 'others' in Figures 5 and 6. In general, representatives of the *Spiniferites* complex dominate the associations, showing an optimum just above the Berg en Terblijt Horizon. In the clay layers, however, their percentages are suppressed, and the other groups are more abundant, notably *Cribroperidinium* sp. A (Figures 5, 6). It may be noted that cysts presumably derived from heterotrophic dinoflagellates, viz. the peridinioids, are rare or absent in all samples (Figure 6).

Biostratigraphic analysis

Although detailed information on the stratigraphic distribution of dinoflagellates across the K/T boundary in the Netherlands is not available, comparisons may be made with the data from relatively nearby Denmark. The classic sections across the Fish Clay at e.g. Stevns Klint, Nye Kløv and Dania were investigated by amongst others J.M. Hansen (1977, 1979), Kjellström and J.M. Hansen (1981), Hultberg (1985, 1986), and Damassa (1988). Subsurface sections through the Maastrichtian and Danian in the Danish North Sea Sector were recently reported on by Schiøler and Wilson (1993). All these papers stress the importance of the last occurrence (LO) of *Palynodinium grallator* at the K/T boundary, and the first occurrences (FOs) of *Damassadinium californicum, Senoniasphaera inornata* and *Carpatella cornuta* above the boundary. The uppermost Maastrichtian succession in Denmark is claimed to be characterized by the co-occurrence of *Thalassiphora pelagica* and *Palynodinium grallator* (e.g. J.M. Hansen 1977). According to J.M. Hansen (1977, 1979) and Hultberg (1985, 1986), the upper part of the lower Danian may be characterized by the successive FOs of several *Xenicodinium* or *Tectatodinium* species (see also Powell 1992). Notably the FO of *Damassadinium californicum* is of global significance for the recognition of the K/T bound-

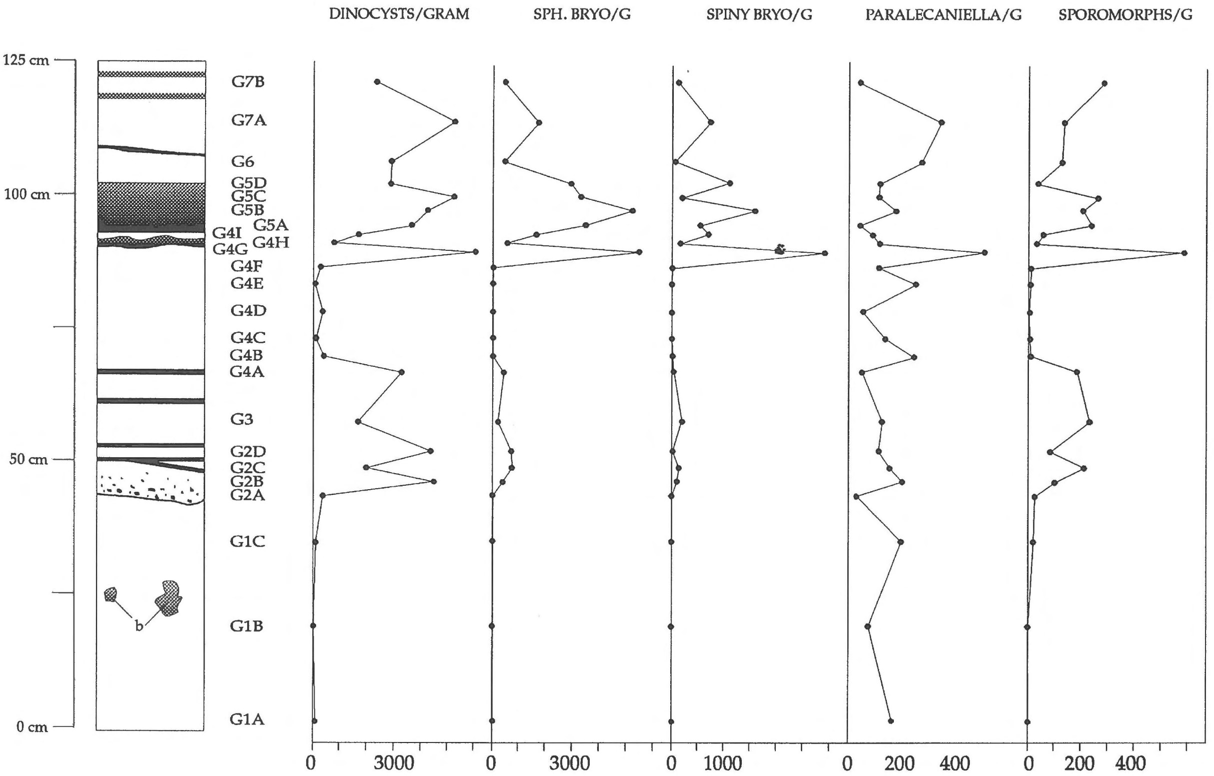

Figure 4. Concentration of selected palynomorph categories per gram in the Geulhemmerberg main section; SPH.BRYO = spherical bryophyte spores; SPINY BRYO = Spiny bryophyte spores.

ary, as has been shown in Tunisia (Brinkhuis and Zachariasse 1988) and the USA (Habib et al. 1992; Moshkovitz and Habib 1993). This FO is calibrated against the basal part of the lowermost Danian calcareous nannoplankton NP1 (Martini 1971) and planktonic foraminifer P0 zones (Smit 1982). The FO of *Carpatella cornuta* is also widely used to separate the Danian from the Maastrichtian (Damassa 1988; Habib et al. 1992). Moshkovitz and Habib (1993) recently introduced another typical Danian dinoflagellate cyst, *Lanternosphaeridium reinhardtii*. It was described from Alabama and Georgia (USA), its FO calibrated against the lowermost Danian calcareous nannofossil NP1 Zone and the planktonic foraminifer Pα Zone (see also Habib 1994). In addition, *Disphaerogena carposphaeropsis* first appears in the uppermost Maastrichtian, possibly even above the FO of *Thalassiphora pelagica* (Benson 1976; Brinkhuis and Zachariasse 1988; Moshkovitz and Habib 1993; Habib 1994). The morphologically similar *Thalassiphora patula* has never been recorded as deep stratigraphically as in the present study. Its FO may thus be of importance for the characterization of the uppermost Maastrichtian (Tables 1, 2).

In his pioneering paper on dinoflagellate cysts from the K/T boundary sections in Denmark, including the Stevns Klint section, J.M. Hansen (1977) claims a simultaneous incoming of Tertiary species at the K/T boundary, viz. the FOs of *Senoniasphaera inornata, Damassadinium californicum* and *Carpatella cornuta*. However, in a later paper on Stevns Klint by H.J. Hansen et al. (1986), it appears that the FOs of *Carpatella cornuta* and *Senoniasphaera inornata* are recorded some 2–3 cm above the K/T boundary, while *Damassadinium californicum* is not recorded in the boundary clay at all at this site (cf. Hultberg 1985, 1986). Moreover, recent work of Habib (1994) on sections from Alabama suggests that only the FO of *Senoniasphaera inornata* more or less coincides with the boundary, calibrated against planktonic foraminifer Zone P0. According to Habib (1994), the FOs of *Damassadinium californicum* and *Carpatella cornuta*

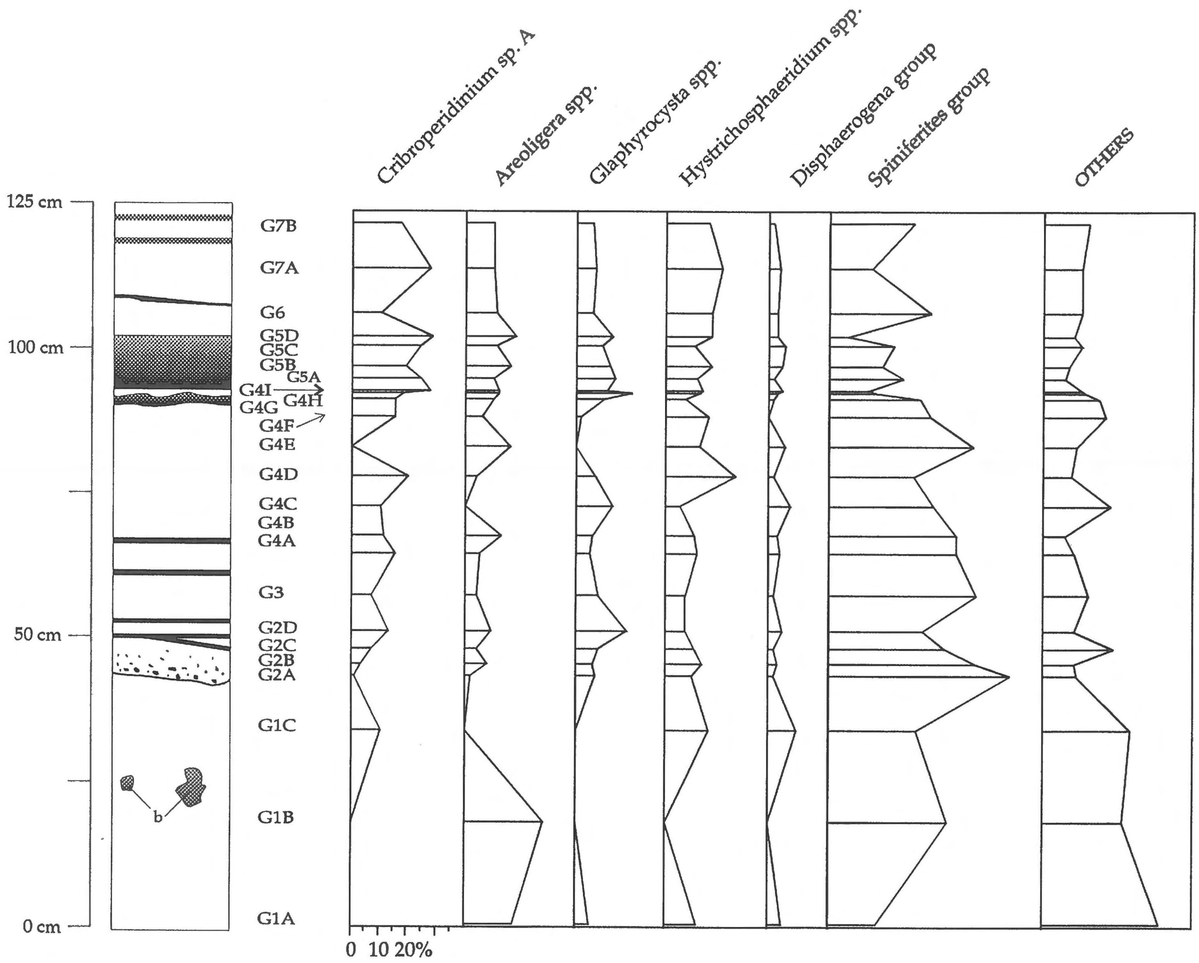

Figure 5. Distribution of the quantitatively most important dinoflagellate cyst taxa and groups of morphologically closely related taxa in the Geulhemmerberg main section.

occur slightly higher, in planktonic foraminifer Zone Pα. Furthermore, Habib (1994) claims that the LO of *Palynodinium grallator* occurs in the early Danian, at a horizon in the basal part of planktonic foraminifer Zone P1a. Comparison of the evidence from Tunisia (Brinkhuis and Zachariasse 1988) and Alabama (Habib 1994) indicates that *Damassadinium californicum*, and possibly also *Carpatella cornuta* (recorded as '*Kenleyia nuda*' in Tunisia), might have migrated into higher latitudes during the earliest Danian, their FOs being diachronous along a low- to high-latitude transect.

Most of the above mentioned taxa, viz. *Palynodinium grallator, Senoniasphaera inornata, Thalassiphora pelagica, Disphaerogena carposphaeropsis* and *Lanternosphaeridium reinhardtii*, have been recorded from one or more Geulhemmerberg samples (Tables 1, 2). Conspicuously, *Damassadinium californicum* and *Carpatella cornuta* have not been identified. However, some of the specimens assigned to *Cribroperidinium* sp. A develop relatively thick, 'spongy' walls, notably in samples from the E clay, and are difficult to separate from *Carpatella cornuta*. The development of a clear antapical protrusion in these specimens, the definitive identification criterion to separate *Cribroperidinium* species from *Carpatella cornuta* (Damassa 1988), was not observed.

When analysing the distribution pattern of the stratigraphically important taxa, it may be noted that 1) *Thalassiphora pelagica, Palynodinium grallator, Disphaerogena carposphaeropsis*, and *Thalassipho-*

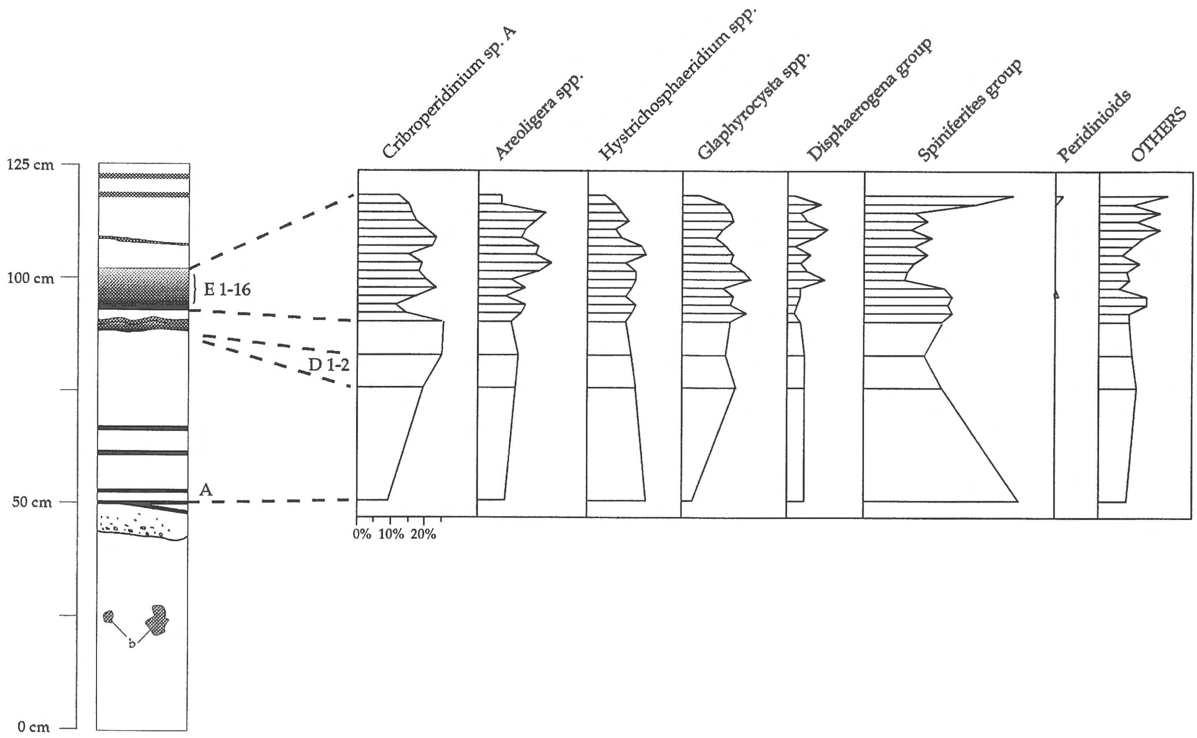

Figure 6. Distribution of the quantitatively most important dinoflagellate cyst taxa and groups of morphologically closely related taxa in the selected clay layers at the Geulhemmerberg.

ra patula co-occur in the lowest sample, 2) *Palynodinium grallator* ranges, albeit scattered, throughout the entire sequence, 3) *Senoniasphaera inornata* first appears in the lowermost clay layer (A clay), and that 4) *Lanternosphaeridium reinhardtii* first occurs in the E clay, where it is very rare. The relatively young occurrences of *Palynodinium grallator* may be explained by reworking, since quite a large number of typical Late Cretaceous species have similar scattered records throughout the section, e.g. *Palaeohystrichophora infusorioides, Dinogymnium* spp., *Gillinia hymenophora* and *Surculosphaeridium longifurcatum*. On the other hand, it may represent its final demise during earliest Tertiary times (cf. Habib 1994). Figure 7 provides a summary of important palynostratigraphic events.

In conclusion, it may be suggested that 1) the lowermost part of the Geulhemmerberg K/T boundary section represents (part of) the latest Maastrichtian, and that 2) an early Danian, but not necessarily earliest Danian, age may be assigned to sediments from the Berg en Terblijt Horizon upwards, based on the FO of *Senoniasphaera inornata*. The FO of *Lanternosphaeridium reinhardtii* may indicate that the succession from the E clay upwards may possibly be assigned to planktonic foraminifer Zone Pα, or younger. This age assessment markedly contrasts with results of the calcareous nannoplankton investigation (Romein et al., this issue), but may be reconciled with the planktonic foraminifer distribution described by Smit and Zachariasse (this issue), although the latter authors do not record evidence for the presence of the P1a or Pα zones. The absence of the classic diagnostic basal Tertiary dinoflagellate cysts like *Damassadinium californicum* and *Carpatella cornuta* may be due to 1) the succession being slightly older than their FO horizon, 2) their possible 'delayed' appearance at higher latitudes, 3) unfavourable environmental conditions, and/or 4) their extreme scarcity in the basal Danian of the Geulhemmerberg.

Palaeoenvironmental interpretation

As mentioned above, the relative distribution pattern of the broad categories of palynomorphs and their

Table 1. Distribution chart of dinoflagellate cysts in the Geulhemmerberg main section; asterisks indicate presence outside count.

SAMPLES TAXA	G1A	G1B	G1C	G2A	G2B	G2C	G2D	G3	G4A	G4B	G4C	G4D	G4E	G4F	G4G	G4H	G4I	G5A	G5B	G5C	G5D	G6	G7A	G7B
Xenikoon sp. A F.&R. 1977	3			1		2				1		1	1											
D. acuminatum	1			2		1				1			1		2									
P. lidiae	1					1			*						1					1				
C. fibrospinosum	1			*	2	1	1	1	3	1	1				5	1	4		1	3	1	2	3	
C. saeptum	1	1	2	2	2	1		4	1	1		1	1	1	4	1	7	1	2	1	5	5	10	
T. patula	*			*			1	2	1				1		1			1	1	*	2		1	
C. velatum	1		2	2			3		2			1					1		1	2	5	5	5	
H. tubiferum tubiferum	2		3	11	20	21	17	18	52	8	2	35	4	7	26	12	26	29	19	16	28	61	72	27
L. globosa	1					36	6	10			6	3		3	1							3		9
P. grallator	*	*	*																			1		1
A. senonensis	3	2		2	12	14	19	8	17	7		4	4	3	24	8	19	22	16	15	17	25	22	8
S. ramosus	3	3	6	85	109	132	99	153	227	43	13	51	16	16	120	17	35	70	26	45	15	151	62	55
D. carposphaeropsis	1		1	1	3	4	8	1	13	1	2	2	1		2	1	5	3	3	4	6	3	7	1
G. perforata	1			10	13	27	57	26	26	6	5	13		1	41	20	27	41	17	17	26	29	30	12
L. rhombiforme		1				1																		
C. fimbriata		1		1	*	1	5	1	2			6			1	1	1	1	1	1	1	4	4	2
G. pastielsii		1			1	1		1	1	1	1		1		1	1	1	1	1	1	1	1	1	1
C. striolata		1		1	2	1	1	1		1					1	2	1	1	1	1		1	1	1
N. perforatum		1			3	1	1		5						1	2	4	1	2	1	4		3	1
C. intermedia			1			1	1		5						*		1				1			
F. ovalis			1	1		*	2	1	1	1							2	1		1	*	1	1	
A. coronata			1	1	1	1	1	1		1			1				1	1	1				1	
F. axialis			1	1	1	1		1	1		1	2	1			2		1		2		2	1	
P. silicorum			1	2	2	9	4	2	2				1		6	1	1					1		1
C. speciosum			*	1	1	1	1				1	1	1	1	7				1			1		4
Indet. skolochorates			1	1	8	25	7	16	28	3	1			1	25	7	10	15	3	11	5	23	15	7
Cribroperidinium sp. A			2	2	8	25	42	23	79	11	4	35		7	61	18	66	68	28	47	54	45	109	32
S. delitiense				1																				
A. biannii				2	1													1						
P. cayeuxii				1																1		2	1	
A. buccinum				1	2	1	1	4	1	1	1	1	*	2	4	1	1	3	*	2	1	4	2	1
H. arborispinum Marh. 1992				1	8	11	4	1	3	2		6	1				1	1	3	3		4	8	1
E. bifidum				1	2	1	1	2	2		*	1			1		*	1		2		2	2	1
H. borisii					1	1																		
F. aculeata					1												1							
H. coninckii					1		1											1						
A. volata					6	2	12	6	12	6		3	1		16	4	10	8	7	7	18	25	18	11
H. bulbosa					1		2										2		*		1	1		1
O. pulcherrimum					*	1	1	1	4	1			1		1		1			1				1
Tanyosphaeridium spp.					4		2	1	1	1		1	1		1		1	2	1	1		1	4	1

absolute concentration (Figures 2, 3) closely match the lithological development. The calcarenitic units, characterized by relatively poor assemblages dominated by *Paralecaniella* spp., can clearly be separated from the more argillaceous layers, which are dominated by bryophyte spores and/or dinoflagellate cysts.

Terrestrial components

Although the studied interval is evidently entirely marine in origin, the marked abundance of terrestrial palynomorphs in the clay-rich layers confirms an important continental input. These palynomorphs are thought to be almost all derived from bryophytes. Pollen and spores derived from vascular landplants only play a minor role. Since 1) the bryophyte spores

Table 1. Continued.

SAMPLES TAXA	G1A	G1B	G1C	G2A	G2B	G2C	G2D	G3	G4A	G4B	G4C	G4D	G4E	G4F	G4G	G4H	G4I	G5A	G5B	G5C	G5D	G6	G7A	G7B
A. ramulifera					2	2	5		1		1	2												1
T. bononiensis						1																		
S. terminus						2									4			3						
H. duplum						3	1	2	2			2	*		2	*		1	*		1	2	1	
C. aceras						2			1						2		1		1	1	1		1	
F. ferox						*						1			1		1						1	2
Impletosphaeridium spp.						1				*						1	1			1				1
G. hymenophora						1		4		1		2		1	4		1	1			1			1
Turbiosphaera sp. A						1	6		1						2		3	2	4			3	1	2
C. inodes						1																1	1	1
C. oceanica							1																	
K. truncatum							1	1																
S. longifurcatum							1														*	3	1	
M. polycladiata							3	1	1			2		1	1		1	2	1	2		1	2	
C. armatum							1			1					1		1	1	1	1	1		1	
Dinogymnium spp. undiff.								1																
F. mantellii								1	1						5				2	2				
I. rigidaseptatum									*						1		2	1						
P. australinum									*						1					1		1		
A. wilsonii									1						1					1		2	7	
O. complex										1							1							
H. tub. brevispinosum												1					2	1			1	3		1
R. fucatum													1											
M. ornatum													1											
Trigonopyxidia spp.															1									
P. golzowense															1					1				
P. infusorioides															5		1					2		
A. circumtabulata															1		1					1	1	
S. inornata																1								
S. ramosus ssp. A																1								
P. cingulatum																1								
A. cf. reticulata																		1						
H. membraniphorum																		1						
C. tocherii																					1			
L. reinhardtii																					*			
H. ovum																						1		
C. discreta																						1		
R. borussica																						1		1
F. annetorpense																							1	

are particularly well preserved, and, perhaps more importantly, 2) the recorded abundance of bryophyte spores in a marine succession is unparallelled in palynological literature, we suggest that the site was close to land. Moreover, we suggest that sedimentation rates were relatively high, and/or bottom conditions were anoxic, resulting in optimal preservation.

The interpretation of the 'sudden' proliferation of elements assignable to Bryophyta is problematic, as it is a poorly studied category of palynomorphs. As suggested above, the encountered elements may be related to certain species of extant Pottiaceae (Bryophyta). It may also be noted that identical palynomorphs occur scattered throughout marine Maastrichtian and Danian successions, e.g. in other sections in the Netherlands, and in Denmark and the USA (H. Brinkhuis, unpublished data), albeit possibly only from higher-latitude-sites, and never in abundance. This indicates at least that they are already present in terrestrial ecosystems during the latest Cretaceous. Furthermore, they may very well reflect coastal vegetation, as was suggested above on the basis of the ecology of some

Table 2. Distribution chart of dinoflagellate cysts in selected clay layers at the Geulhemmerberg; asterisks indicate presence outside count.

TAXA \ SAMPLES	A	D-2	D-1	E-16	E-15	E-14	E-13	E-12	E-11	E-10	E-9	E-8	E-7	E-6	E-5	E-4	E-3	E-2	E-1
A. antleriformis	*																		
C. discreta	*																		
Dinogymnium spp. (undiff.)	*																		
P. maastrichtiense	*																		
Xenikoon sp. F & R 1977	*																		
Impletosphaeridium spp.	*	1																	
D. pseudocolligerum	3	*																	
R. borussica	*	*																	
R. veligera	*	*																	
D. pastielsii	*	*																	
H. tenuitubatum	*		1																
Diconodinium spp. (undiff.)	*		1																
S. membranaceus	1			*															
F. aculeata	*	*		*															
C. inodes	*	*	*	*	*														
Diphyes spp. (undiff.)	*				*														
A. coronata	3	4	3	*		*													
R. granulata	*	1				*													
D. acuminatum	*		*		*	*													
P. infusorioides	*		*		1	1													
H. membraniphorum	*					*													
P. golzowense	*	*	*				1												
H. salpingophorum	*		*				1												
H. proprium proprium	*	*	*					*											
T. pelagica	1	*				*	*	*	*										
O.complex	*		*	*					*										
P. silicorum	1	1	3	1	*	2				1									
A. ramulifera	*	1	*			*		*					*						
L. globosa	*	*													*				
H. coninckii	*	*	*			*	*						*		*				
C. fimbriata	*	1	*			*		1	*	1	*	3	*	2	*				
S. inornata	*	*	*	*		*		*		1			*	*			*		
Alterbidinium spp. (undiff.)	*	*													1		1		
S. longifurcatum	*	*	1		*	*					*	*	*	1				*	
C. striolata	*	*	1	1	*	*	*	*	*	3	1	*	*	*	3	3	3	1	
C. armatum	*	3	2	1	1	2	2		1				*					1	
Tanyosphaeridium spp. (undiff.)	*	*	*	1	1	3	1	*	*		*		1		1		1	*	
A. biannii	1	*	*	*	*	1	1	*	*	*		*	*	*	*	1	*	*	
C. speciosum	*	*	*		1	*	1			1								*	4
H. duplum	*	*	*	1	1	*	*	1	1	1	2	2	1	*	*		1	*	*
C. intermedia	1	*	*	*	1	*	*	1	2	*	*	*	*	*	*	*	2	*	*
H. proprium brevispinosum	*	1	*	*	*		*	*		*	*	*	*	*			*	*	1
C. velatum	*	1	*	*	3	*				*	1	*						*	1
Cribroperidinium sp. A	13	23	35	36	25	25	36	38	28	27	29	36	31	46	25	23	28	22	17
C. aceras	*	*	*								*	1	*	2	1	*	*	1	*
H. tubiferum tubiferum	12	16	15	13	20	33	18	19	15	18	13	32	19	13	4	13	14	11	5
D. carposphaeropsis Cpx	*	2	4	7	1	2	3	3	6	6	2	8	2	9	9	1	3	2	*
Skolochorates Indet.	3	*	2	1	*	105	111	2	3	2	5	5	4	6	7	5	4	*	1
A. buccinum	2	3	*	3	1			2	*	1	4		2	*	1	1	1	*	2
M. polycladiata	*	2	*	1	*	2	5	2	4	2	4	3	*	7	*	1	2	1	9
I. rigidaspetatum	*	*	*	*	*	*	*	*	*	*	*	2	1	*	*		*	*	*
N. perforatum	*	*	2	1	3	2	*	*	*	1	*	2	1	2	2	1	6	2	1

living representatives of the Pottiaceae. This would explain their optimal preservation in marine successions. Their possible preference for limestone and/or clay substrates may also play a key role in their spatial distribution. Their abundance at Geulhemmerberg may thus be related to the abundance of clays on the coastal plains directly following the K/T event(s) and to the fact that these clays were transported into the marginal marine environment from coastal settings. The 'bryophyte event' may hence be associated merely with the enhanced terrigenous input into the sea following the K/T crisis. In this sense, the event as recorded at the marginal marine Geulhemmerberg site may also be related to a short-term drop in sea-level, either associated with the K/T event(s), or occurring directly afterwards.

Table 2. Continued.

SAMPLES TAXA	A	D-2	D-1	E-16	E-15	E-14	E-13	E-12	E-11	E-10	E-9	E-8	E-7	E-6	E-5	E-4	E-3	E-2	E-1
A. senonensis	8	11	8	10	15	26	12	17	11	15	23	19	10	15	10	12	21	4	3
O. pulcherrimum	1	1	*	1		*	1	*		2	*	1	1	1		1	1	*	*
Operculodinium spp. (undiff.)	*	1	1	*	*	*	*	*	2	*	2	2	3	3	2	1	5	4	5
C. fibrospinosum	2	2	*	*	1	1	3	3	1	*	2	2		1	*			2	*
P. grallator	*	*	1			*					*								*
A. volata	*	*	5	5	9	7	4	6		11	7	18	12	8	6	8	12	5	6
P. lidiae	*	*	*			1	2		*									*	*
A. deflandrei	*	*		*	*	*		*	*	1	1	*			1			*	*
E. bifidum	3	2	*	*	1	*	1	*	2	1	*	2	1	1	1	1		*	1
C. saeptum	*	3	1	*		*	2	3	*	*	*	2	2	3	1	1	3	1	2
F. axialis	1	*	*	*	1	1	*	*	1	*	*	1	*	1	2	1	1	1	*
F. ferox	*	*	*	*		*			1								1		1
F. mantellii	*	*	*	*															1
F. ovalis	1	*	*	*		1	*	*	1	*	*	1	*		*	1	*	*	*
Fibrocysta sp. A	*	*	*	*	*	*	1	*	2	1	2	1	*	*	*	*	1	*	*
S. multibrevis	1	*	*	1	1	*	*	*	*	*	*	1	*	1	*	*		*	4
S. ramosus gracilis	1	9	3	2	1	*	1	4	*	*	*	2	*	2	*	*	*	*	5
S. ramosus granosus	165	1	1	1	1		1	1	*	*	*	1	*	1	*	*		*	1
S. ramosus ramosus	41	20	20	13	27	31	35	25	14	19	19	34	15	29	15	25	22	42	50
S. terminus	*	*	1		1	1	1						1	*	1	*		*	1
T. bononiensis	*		*																*
T. filosa	*	*	*	*	1	4	*	1	2	*		1	1	4	3	4	2	8	1
T. magdalium	*	*	*	1	1	2	2	*	*	1	*		1	*	1	1	1	*	1
T. patula	*	1	3	*	*	*	1	*	*	2	*	1	*	*		*	*	1	*
G. perforata	5	22	19	21	34	33	31	20	28	26	21	37	19	20	15	20	25	18	7
H. arborispinum	11	1	3	1	2	1	2	2	3	*	2	5	1	7	6	3	2	1	1
H. bulbosa	*		*		*	*	1	*	1	1		1			*		*	*	*
Senegalinium spp. (undiff.)		*																	
X. ceratoides		*																	
Batiacasphaera spp. (undiff.)		*		*		*	*												
D. fibrosa		*	*					*	*										
G. hymenophora		*				2												*	1
A. circumtabulata		*	*	*	1	*							*	*					*
H. pulchrum			1																
P. cayeuxii			*		1	*												1	
Acanthaulax spp. (undiff.)				1		1	1												
P. sonciniae				1	1	*	1				1								
G. pastielsii				*		1	1	1	4	2	3	4	3	4	2	3	3	2	2
S. ramosus ssp. A				15	14	25	16	9	3	1	4	6	4	6	2	*	4	5	*
C. edwardsii						*													
L. reinhardtii						*	*						*		*			*	
A. wilsonii							*	*										1	
O. operculata								*				*			*				
Polysphaeridium spp. (undiff.)									*										1
A. cf. reticulata												1		*	*		*		
Turbiosphaera sp. A																		*	
Impagidinium spp. (undiff.)																		1	
Manumiella spp. (undiff.)																		1	

Alternatively, however, the sudden abundance of bryophyte spores may be related directly to the K/T event(s) itself. The bryophyte event may reflect a major change in the terrestrial ecosystem. Present-day Bryophyta are well-known for their pioneering character. They are the first to colonize environments where most higher landplants fail, and they are the first to rapidly occupy areas where vegetation was destroyed. In addition, their proliferation may reflect severe climatic perturbations. In effect, the Geulhemmerberg succession may provide the first evidence for significant continental environmental change related to the K/T event(s) in NW Europe. The phenomenon may be tentatively compared with the well-known 'fern-spike' event reported from several continental K/T successions in North America (e.g., Nichols et al. 1992).

In any case, since the bryophyte spores first occur in relatively large numbers above the Berg en Terblijt Horizon, it may be suggested to position the K/T boundary at this hardground, in line with the dinoflagellate evidence.

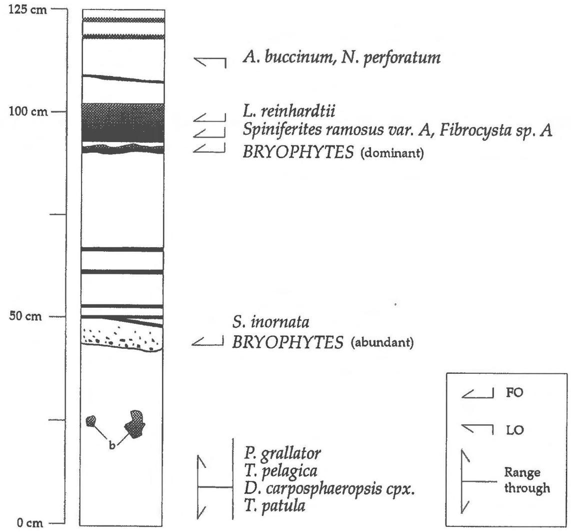

Figure 7. Summary of important palynostratigraphic events across the K/T boundary at the Geulhemmerberg. FO = first occurrence, LO = last occurrence.

Aquatic components

Several groups of algae have been recorded in the samples (Figure 2). The most important categories appear to be representatives of the acritarch genus *Paralecaniella* and dinoflagellate cysts. *Paralecaniella* spp. have been reported from Upper Cretaceous and Tertiary successions world-wide. Their palaeoenvironmental significance is as yet poorly understood. Elsik (1977) considered them to represent either schizosporous algae or acritarchs and mentioned that they were most abundant in marginal marine successions, indicating a tolerance for inner neritic, possibly brackish conditions.

Although several fresh-water dinoflagellate cysts have been described from Upper Cretaceous and Tertiary deposits, none of these species have been recorded at the Geulhemmerberg. It is therefore suggested that the encountered dinoflagellate cysts are all of marine origin. However, taxa typically representing relatively offshore and/or oceanic conditions, like *Impagidinium* spp. and *Nematosphaeropsis* spp. (Wall et al. 1977, papers in Head and Wrenn 1992) occur only in trace amounts, and could be reworked. The most abundant taxa and/or groups of morphologically related taxa recorded from the Geulhemmerberg succession (Tables 1–2) are usually found in similar abundances in relatively marginal marine successions throughout the Mesozoic and Cenozoic (Downie et al. 1971; Hultberg and Malmgren 1986; Brinkhuis and Zachariasse 1988; Brinkhuis 1994). Of these groups, only representatives of the *Spiniferites* complex still occur today. They typically occur in outer neritic waters (Wall et al. 1977, papers in Head and Wrenn 1992).

The depositional environment

The relative abundance of *Paralecaniella* spp. in the assemblages associated with calcarenitic, coarse-grained intervals, may indicate a marginal marine to restricted marine influence, or may reflect increased transport from such settings. The clay-rich intervals, contain rich and well-diversified dinoflagellate cyst associations, and may be regarded to reflect open marine, neritic conditions. In this way, the alternation of the assemblages may be explained in terms of relative sea-level fluctuations. However, in such a scenario one would expect terrestrial elements, viz. bryophyte spores, to be abundant in the *Paralecaniella*-dominated assemblages and less abundant in the dinoflagellate-dominated assemblages, which contrasts with our findings. Rather, the fact that the alternating assemblages mimic the alternating clay-poor and clay-rich intervals leads us to suggest that the alternations are due to differing hydrodynamic conditions at similar water depths. *Paralecaniella*-dominated assemblages were deposited during hydrodynamically higher energy conditions under which most clay-sized particles remained in suspension, leading to apparently impoverished palynological assemblages. The dinoflagellate-dominated assemblages are the result of hydrodynamically lower energy conditions, when pelagic sedimentation prevailed. The dinoflagellate-dominated assemblages from the coarse-grained unit directly above the Berg en Terblijt Horizon are thought to be derived largely from the displaced clay flakes present in this unit. This unit may hence be regarded to reflect the highest level of hydrodynamic energy preserved in the Geulhemmerberg succession, located directly above a hiatus. This idea supports the suggestions of Roep and Smit, and Zijlstra et al. (both this issue); they interpret the sedimentology in terms of varying hydrodynamic energy due to varying storm activity and intensity.

Nevertheless, the relative optima of the *Spiniferites* group in the essentially marginal marine, probably inner neritic assemblages of the Geulhemmerberg may reflect intervals with the most significant open marine influence. Such optima are located just above the Berg en Terblijt Horizon, in sample G2A, and near the top of the E clay (Figure 7). The higher relative abundance of the *Spiniferites* group in sample G2A supports considerations claiming that this hardground may represent a relative transgression following a short-term sea-level fall. The subsequent *Spiniferites* optimum associated with the E clay may reflect a subsequent relative sea-level high. If linked to sea-level fluctuations, these must have been of higher order than the 'third-order' cycles of Haq et al. (1988) as all the deposits above the final Maastrichtian Berg en Terblijt hardground in the cave are placed in the early Danian, corresponding to part of the planktonic foraminifer P0 Zone, thought to represent only some 20–30 Ka (Smit and Zachariasse, Smit and Brinkhuis, both this issue).

In summary, the evidence suggests that the Geulhemmerberg succession represents relatively marginal marine, probably inner neritic conditions, with nearby landmasses providing an important terrestrial input. The differing compositions of the palyno-assemblages are clearly linked to the type of sediment, calcarenite or clay, from which the samples were taken. This is thought to be related to differing hydrodynamical conditions, possibly combined with slightly varying waterdepths, increased transport of remobilized land-derived material and/or the introduction of restricted marine conditions (cf. Roep and Smit, this issue). The quantitative distribution of the main dinoflagellate groups does not change dramatically throughout the succession, indicating that the general depositional setting did not change significantly. However, high relative abundances of representatives of *Spiniferites* appear to indicate intervals of maximum open marine influence.

Conclusions

The K/T succession in the Geulhemmerberg caves generally contains rich and well-preserved palynological assemblages. On the basis of the recorded stratigraphically diagnostic dinoflagellate cysts, it is suggested that the lowermost part of the succession represents the latest Maastrichtian, and that an early Danian age may be assigned to sediments above the Berg en Terblijt Horizon.

The Geulhemmerberg succession probably represents a relatively marginal marine, inner neritic depositional setting, with nearby landmasses providing terrestrial input. The terrestrial palynological elements are interpreted to be almost all derived from Bryophyta. Their sudden proliferation at the K/T boundary may be associated with increased transport from the coastal plain, and/or it may reflect a major change in the terrestrial ecosystem at K/T time.

The main changes in the palynomorph distribution within the succession are related to the sedimentological development; the two main types of sediment, calcarenite and clay, are reflected by two markedly different palynological assemblages. Differing hydrodynamical conditions, possibly combined with slightly varying water depths, increased transport of remobilized land-derived material and/or the introduction of restricted marine conditions are suggested as underlying depositional mechanisms.

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Appendix

Dinoflagellate taxonomy

Characteristic dinoflagellate cysts from the Maastrichtian and Danian of the Geulhemmerberg are illustrated on Plates 1–3. An alphabetic list of all recorded taxa is provided below. Species which are considered reworked are indicated with (R), those possibly reworked with (R?). Previously undescribed taxa and grouped taxa are briefly treated under 'Taxonomic remarks'. Most taxonomic citations may be found in Lentin and Williams (1993). Citations for described species not included in, or not accepted by Lentin and Williams (1993) are referenced below. The material is stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands.

List of taxa

Acanthaulax spp. (pars.) (R)
Acathaulax wilsonii (R)
Achilleodinium bianii
Achomosphaera antleriformis (R?) Schiøler, 1993
Achomosphaera ramulifera
Adnatosphaeridium buccinum, Plate 1, Figure 1
Alisocysta circumtabulata
Alisocysta sp. cf. *A. reticulata*, Plate 1, Figures 2, 3
Alterbidinium spp. (R?)
Apteodinium deflandrei (R)
Areoligera coronata
Areoligera senonensis, Plate 1, Figure 4
Areoligera volata
Batiacasphaera spp.
Caligodinium aceras
Cassiculosphaeridia? tocheri Schiøler, 1993 (R?)
Cassiculosphaeridia intermedia Slimani, 1994
Cerodinium speciosum
Chlamydophorella discreta (R?)
Cladopyxidium saeptum
'Cladopyxidium velatum' sensu Marheinecke, 1992
Cleistosphaeridium armatum (R? in post-K/T samples)
Conneximura fimbriata
Cordosphaeridium fibrospinosum, Plate 3, Figure 5
Cordosphaeridium inodes
Coronifera striolata
Cribroperidinium edwardsii (R)
Cribroperidinium sp. A, Plate 1, Figures 5, 6
Damassadinium fibrosum (Hultberg) Fensome et al., 1993
Dapsilidinium pastielsii
Dapsilidinium pseudocolligerum
Diconodinium spp. (R?)
Dinogymnium acuminatum (R in post-K/T samples)
Dinogyminium spp. (R in post-K/T samples)
Diphyes spp.
Disphaerogena carposphaeropsis complex, Plate 1, Figure 7
Exochosphaeridium bifidum
Fibradinium annetorpense
Fibrocysta axialis
Fibrocysta ovalis
Fibrocysta sp. A, Plate 1, Figure 8
Florentinia aculeata
Florentinia ferox
Florentinia mantellii
Gillinia hymenophora (R)
Glaphyrocysta perforata, Plate 2, Figure 1
Glaphyrocysta pastielsii
Hystrichodinium pulchrum (R)
Hystrichokolpoma bulbosa
Hystrichosphaeridium arborispinum sensu Marheinecke, 1992
Hystrichosphaeridium duplum
'Hystrichosphaeridium proprium brevispinosum' sensu Marheinecke, 1992
'Hystrichosphaeridium proprium proprium' sensu Marheinecke, 1992
Hystrichosphaeridium salpingophorum
'Hystrichosphaeridium tenuitubatum' sensu Marheinecke, 1992
Hystrichosphaeridium tubiferum tubiferum
Hystrichosphaeropsis borisii Schiøler, 1993 (R?)
Hystrichosphaeropsis ovum (R)
Hystrichostrogylon coninckii
Hystrichostrogylon membraniphorum
Impagidinium spp.
Impagidinium rigidaseptatum Slimani, 1994
Impletosphaeridium spp.
Kleithriasphaeridium truncatum (R?)
Laciniadinium rhombiforme (R?)
Lanternosphaeridium reinhardtii Moshkovitz and Habib, 1993, Plate 2, Figures 2, 3
Lejeunecysta globosa
Manumiella spp.
Membranilarnacia polycladiata
Microdinium ornatum
'Neonorthidium perforatum' sensu Marheinecke, 1992
Odontochitina operculata (R)
Oligosphaeridium complex
Oligosphaeridium pulcherrimum (R?)
Operculodinium spp.
Palaeocystodinium australinum
Palaeocystodinium golzowense
Palaeocystodinium lidiae
Palaeohystrichophora infusorioides (R)
Palaeotetradinium maastrichtiense
Palaeotetradinium silicorum
Palynodinium grallator (R? in post-K/T samples), Plate 2, Figures 4, 5
Phanerodinium cayeuxii
'Phanerodinium sonciniae' sensu Marheinecke, 1992
Phanerodinium veligerum
Polysphaeridium spp.
Pterodinium cingulatum
Raphidodinium fucatum (R)
Rottnestia borussica
Rottnestia granulata
Senegalinium spp.
Senoniasphaera inornata, Plate 2, Figure 6
Spiniferites membranaceus
Spiniferites multibrevis
Spiniferites ramosus gracilis
Spiniferites ramosus granosus
Spiniferites ramosus ramosus
Spiniferites ramosus spp. A, Plate 2, Figure 2
Spiniferites terminus
Spongodinium delitiense
Surculosphaeridium longifurcatum (R)
Tanyosphaeridium spp.
Thalassiphora bononiensis, Plate 3, Figure 1

Thalassiphora inflata
Thalassiphora patula, Plate 3, Figure 2
Thalassiphora pelagica
Trigonopyxidia spp.
Turbiosphaera filosa
Turbiosphaera sp. A, Plate 3, Figures 3, 4
Xenascus ceratioides (R)
Xenikoon sp. A of Foucher and Robaszynski, 1977 (R?)

Taxonomic remarks

Alisocysta sp. cf. *A. reticulata*
Plate 1, Figures 2, 3
Remark: this taxon is similar to *Alisocysta reticulata*, but both the reticulation and the penitabular ridges are only poorly developed. It occurs in the E clay only.

Cribroperidinium sp. A
Plate 1, Figures 5, 6
Remark: this taxon is similar in overall appearance to *Cribroperidinium pyrum, C. wetzelii* and/or *C. giuseppei* in terms of its general shape and short apical horn but it differs by its weakly developed paratabulation, and its thin but spongy or fibrous autophragm. In some specimens the wall is somewhat thicker, approaching that described in *Carpatella cornuta* (Damassa, 1988). In addition, an antapical bulge may occur on some specimens, making it difficult to separate them from *Carpatella cornuta*. However, a clearly defined blunt antapical horn was not observed.

Disphaerogena carposhaeropsis complex
Plate 1, Figure 7
Remark: forms assigned to the *Disphaerogena carposphaeropsis* complex display a large morphological variability. Although the major part of the recorded specimens may be reconciled with the original description of *Disphaerogena carposphaeropsis* (or that of its junior synonym *Cyclapophysis monmouthensis* Benson; see Lentin and Williams, 1993), many specimens display features that suggest transition to forms attributable to any of the genera *Cordosphaeridium, Thalassiphora, Lanternosphaeridium, Turbiosphaera, Carpatella* and even *Danea*. One of the features observed in the complex is the development of distinct apical and antapical horns in samples close to the presumed K/T boundary (Plate 1, Figure 7). The latter feature is characteristic for representatives of *Danea* and *Carpatella*, the basal Tertiary 'markers', and also for *Lanternosphaeridium reinhardtii*. It was chosen herein to apply the definition of the latter six genera rather strictly, and place all the transitional forms within the '*Disphaerogena carposphaeropsis* complex'.

Fibrocysta sp. A
Plate 1, Figure 8
Remark: most specimens assigned to *Fibrocysta* sp. A are similar to *Fibrocysta axialis*, but differ by having only poorly developed, extremely short processes. Since only a few specimens have been recorded, it is suggested that they may represent a variety of *Fibrocysta axialis*, or poorly developed representatives of this species. In overall appearance, however, they also show a great similarity to *Carpatella cornuta*.

Spiniferites ramosus ssp. A
Plate 2, Figure 7
Remark: this subspecies of *Spiniferites ramosus* is characterized by its relatively large size (overall diameter up to 100 μm) and its extremely thin and delicate autophragm.

Turbiosphaera sp. A
Plate 3, Figures 3, 4
Remark: this taxon, provisionally attributed to *Turbiosphaera*, is similar to *Cordosphaeridium fibrospinosum* but differs from this taxon by the irregular outgrowths of the outer wall layers. This phenomenon causes proximal interconnection of the processes, notably in the paracingular area, typical for *Turbiosphaera*.

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