Geologie en Mijnbouw **75:** 215–231, 1996.

Calcareous dinocysts from the Geulhemmerberg K/T boundary section (Limburg, SE Netherlands)

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Received 21 April 1994; accepted in revised form 9 May 1996

Key words: Bonetocardiella, Calciodinellaceae, K/T survivors, sea-level changes

Abstract

Calcareous dinoflagellate cyst (calcdinocyst) associations from the Cretaceous/Tertiary (K/T) boundary section of the Geulhemmerberg comprise 31 morphotypes in total. In addition, two incertae sedis organisms, morphologically related to the genus *Bonetocardiella*, occur. In the uppermost Maastrichtian and lowermost Danian, the quantitatively dominant calcdinocysts are Pithonelloideae, nearly exclusively *Pithonella sphaerica*, accompanied by up to 14% *Bonetocardiella* spp. In the uppermost Maastrichtian, *Pithonella* and *Bonetocardiella* make up the entire association. They are joined by Obliquipithonelloideae and Orthopithonelloideae in the lowermost Danian. Most calcdinocyst species (22 of the 31 species) appear to survive the K/T boundary event(s), while eight species first appear above the boundary.

The distribution of the Obliquipithonelloideae and Orthopithonelloideae is related to the lithofacies. With up to 18 species, the diversity is highest in the clay layers, notably in the A, B, C and E clays. In these layers, the number of orthopithonelloids increases in comparison to the obliquipithonelloids.

The cyclic diversity distribution of calcdinocyst morphotypes may possibly be attributed to sea-level changes, with maxima correlating to the diversity maxima as found in the A, B, C and E clays.

Introduction

Calcareous dinoflagellate cysts of the family Calciodinellaceae Deflandre 1947 are significant contributors to the microfossil content of Mesozoic and Cenozoic marine sediments. Especially during the Cretaceous they are of considerable importance (Keupp 1981; Willems 1988). According to the few investigations made, the same seems to be true for the Paleogene (Kohring 1993) and Neogene (Versteegh 1993). The first occurrence of these mostly hollow, spherical to ovoid organisms, also called 'calcispheres', goes back to the Karnian (Late Triassic; Janofske 1992). Data from recent dinoflagellates that produce calcareous cysts are available from Wall and Dale (1968), Wall et al. (1970), Matsuoka et al. (1990), Lewis (1991), Montresor et al. (1993) and others.

Since the first detailed investigations by Villain (1975, 1977) on the Maastrichtian limestones of Limburg (the Netherlands), it has been well known that calcareous dinoflagellates play a prominent role in these marine sediments. In stratigraphically comparable sections of France, England and Germany, these fossils are of great significance, and in some cases they even occur in rock-forming proportions mainly so in the Maastrichtian chalk facies (Willems 1988, 1992). For further details and overviews on the history of systematic investigations on calcareous dinoflagellates reference is made to Fütterer (1990) and Kohring (1993).

Very little is known about the stratigraphic distribution of calcareous dinocysts close to the Cretaceous/Tertiary (K/T) boundary. The few data available have been published by Fütterer (1984, 1990) from the south-eastern Atlantic and the eastern Weddell Sea, and recently by Kienel (1994) from several localities in Denmark and northern Germany. According to the investigations of Kohring (1993) on the Middle and uppermost Eocene of Jutland (Denmark) and the Paris Basin (France), it seems that a relatively high proportion of the Calciodinellaceae are long-lived forms, because many of the morphotypes he describes are already known from different stages of the Cretaceous. This is at least true for the two highly diverse groups of the Orthopithonelloideae and the Obliquipithonelloideae.

The Pithonelloideae first appeared in the late Barremian, and reportedly became extinct at the K/T boundary (Keupp 1990). Among the calcareous dinoflagellates, this subfamily plays quantitatively an extraordinary, often even rock-forming role in the Upper Cretaceous chalk facies. Kienel (1994) for the first time showed that the two most prominent species of Pithonelloideae (*Pithonella sphaerica, P. ovalis*) including the newly described *Lentodinella danica* cross the K/T boundary. However, the two prominent Late Cretaceous species appear not to have existed after the early Danian Zone NP1 (Martini 1971). They are quantitatively gradually substituted by *L. danica*, which first appears in the uppermost Maastrichtian, and slowly disappeared within the *Cruciplacolithus intermedius* Zone. According to Fütterer (1990), the extinction of Cretaceous taxa and the evolution of new Cenozoic taxa at the K/T transition was caused by one event, even though several of the Cretaceous taxa still occur within the NP1. Parallel to the extinction period, lasting from the K/T boundary through the NP1 (Kienel 1994), new forms of calcareous dinoflagellates evolved, with a proliferation of new forms dominated by *Obliquipithonella operculata* in the upper NP1. The blooming of this new species has been referred to as the '*Thoracosphaera*' event in the early Danian as mentioned in many nannoplankton papers of the Ocean Drilling Project (Thierstein 1981) or in other K/T boundary studies (Percival and Fischer 1977; Eshet et al. 1992).

Until now, investigations on calcareous dinocysts were concentrated on the taxonomic recording of Cretaceous forms mainly. First remarks on the paleoecological impacts on the distribution and phenotypic variability of calcdinocysts are given by Keupp (1981). Kohring (1993) pointed out that the distribution of Eocene calcdinocysts seems to be controlled by combinations of paleogeographical, paleoecological and paleoclimatological factors. Recently, a few papers have demonstrated that some of the ecological parameters controlling the distribution of these organisms can be related to transgressive and regressive trends (Keupp 1993; Keupp and Ilg 1989; Keupp and Kowalski 1992; Zügel 1994).

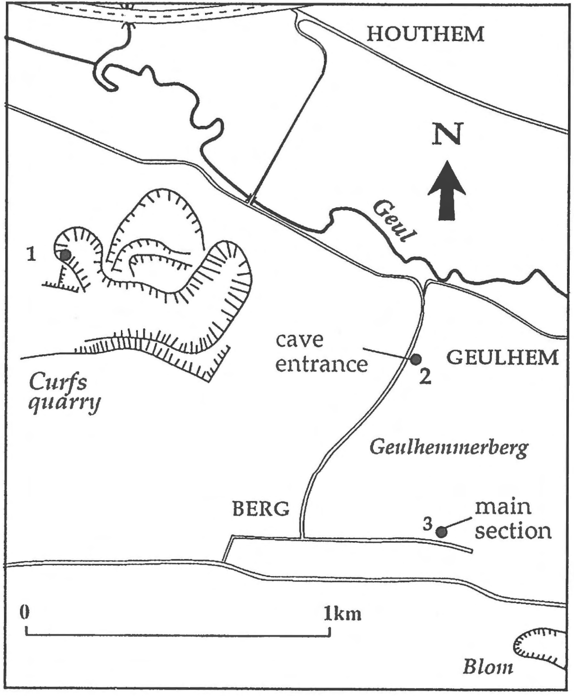


Figure 1. Location map of the Geulhemmerberg K/T boundary section (loc. 3), 6 km ENE of Maastricht, Limburg, SE Netherlands.

Samples

The material studied is derived from 24 samples of a 146-cm-thick section from the cave systems of Geulhemmerberg, a few kilometres west of Valkenburg in Limburg (SE Netherlands, Figure 1; see also Brinkhuis and Smith, this issue). The K/T boundary in this part of the Maastrichtian type area has often been equated with the Vroenhoven Horizon, a hardground marking the boundary between the Maastricht and Houthem formations (Albers and Felder 1979). Below this horizon, another irregular hardground surface (Berg en Terblijt Horizon) represents an unconformity at the top of a Late Cretaceous paleorelief. The section at Geulhemmerberg is situated in a paleodepression of this relief and was therefore expected to represent a more complete K/T boundary section (Brinkhuis and Smit, Roep and Smit, this issue).

According to the calcareous nannoplankton zonation (Romein et al., this issue) and to palynological data (Brinkhuis and Schiøler, this issue), the sampled interval seems to include the K/T boundary. Light-microscopical analysis of coccoliths indicates the presence of the late Maastrichtian *Nephrolithus frequens* Zone (samples G1A–G1C in Figure 2) and the early

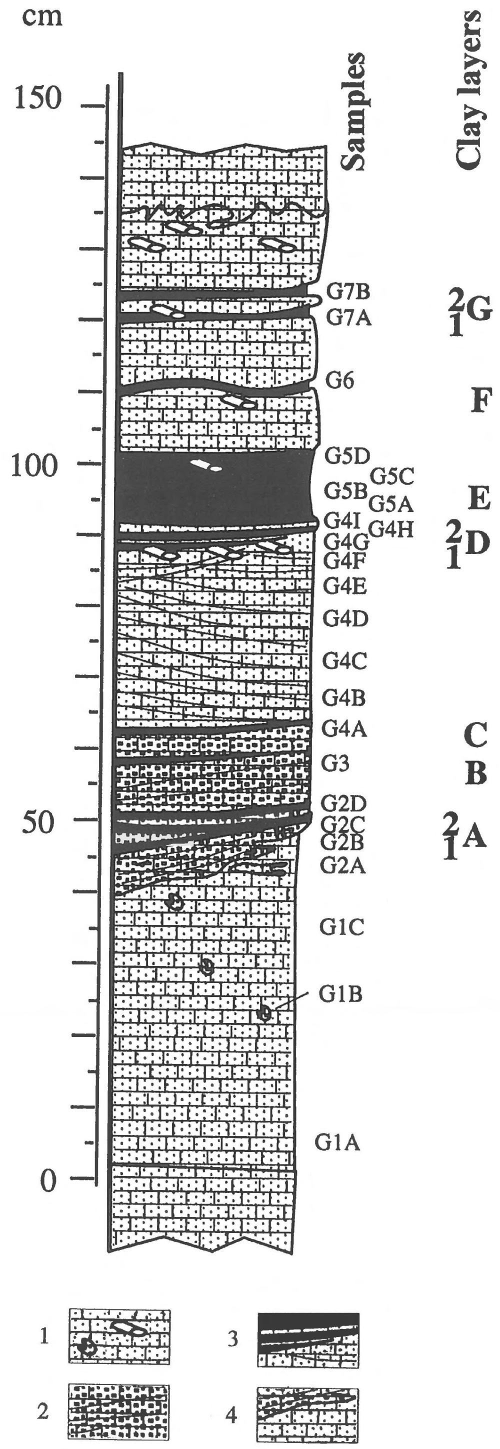


Figure 2. Lithological column of the Geulhemmerberg K/T boundary section (loc. 3 in Figure 1). 1 = Calcarenites, fine- to medium-grained, with burrows; 2 = calcarenites, coarse-grained; 3 (black) = clay layers and clayey intercalations; 4 = hardground. See Brinhuis and Smit (this issue) for stratigraphy. The hardground between samples G1C and G2A is the Berg en Terblijt Horizon.

Danian *Biantholithus sparsus* Zone (samples G2A–G7B). Scanning electron microscope analysis, however, indicates the presence throughout the section of *Neobiscutum romeinii, N. parvulum* and small forms of *Cruciplacolithus primus*, taxa so far reported only from the early Danian. Therefore, a Danian age of the whole Geulhemmerberg section cannot be excluded. The stratigraphic data obtained from the calcareous dinocysts have to be considered with caution, as only little is known about their stratigraphic usefulness.

Lithologically, the studied section can be divided into several parts (Figure 2). The bottom part (samples G1A–G1C) below the Berg en Terblijt Hardground consists of fine-grained yellow calcarenites containing many burrows. The irregular hardground surface is covered by channel-like irregular depression infillings of the lowermost Danian (Roep and Smit, this issue). It consists of an overall thinning- and fining-upward sequence (samples G2A–G5D) starting with coarse-grained calcarenites and fossil hash (shells, echinoids) at the base. A few centimetre-thick irregular clay layers are intercalated in this sequence (samples G2A–D, G3, G4A). These clay layers, each of which may be formed by two or more thinner horizons, are named clays A to C (Brinkhuis and Smit, this issue). The middle part of the section consists of medium-grained yellow calcarenites (samples G4B–G4F), grading upwards first into a thin clay layer (D Clay, sample G4G) and then into a 10-cm-thick clay layer (E Clay, samples G4I, G5A–G5D) with a fine calcarenitic ripple flaser at its base (sample G4H). Overlying the E Clay, a new fining-upward sequence starts with a 10-cm-thick calcarenitic bed. Following are irregular but more or less parallel-laminated fine-grained calcarenites with several centimetre-thick clay intercalations (clays F and G, samples G6, G7A–G7B). The top part of the section consists of brownish marly calcarenites which are thoroughly homogenized, probably by intense burrowing.

Methods

For the investigation of calcareous dinoflagellates, which mostly are 30 to 60 μm in diameter, the preparation of the calcarenites as well as the clays follows the methods of Willems (1985). The method combines 25% Glauber's salt ($Na_2SO_4 \times 10\ H_2O$) solution with freezing. After the near-complete disintegration of about 1 cm^3 of sample, the sample was sieved and the fraction of 20–125 μm separated. The cysts were

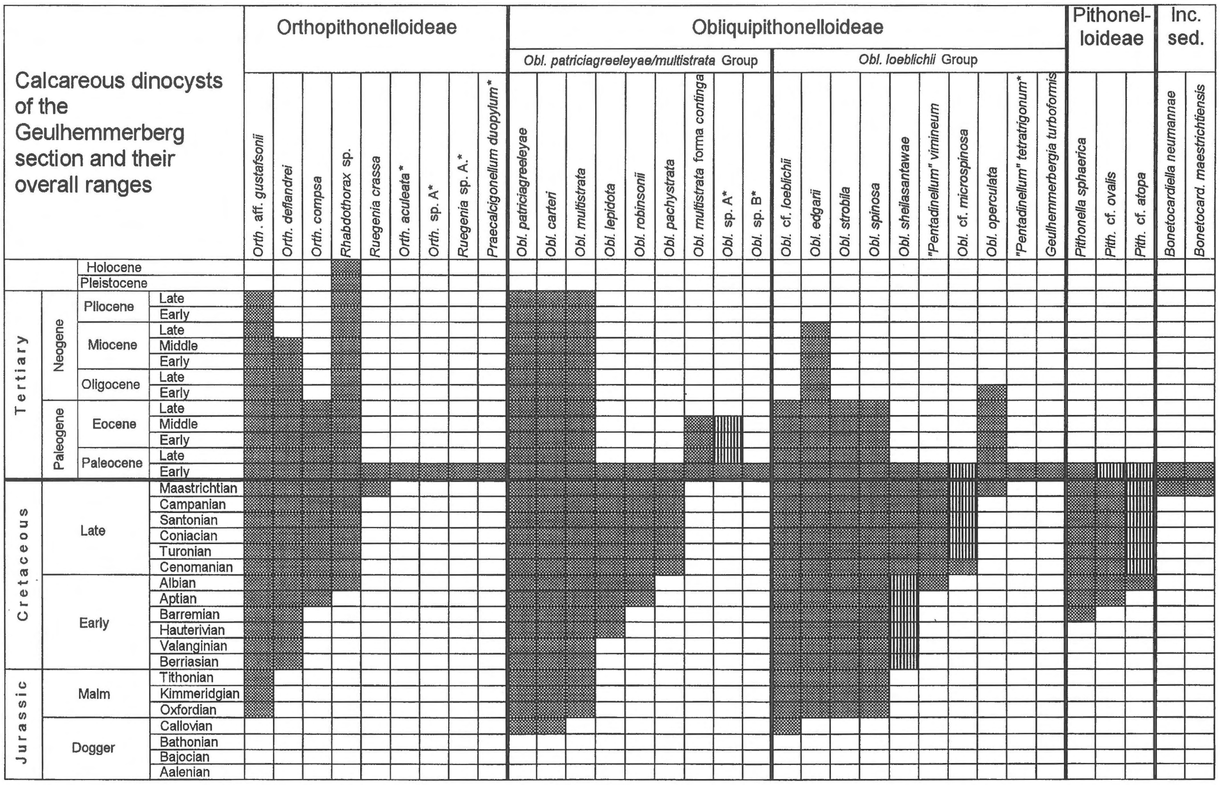


Figure 3. Overall stratigraphic distribution of the calcareous dinocysts and the two species of *Bonetocardiella* spp. found in the K/T boundary section of the Geulhemmerberg, with additional data from the literature. Species marked with an asterisk* are newly described from Geulhemmerberg. Fields of vertical lines mark a stratigraphic range not positively identified in the literature.

picked under the binocular microscope with at least 80 × magnification, and placed on a standard stub provided with an adhesive conductive sticker for SEM studies. After sputtering with gold, the specimens were investigated using a gun potential of 15–20 kV.

For the paleoecological interpretation, a rough calculation of the relative distributions of the different species and morphotype groups was made by collecting the first 100 specimens from each sample. In a few samples, nearly no specimens were recognised, even after searching for several hours. The total amount of calcareous dinocyst specimens investigated was 2098.

The formal systematic descriptions of the taxa mentioned in the Appendix will be published in a forthcoming contribution (Willems, submitted).

Discussion

In the K/T boundary section of the Geulhemmerberg, a high diversity of 31 species of calcareous dinocysts occurs. Among these, five species and one monospecific genus are described for the first time (Willems 1995; submitted). Furthermore, two species of the Incertae Sedis genus *Bonetocardiella* have been recognised. This paper completely documents the calcareous dinoflagellate flora. The following statements regarding the stratigraphic range and paleoecological value of the dinocysts have to be considered with some reservation, because some of the lowermost Danian sediment contains abundant reworked Maastrichtian and Campanian nannofossils.

Based on the stratigraphic results derived from the calcareous nannoplankton (Romein et al., this issue), the Geulhemmerberg section covers the time from the latest Maastrichtian (samples G1A–G1C) to the earliest Danian *Biantholithus sparsus* Zone (samples G2A–

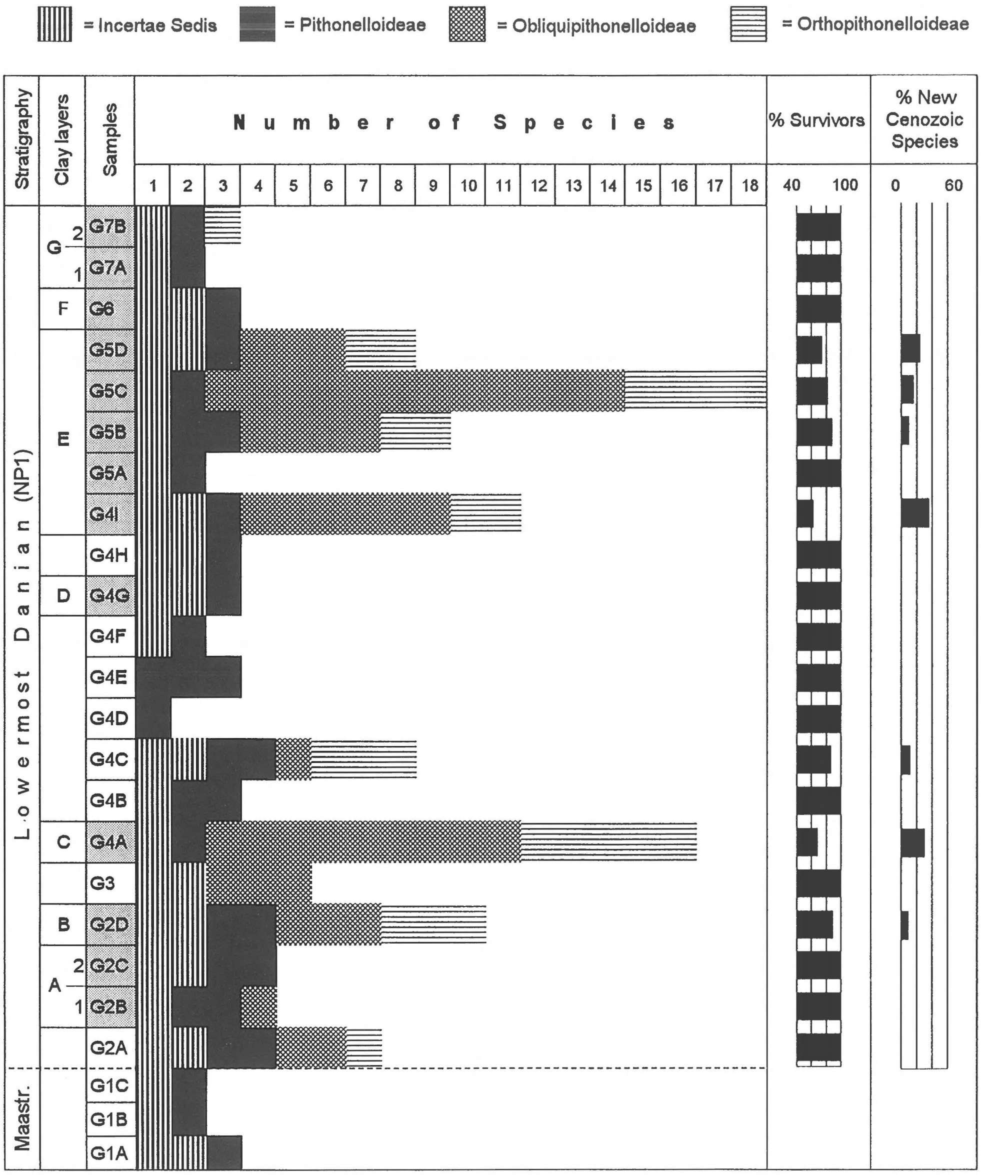


Figure 4. Species distribution and diversity of calcareous dinocysts and *Bonetocardiella* spp. in the samples of the Geulhemmerberg K/T section. On the right, the percentages of K/T survivors and new Cenozoic species occurring just above the boundary. Sample numbers shaded grey indicate clays.

G7B). A hiatus occurs at the base of the lowermost Danian. The occurrence of calcdinocysts shows two remarkable features at this hiatus. First, the samples G1A–G1C consist exclusively of Pithonelloideae and *Bonetocardiella* spp. (Figure 4). Starting with sample G2A, ortho- and obliquipithonelloid calcdinocysts first appear, including *Obliquipithonella operculata* which is a typical species for the lowermost Danian, even though it is also known from the Upper Maastrichtian (Kienel 1994). Secondly, the major representative of the Pithonelloideae, *Pithonella sphaerica*, shows a slowly decreasing abundance above sample G1C. In addition, *P. sphaerica* tests show a distinct reduction of their average diameter from samples G2A/B upwards. The same phenomenon has been pointed out by Kienel (1994) to be a typical feature of this species within the

Stratigraphy	Samples	Orthopithonelloideae									Obliquipithonelloideae																			Pithonelloideae			Incertae sedis	
											Obl. patriciagreeleyae/multistrata Group									*Obl. loeblichii* Group														
		Orthopithonella aff. *gustafsonii*	*Orth. aculeata**	*Orth. compsa*	*Orth. deflandrei*	*Orth.* sp. A*	*Rhabdothorax* sp.	*Ruegenia crassa*	*Ruegenia* sp. A*	*Praecalcigonellum duopylum**	*Obliquipithonella patriciagreeleyae*	*Obl. multistrata*	*Obl. multistrata* forma *continga*	*Obl. carteri*	*Obl. pachystrata*	*Obl. robinsonii*	*Obl. lepidota*	*Obl.* sp. A*	*Obl.* sp. B*	*Obl.* cf. *loeblichii*	*Obl. sheilasantawae*	*Obl. strobila*	*Obl. spinosa*	*Obl. edgarii*	*Obl.* cf. *microspinosa*	*Obl. operculata*	*'Pentadinellum' vimineum*	*'Pentadinellum' tetratrigonum**	*Geulhemmerbergia turboformis**	*Pithonella sphaerica*	*Pith.* cf. *ovalis*	*Pith.* cf. *atopa*	*Bonetocardiella neumannae*	*Bonetocard. maestrichtiensis*
Lowermost Danian (NP 1)	G7B						1																							86			6	
	G7A																													79			1	
	G6																													79			6	6
	G5D		5				3									1			1					1						66			4	3
	G5C		1			1	3	1			1				4	1	3		1	1		1	2	4	1	1			2	45				1
	G5B				1				1					1	1							2		3						56		1		3
	G5A																													8				1
	G4 I		5				4				2	1	1						1							1			1	75			2	1
	G4H																													66			3	1
	G4G																													60			4	1
	G4F																													10			2	
	G4E																													81	2	1		
	G4D																													2				
	G4C		1	1			2																2							78		4	13	5
	G4B																													78	7			4
	G4A	13	12		1		15			2				1	2		1	2			1	1				3	1	5		37			2	
	G3				1			1																						94			3	1
	G2D	4	7	1									2	3								2								57		2	12	2
	G2C																													72	1		12	1
	G2B																						1							82			4	
	G2A						1							1									3							80		1	4	1
Maastr	G1C																													88		1	2	
	G1B																													87			1	
	G1A																													81			5	6

Figure 5. Distribution chart of calcdinocysts and *Bonetocardiella* spp. in the Geulhemmerberg K/T boundary section. The numbers of specimens found result from the counting of up to 100 tests per sample. In spite of long picking times, some of the samples (e.g. G5A) yielded hardly any specimens.

Biantholithus sparsus Zone. However, there is no clear evidence whether these observations are sufficient to use calcdinocysts as indicators for the K/T boundary.

The abundance of calcdinocysts is generally very high throughout the section. It is low in only two layers in the lowermost Danian: calcarenites of sample G4D and the lower part of the E Clay (sample G5A). The only species found in these layers are rare poorly preserved *P. sphaerica*, in sample G5A accompanied by one *Bonetocardiella maestrichtiensis*. The two species of *Bonetocardiella* occur with an abundance of up to 14% in nearly all other layers, except for samples G4D and G4E.

In the three samples G1A–G1C dated as latest Maastrichtian, the species diversity is restricted and dominated by an abundance of *P. sphaerica*, accompanied only by rare *Bonetocardiella neumannae* and *B. maestrichtiensis*. This phenomenon has also been reported from other localities in the uppermost Cretaceous of Europe (Villain 1975, 1977; Willems 1992; Kienel 1994). In contrast, the lowermost Danian samples are characterised by a diverse dinocyst assemblage starting abruptly with sample G2A at the very basal layer of the Danian.

Taking the literature into consideration, 22 (= 71%) of the 31 species found in the lowermost Danian cross the K/T boundary (Figure 3). Concerning the Ortho- and Obliquipithonelloideae, this has already been known for some species from studies by Kohring (1993) in the Eocene of Denmark and the Paris Basin, and by Kienel (1994) at the K/T boundary in eastern Germany and Denmark. According to these authors, species such as *Orthopithonella* aff. *gustafsonii, Orth. compsa, Orth. deflandrei, Rhabdothorax* sp., *Obliquipithonella multistrata, Obl. patriciagreeleyae, Obl. carteri, Obl. loeblichii, Obl. strobila, Obl. spinosa* and *Obl. edgarii* are long-lived forms, many of which can be traced back into the Late Jurassic. At Geulhemmerberg, it has been shown for the first time that *Obl. pachystrata, Obl. robinsonii, Obl. lepidota, Obl. sheilasantawae, Obl.* cf. *microspinosa*, and *'Pentadinellum' vimineum* are K/T survivors as well.

This also applies to the Pithonelloideae representatives *P. sphaerica, P.* cf. *ovalis* and *P.* cf. *atopa*, the former two having recently been recognised as survivors by Kienel (1994). For the first time, however, it has been shown that the Incertae Sedis species *Bonetocardiella neumannae* and *B. maestrichtiensis*, which so far were known only from the Maastrichtian, also crossed the K/T boundary. Two other surviving dinocysts appeared just before the boundary: *Ruegenia crassa* and *Obl. operculata*. Newly described species which appear after the K/T boundary are *Orth. aculeata, Orth* sp., *Ruegenia* sp., *Praecalcigonellum duopylum, 'Pentadinellum' tetratrigonum, Geulhemmerbergia turboformis*, as well as two unknown *Obliquipithonella* morphotypes, spp. A and B, and the already described *Obl. multistrata* forma *continga*.

As in the uppermost Maastrichtian, the dominant dinocysts in the lowermost Danian are the Pithonelloideae (mainly *P. sphaerica*), in most cases, except samples G4D and G4E (Figure 4), accompanied by *Bonetocardiella* spp. The qualitative and quantitative distributions of the ortho- and obliquipithonelloid calcdinocysts in the lowermost Danian depend strongly on the lithology. The diversity of up to 18 species generally is the highest within the clay layers, especially in the B (sample G2D), the C (G4A) and the E Clay (G4I, G5C). Most of the newly described lower Danian dinocysts appear in these clay layers. However, the survivors from the Cretaceous are relatively few in the same layers. Sample G5A within the E Clay is an exception, because its species diversity and abundance are extremely low. As for Ortho- and Obliquipithonelloideae, the latter group always, except for G4C, plays the more important role with regard to diversity. It is remarkable that the orthopithonelloid abundance increases with the calcdinocyst diversity.

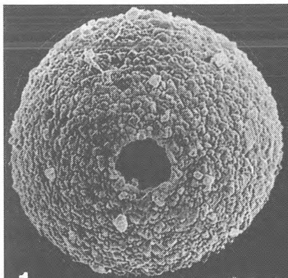
In general, the lowest calcdinocyst diversity occurs in the calcarenites, and in intervals of lowest overall abundance (especially G4D, G4F). The frequency and diversity of the cysts appear to be positively correlated. In the layers with the lowest diversity, the assemblage is essentially composed of Pithonelloideae, in most cases accompanied by *Bonetocardiella* spp. In the same layers, the representatives of the Ortho- and Obliquipithonelloideae are nearly exclusively survivor forms.

Little is known about the factors controlling the paleogeographic distribution of calcareous dinocysts. Only recently, the studies carried out by Keupp (1993), Kohring (1993) and Zügel (1994) supplied information on ecological control mechanisms, which have to be considered carefully before they are applied to other cases. Within the Pithonelloideae, there is an absolute dominance of *P. sphaerica* in all Geulhemmerberg samples. Compared with the investigations by Zügel (1994) of the Cenomanian–Turonian in the Anglo-Paris Basin, this may indicate open, proximal to distal shelf environments. Taking into consideration hints given by Villain (1981), the pithonelloids seem to migrate into more proximal shelf areas during the late Cretaceous. This would agree with the regular occurrence of *Bonetocardiella* spp. which, if not redeposited, points to inner shelf environments (Villain 1981).

The described variable distribution pattern of the calcdinocysts (Figure 4) may possibly be attributed to sea-level changes. Kohring (1993) found that an increase in species diversity is positively correlated with a greater distance from the coast. He also has shown that the species diversity of orthopithonelloids increases offshore in comparison with that of obliquipithonelloids. Based on these observations, some trends can be discussed in the Geulhemmerberg section. The higher species diversity of obliquipithonelloids compared to orthopithonelloids in samples where both subfamilies occur, indicates a generally more proximal shelf position (Keupp 1993; Kohring 1993). The maximum transgression thus would be in the C Clay (G4A) and in the upper half of the E Clay (G5C), correlating with the highest orthopithonelloid diversity. A transgressive setting or deepening of the sea is assumed from the general thinning-upward character of the interval between G2A to G5D. The maximum regressive trends would be located at the top of the uppermost Maastrichtian (sample G1C) and especially in the lowermost Danian sample G4D, where orthopithonelloids as well as obliquipithonelloids are missing. There are indications of a further regressive trend in the uppermost part of the studied section (samples G7A and B).

Acknowledgements

My special thanks are for Henk Brinkhuis (Utrecht) and Jan Smit (Amsterdam) and the whole 'Deep Dark Hole' Working Group for placing the material at my disposal. J. Pospichal (Tallahassee) gave important hints for improving the text. I also thank Ms. Angelika Freesemann for the preparation of the material, Ms. Anne Meyer for carrying out photographic work, Hartmut Mai for the SEM work, Ms. Tania Hildebrand-Habel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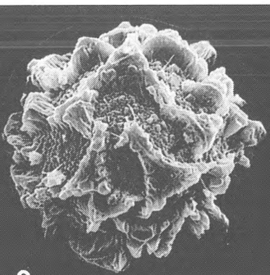
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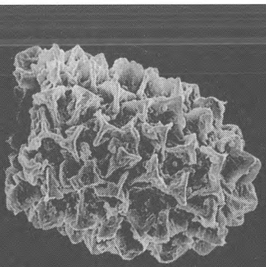
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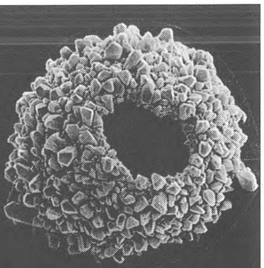
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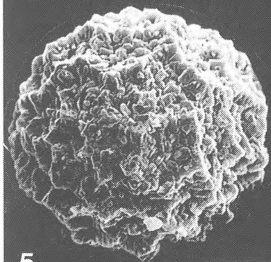
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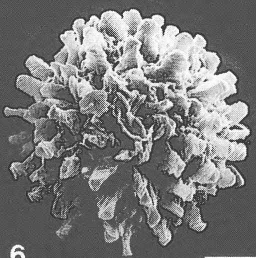
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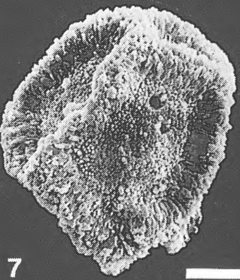
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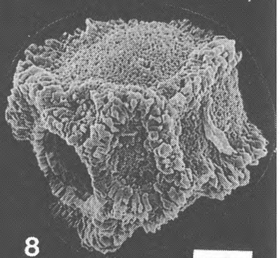
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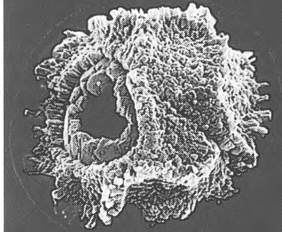
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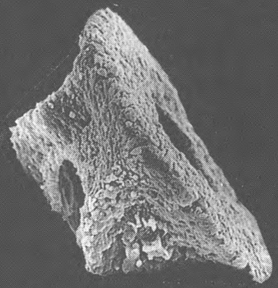
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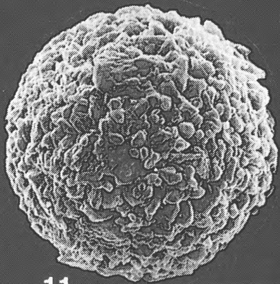
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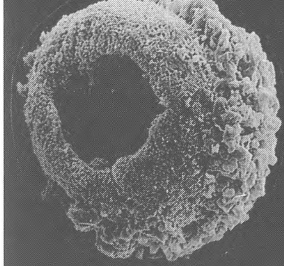
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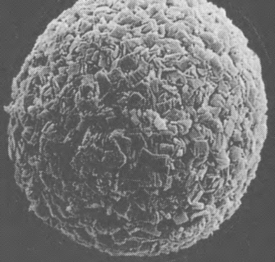
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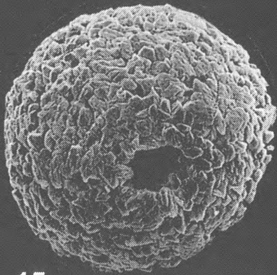
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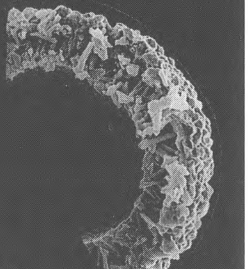
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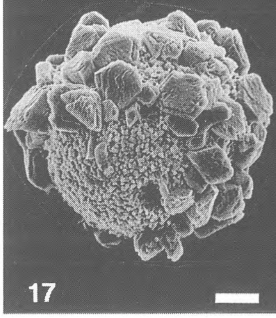
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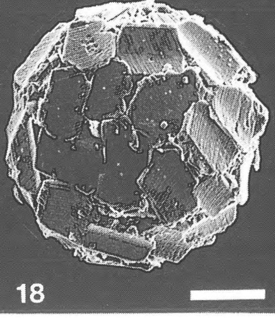
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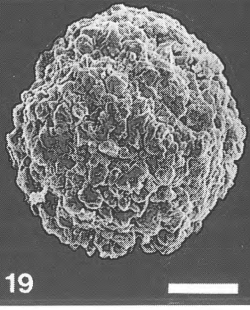
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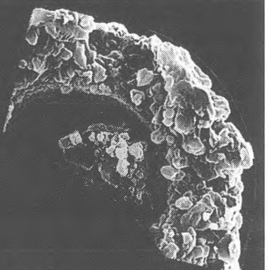
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Plate 1. Calcareous dinoflagellate cysts from the Geulhemmerberg K/T boundary section. All scale bars 10 μm.
Figures 1–10. Calcdinocysts of the subfamily Orthopithonelloideae Keupp 1987 – 1. *Orthopithonella* aff. *gustafsonii* (Bolli 1974). – Cyst no. 100, sample G2D. – 2. *Orthopithonella aculeata* Willems (submitted). – Cyst no. 92, sample G5C. – 3. *Orthopithonella compsa* (Keupp 1982). – Cyst no. 8, sample G4C. – 4. *Orthopithonella deflandrei* (Kamptner 1956). – Cyst no. 16, sample G3. – 5. *Orthopithonella* sp. A. – Cyst no. 39, sample G5C. – 6. *Rhabdothorax* sp. – Cyst no. 96, sample G5C. – 7, 8. *Ruegenia crassa* Kienel 1994. – 7: Cyst no. 53, sample G3; 8: Cyst no. 5, sample G5C. – 9. *Ruegenia* sp. A. – Cyst no. 12, sample G5B. – 10. *Praecalcigonellum duopylum* Willems 1995. – Cyst no. 92, sample G4A.
Figures 11–20. Calcdinocysts of the *Obliquipithonella patriciagreeleyae/multistrata* Group of the subfamily Obliquipithonelloideae Keupp 1987 – 11. *Obliquipithonella patriciagreeleyae* (Bolli 1974). – Cyst no. 22, sample G4I. – 12. *Obliquipithonella multistrata* (Pflaumann & Krasheninnikov 1978). – Cyst no. 83, sample G4I. – 13. *Obliquipithonella multistrata* forma *continga* Kohring 1993. – Cyst no. 2, sample G2D. – 14. *Obliquipithonella carteri* (Bolli 1974). – Cyst no. 68, sample G2D. – 15, 16. *Obliquipithonella pachystrata* Zügel 1993. – 15: Cyst no. 59, sample G5C; 16: Detail of wall structure. – Cyst no. 31, sample G4A. – 17. *Obliquipithonella robinsonii* (Bolli 1974). – Cyst no. 63, sample G5C. – 18. *Obliquipithonella lepidota* (Keupp 1982). – Cyst no. 75, sample G5C. – 19, 20. *Obliquipithonella* sp. A., Figure 20 showing detail of wall structure. – Cyst no. 83. sample G4A.

and Ms. Maike Werther for picking out the specimens and Ms. Erna Friedel for helping with the English text.

Appendix

Taxonomy of calcareous dinoflagellate cysts

The taxonomy of calcareous dinocysts adopted in this paper follows Keupp (1987), who established three subfamilies of the family Calciodinellaceae Deflandre 1947 within the order Peridiniales Haeckel 1894. This division is based on the orientation of the morphological long axis of the skeletal calcite crystallites in the outer cyst wall relative to the test surface:

- Orthopithonelloideae Keupp 1987 have a strictly radial orientation of outer wall crystals: those of the inner wall may be oriented the same way or irregularly obliquely.
- Obliquipithonelloideae Keupp 1987 have an irregularly oblique or even tangential orientation in each wall layer.
- Pithonelloideae have a thick inner, and a (very) thin outer wall: both layers show a uniquely oblique orientation of the crystals in regular rows, thus forming a parquet-like proximal and distal surface pattern.

Division Pyrrophyta Pascher 1914
Class Dinophyceae Frisch 1929
Order Peridiniales Haeckel 1894
Suborder Peridiniinaea (Fott 1959), Bujak and Davies 1983
Family Calciodinellaceae (Deflandre 1947), Bujak and Davies 1983

Subfamily Orthopithonelloideae Keupp 1987

Genus *Orthopithonella* Keupp 1984

Orthopithonella sp. aff. *gustafsonii* (Bolli 1974)
Plate 1, Figure 1
O. aff. *gustafsonii*, which is characterised by a simple round archaeopyle, is restricted to the B and C clays. This group is known from the Late Jurassic (Keupp 1992a) to the Late Eocene (Kohring 1993). The cryptotabulate form group around *O. gustafsonii*, which is characterised by a polygonal archaeopyle, however, seems to be stratigraphically restricted to the middle Aptian to Albian (Keupp 1992a).

Orthopithonella aculeata Willems (submitted)
Plate 1, Figure 2
This newly described species is closely related to the morphotype group *O. gustafsonii*. It occurs more or less continuously throughout the lowermost Danian of the section, and is particularly common in the clay layers. A comparable morphotype was described as *Orthopithonella* cf. *gustafsonii* forma *salebra* in Kienel (1994), from the Danian of various localities in Denmark and eastern Germany.

Orthopithonella compsa (Keupp 1982)
Plate 1, Figure 3
In contrast to the original description, the tests observed here (samples G2D, G4C) have an ovoid outer shape. The oldest representatives of the typical spherical forms of *O. compsa* were described by Keupp (1982) from the Upper Aptian of northern Germany. Kohring (1993) reported them from the Upper Eocene of Jutland in Denmark.

Orthopithonella deflandrei (Kamptner 1956)
Plate 1, Figure 4
The fact that various orthopithonelloid calcareous dinoflagellates have been included previously within *O. deflandrei* in the literature, possibly explains the wide stratigraphic range of the species. It ranges from the ?late Berriasian (Keupp 1992b), or Neocomian (Stradner 1961) into the Middle Miocene (Fütterer 1977). Kamptner (1956) described the species from the Eocene of France. In Geulhemmerberg, the form occurs mainly in the C and E clays.

Orthopithonella sp. A
Plate 1, Figure 5
The morphotype, which is characterised by an irregular ridge pattern (paratabulation?) on the test surface, is restricted to the E Clay. This is in accordance with the occurrence of the morphologically similar *Orthotabulata obscura* Kienel 1994 in the Danian of Jutland and Zealand in Denmark.

Genus *Rhabdothorax* Kamptner 1958

As mentioned by Fütterer (1977), this genus exhibits remarkable morphologic similarities with the calcareous cysts of *Scrippsiella trochoidea* (Stein) Lemmermann, which is described from the Recent exclusively.

Rhabdothorax sp.
Plate 1, Figure 6
The oldest tests comparable to *Rhabdothorax* sp. have been described by Keupp (1987) from the Albian of northern France. Recent occurrences of corresponding forms were described by Kamptner (1937) from the Mediterranean. In the Geulhemmerberg section, the species occurs in several calcarenites (samples G2A, G4C) and clay layers (samples G4A, G4I, G5C, G5D).

Genus *Ruegenia* Willems 1992

Ruegenia crassa Kienel 1994
Plate 1, Figures 7, 8
This species only occurs in two samples (G3, G5C). So far, it has only been described (Kienel 1994) from the Maastrichtian and Danian of Nennhausen (eastern Germany).

Ruegenia sp. A
Plate 1, Figure 9
This form is distinguished from *R. crassa* by the differing outer paratabulation pattern. It will be first described in detail in Willems (submitted). Its occurrence is restricted to the E Clay.

Genus *Praecalcigonellum* Keupp & Versteegh 1989

Species of this genus are generally rare and have been recorded from the Early Cretaceous (Hauterivian) to Quaternary (Keupp and Versteegh 1989). They have been found in Recent sediments from Bermuda, and in plankton samples off Woods Hole, Massachusetts (Wall and Dale, 1968).

Praecalcigonellum duopylum Willems 1995
Plate 1, Figure 10
This newly described species is very rare and has been found exclusively in Clay C.

Subfamily Obliquipithonelloideae Keupp 1987

Genus *Obliquipithonella* Keupp 1984

Obliquipithonella patriciagreeleyae/multistrata Group sensu Keupp 1981
In this group, the wall layers are characterised, in their initial position, by long-stemmed crystallites or rhombohedrons (Keupp 1992a). They are arranged in cross-lamellar structure or in a mainly irregularly tangential orientation. They differ from those of the *O. loeblichii* Group by the existence of the thin initial layer of fine-stemmed crystals in the basal area of the outer wall.

Obliquipithonella patriciagreeleyae (Bolli 1974)
Plate 1, Figure 11
This species was found in two samples from the E Clay. It is known to cross the K/T boundary from its descriptions in Kohring (1993) from the Late Eocene, and in Versteegh (1993) from the Late Pliocene. The stratigraphic range of the species starts in the Late Callovian (Keupp and Ilg 1989).

Obliquipithonella multistrata (Pflaumann & Krasheninnikov) 1978
Plate 1, Figure 12
The morphotypes that comprise the *O. multistrata* Group sensu Keupp (1981) are morphologically very variable. They have been found from the Oxfordian (Keupp and Ilg 1989) to the Late Pleistocene (Versteegh 1993) and have a global distribution. The only test was found in the E Clay (sample G4I).

Obliquipithonella multistrata forma *continga* Kohring 1993
Plate 1, Figure 13
According to the first description in Kohring (1993), this form is only known from the Middle Eocene of Schleswig-Holstein in northern Germany. The occurrence in the Geulhemmerberg B and E clays now extends the stratigraphic range down into the lowermost Danian.

Obliquipithonella carteri (Bolli 1974)
Plate 1, Figure 14
The species occurs in low numbers throughout the lowermost Danian section, and preferably in the B, C and E clays. The cyst seems to represent the morphologically similar *O. multistrata* forma *carteri*, shown by Kohring (1993) which is known from the late Callovian to the Pleistocene.

Obliquipithonella pachystrata Zügel 1993
Plate 1, Figures 15, 16
Zügel (1993) first described *O. pachystrata* from the Cenomanian and Turonian of the Paris Basin and from Wunstorf in northern Germany. The findings in the Geulhemmerberg C and E clays now extend the stratigraphic range into the lowermost Danian.

Obliquipithonella robinsonii (Bolli 1974)
Plate 1, Figure 17
Previously, this cyst has been described from the Upper Aptian to Late Cenomanian (Bolli 1974; Keupp 1982; Zügel 1993). Its wide global distribution is illustrated by its presence at various localities from northern Europe to the Indian Ocean. At Geulhemmerberg, two samples of the E Clay contain one individual each. Its stratigraphic range thus has to be extended considerably.

Obliquipithonella lepidota (Keupp 1982)
Plate 1, Figure 18
The first occurrence of this species is reported by Keupp (1981) from the Early Hauterivian of Speeton (England). In the Lower Saxony Basin in Germany it occurs from the Upper Aptian to Lower Albian (Keupp 1982). Provided that the forms discussed in this paper are not redeposited, which seems improbable because of the fragile tests, the stratigraphic range should be extended to the lowermost Danian C and E clays.

Obliquipithonella sp. A
Plate 1, Figures 19, 20
This cyst, which cannot be assigned to any of the hitherto known morphotypes within the *O. multistrata/patriciagreeleyae* Group, has only been found in the C Clay. In a broader sense, similar tests have been described by Kohring (1993) from the Middle Eocene (Bartonian) of Chambrécy (France).

Obliquipithonella sp. B
Plate 2, Figure 1
This form is similar to *O. pachystrata*, but shows significant morphological differences. These rare cysts have been found exclusively in the E Clay.

Obliquipithonella loeblichii Group sensu Keupp 1981
In contrast to the *O. patriciagreeleyae/multistrata* Group, this group is characterised by the lack of an initial wall layer of small-sized stem-like crystallites in cross-lamellar structure. The morphotypes are characterised by irregularly arranged, coarsely blocky calcite rhombohedrons that form the basis of the outer wall. In some tests, a thin, single-layered, inner wall of equilateral or stem-like crystallites occurs.

Obliquipithonella sp. cf. *loeblichii* (Bolli 1974)
Plate 2, Figure 2
Morphotypes of *O. loeblichii* have a global distribution and range from late Callovian (Keupp and Ilg 1989) to Late Eocene (Kohring 1993). In the Geulhemmerberg, they are restricted to the E Clay.

Obliquipithonella sheilasantawae (Bolli 1974)
Plate 2, Figure 3
Until now, this species has only been known from the Early Cretaceous (mainly Albian; Bolli 1974; Keupp 1981). From the lower Berriasian of Speeton (England), Keupp and Mutterlose (1984) mention a morphotype that is similar in the broadest sense. The stratigraphic range can now be extended into the lowermost Danian (C Clay).

Obliquipithonella strobila (Keupp in Keupp & Michael 1979)
Plate 2, Figures 4, 5
O. strobila, which occurs in two different morphological configurations, is restricted to the B, C and E clays. It has been recorded from the Early Oxfordian of Normandy in France (Keupp and Ilg 1989) to the Late Eocene of Denmark (Kohring 1993).

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Plate 2. Figures 1–16. Calcareous dinoflagellate cysts from the Geulhemmerberg K/T boundary section. All scale bars 10 μm.
Figure 1. Calcdinocyst of the *Obliquipithonella patriciagreeleyae/multistrata* Group of the subfamily Obliquipithonelloideae Keupp 1987: *Obliquipithonella* sp. B. – Cyst no. 91, sample G5D.
Figures 2–12. Calcdinocysts of the *Obliquipithonella loeblichii* Group of the Subfamily Obliquipithonelloideae Keupp 1987 – 2. *Obliquipithonella* cf. *loeblichii* (Bolli 1974). – Cyst no. 41, sample G5C – 3. *Obliquipithonella sheilasantawae* (Bolli 1974). – Cyst no. 29, sample G4A. – 4, 5. *Obliquipithonella strobila* (Keupp in Keupp & Michael 1979). – 4: Cyst no. 58, sample G2D; 5: Cyst no. 65, sample G2D. – 6. *Obliquipithonella spinosa* (Keupp in Keupp & Michael 1979). – Cyst no. 7, sample G4C. – 7. *Obliquipithonella edgarii* (Bolli 1974). – Cyst no. 45, sample G5C. – 8. *Obliquipithonella* cf. *microspinosa* Zügel 1993. – Cyst no. 19, sample G5C. – 9. *Obliquipithonella operculata* (Bramlette & Martini 1964). – Cyst no. 101, sample G4A. – 10. *'Pentadinellum' vimineum* (Keupp 1987). – Cyst no. 102, sample G4A. – 11. *'Pentadinellum' tetratrigonum* Willems (submitted). – Cyst no. 103, sample G4A. – 12. *Geulhemmerbergia turboformis* Willems (submitted). – Cyst no. 18, sample G4I.
Figures 13–16. Calcdinocysts of the subfamily Pithonelloideae Keupp 1987 – 13, 14. *Pithonella sphaerica* (Kaufmann 1865). – 13: Cyst no. 44, sample G5C; 14: Cyst no. 5, sample G4C. – 15. *Pithonella* cf. *ovalis* (Kaufmann 1865). – Cyst no. 24, sample G4B. – 16. *Pithonella* cf. *atopa* Keupp in Keupp & Kienel 1994. – Cyst no. 96, sample G2A.
Figures 17–19. Calcareous organisms incertae sedis from the Geulhemmerberg K/T boundary section. – 17. *Bonetocardiella neumannae* Villain 1975. – Specimen no. 57, sample G3. – 18, 19. *Bonetocardiella maestrichtiensis* (Visser 1951). – 18: Specimen no. 46, sample G3; 19: Specimen no. 56, sample G4C.

Obliquipithonella spinosa (Keupp in Keupp & Michael 1979)
Plate 2, Figure 6
The species shows a wide stratigraphic range from the Early Oxfordian in Normandy, France (Keupp and Ilg 1989), to the Late Eocene of Moesgard in Denmark (Kohring 1993). It has been described from the Aptian to Early Cenomanian of various localities in northern Europe. It has not yet been found in the Late Cretaceous. In the Geulhemmerberg, it occurs in clays and calcarenites in the lowermost Danian.

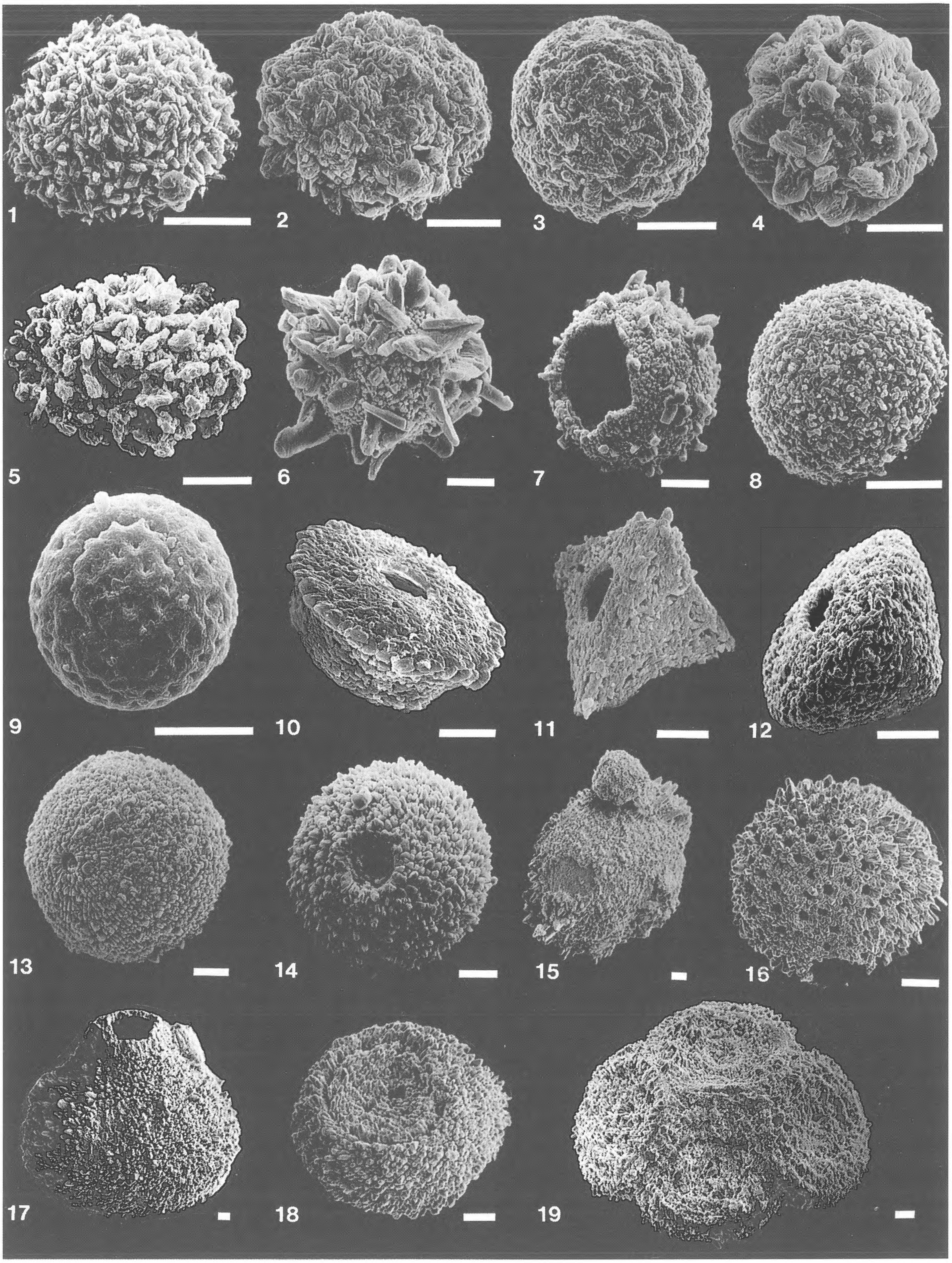
Obliquipithonella edgarii (Bolli 1974)
Plate 2, Figure 7
In the studied material, this species is restricted to the E Clay. On the whole, *O. edgarii* exhibits a wide stratigraphic and regional distribution. The earliest occurrence is reported by Keupp and Ilg (1989) from the early Oxfordian of Normandy, France. Kohring (1993) reported it from the Late Miocene of Algeria. The wide geographic distribution furthermore includes the Indian Ocean (Bolli 1974) and various European occurrences (Keupp 1981, 1987; Kohring 1993).

Obliquipithonella sp. cf. *microspinosa* Zügel 1993
Plate 2, Figure 8
O. microspinosa until now has been described by Zügel (1993) from the Cenomanian of Calais (France) and Wunstorf (Germany). If the form described here is actually *O. microspinosa*, then its stratigraphic range can be extended into the lowermost Danian (E Clay).

Obliquipithonella operculata (Bramlette & Martini 1964)
Plate 2, Figure 9
This form appears only in the C and E clays. Elsewhere, it occurs in masses in the Danian as the so-called *'Thoracosphaera'* event. According to Fütterer (1990), the occurrence of this species in the Late Cretaceous has not yet been demonstrated. Recently, however, Kienel (1994) described its earliest occurrence from the Maastrichtian in a drilling near Nennhausen (Germany). Furthermore, it should be noted that the forms shown in Jafar (1979) and Wise and Wind (1977) from the Late Maastrichtian and Campanian–Maastrichtian are identical with the morphotype presented in this paper. The highest stratigraphic occurrence of *O. operculata* is reported by Kohring (1993) from the Middle Oligocene of the Mainz Basin (Germany).

Genus *Pentadinellum* Keupp 1991

'Pentadinellum' vimineum (Keupp 1987)
Plate 2, Figure 10
Until now, this species has only been known from the middle Albian to early Cenomanian of Folkestone, England, and of the French Channel coast (Escalles, Calais; Keupp 1987; Keupp and Kowalski 1992; Zügel 1993). Its occurrence in the lowermost Danian of the Geulhemmerberg thus extends its stratigraphic range considerably. Its survival across the K/T boundary, however, has to be considered with caution, because the sample, in which the only specimen of *'P.'*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vimineum was found (C Clay), contains abundant redeposited Maastrichtian and Campanian material (mainly coccoliths; Romein et al., this issue).

'Pentadinellum' tetratrigonum Willems (submitted)
Plate 2, Figure 11
This very rare cyst has been found only in the C Clay of the Geulhemmerberg. Comparable forms have never been described in the literature.

Genus *Geulhemmerbergia* Willems (submitted)

Geulhemmerbergia turboformis Willems (submitted)
Plate 2, Figure 12
This very rarely occurring cyst has been found exclusively in the lowermost Danian D and E clays. Comparable morphotypes are not known until now.

Subfamily Pithonelloideae Keupp 1987

Genus *Pithonella* Lorenz 1902

Representatives of the Pithonelloideae have been noted until now from the Late Barremian of Speeton, England (Keupp 1987) to the Late Maastrichtian chalk in Europe (Villain 1975; Willems 1988). The assumed pithonelloid *Centosphaera barbata* (Wind and Wise 1977) has been described from the Danian (Fütterer 1990). It had not been shown until recently, whether the two typical pithonelloid forms, *Pithonella sphaerica* and *P. ovalis*, crossed the K/T boundary. The latest studies by Kienel (1994) of sections in Denmark and Germany gave first hints for such a crossing. The Geulhemmerberg investigations confirm these observations. Both forms cross the K/T boundary at least into the NP1 Zone. Representatives of the Pithonelloideae, described by Weiler (1990) and by Kohring (1993) from the Rupelian of the Mainz Basin in Germany, and from the Ilerdian of the Tremp Basin in Spain, are considered to be reworked.

Pithonella sphaerica (Kaufmann 1865)
Plate 2, Figures 13, 14
At Geulhemmerberg, *P. sphaerica* is nearly the only calcareous dinoflagellate representative in the uppermost Maastrichtian. In the lowermost Danian, it is the quantitatively dominant form (between 50 and 95% in samples G4D and G4E), especially in the clay layers. In most cases, it is accompanied by a more or less great number of other orthopithonelloid and obliquipithonelloid dinocysts. A remarkable feature is that the overall diameter of *P. sphaerica* seems to be generally reduced in the lowermost Danian, a fact comparable to the observations in Kienel (1994).

Pithonella sp. cf. *ovalis* (Kaufmann 1865)
Plate 2, Figure 15
The tests of this taxon found here are very poorly preserved and thus can only be determined with some reservation. In addition, with sizes up to 120 μm, the tests are unusually large. This form occurs very sporadically in the studied material and is restricted to clay layers and calcarenites in the lowermost Danian. It is missing in the Maastrichtian, from which it is well known elsewhere (Willems 1992). As in the case of *P. sphaerica*, its range across the K/T boundary is assumed, as already pointed out in Kienel (1994). Until now, the form has been found almost exclusively from the upper Aptian (Keupp 1987) to the Upper Maastrichtian (Villain 1975, 1977).

Pithonella sp. cf. *atopa* Keupp in Keupp & Kienel 1994
Plate 2, Figure 16
The tests found here differ from the original descriptions in Keupp and Kienel (1994) by their pore pattern, which is usually restricted to the inner wall. Their pores are also clearly visible on the considerably thicker outer wall. *Pithonella atopa*, until now, has only been known from the Upper Albian near Hannover (Germany). In this study it occurs in the uppermost Maastrichtian as well as in the lowermost Danian.

Incertae Sedis

The genus of this morphotype group, which is known from the Upper Albian, has two test types, the systematic position of which is not clear. However, they exhibit a typically pithonelloid wall structure. Therefore, Kienel (1994) and Keupp and Kienel (1994) classify the forms as calcareous dinocysts with the subfamily Pithonelloideae. Villain (1975, 1977) discusses their close relation with the Calpionellidea.

Genus *Bonetocardiella* Dufour 1968, emend. Villain 1975

Bonetocardiella neumannae Villain 1975
Plate 2, Figure 17
Until now, this species has been known exclusively from the Maastrichtian of Limburg in the Netherlands (Villain 1975) and Nennhausen in eastern Germany

(Kienel 1994). It occurs throughout the Geulhemmerberg section in all lithofacies.

Bonetocardiella maestrichtiensis (Visser 1951)
Plate 2, Figures 18, 19
This species has until now only been described from the Maastrichtian of South Limburg (Visser 1951; Villain 1975, 1977). In the Geulhemmerberg, it occurs in all lithologies of the uppermost Maastrichtian and lowermost Danian. A test composed of four individual parts, such as that shown in Plate 2, Figure 18, was found in sample G4C (Plate 2, Figure 19).

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