# Dinoflagellate cyst stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea Basin

STEPHEN LOUWYE\*, MARTIN J. HEAD† & STIJN DE SCHEPPER\*§

\*Palaeontology Research Unit, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium †Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK

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Abstract – Dinoflagellate cysts and other palynomorphs from the Pliocene Kattendijk and Lillo formations, exposed in two temporary outcrops in northern Belgium, provide new information on the biostratigraphic position and sequence stratigraphic interpretation of these units. Dinoflagellate cysts from the Kattendijk Formation indicate an age between about 5.0 Ma and 4.7-4.4 Ma (early Early Pliocene) in our sections, confirming a correlation with standard sequence 3.4 and implying a slightly greater age than the Ramsholt Member of the Coralline Crag Formation of eastern England. The unconformity at the base of the Kattendijk Formation was not seen, but presumably correlates with sequence boundary Me2 at 5.73 Ma. The overlying Lillo Formation is late Early Pliocene or early Late Pliocene (c. 4.2–2.6 Ma) in age, and the unconformity at its base may be correlated with sequence boundary Za2 at 4.04 Ma or Pia1 at 3.21 Ma. The Oorderen Sands and superjacent Kruisschans Sands members (Lillo Formation) are both part of the same depositional cycle. They were probably deposited before 2.74 Ma, and certainly before the onset of Northern Hemisphere cooling at c. 2.6 Ma. Evidence from dinoflagellate cysts indicates that both a shelly unit at the base of the Lillo Formation and the lower part of the overlying Oorderen Sands were deposited during a conspicuously cool climatic phase, with warmer temperatures returning during later deposition of the Oorderen Sands and Kruisschans Sands members. Many dinoflagellate cyst and acritarch species are reported here for the first time from the southern North Sea Basin. Selenopemphix conspicua (de Verteuil & Norris, 1992) stat. nov. is proposed.

Keywords: palynology, dinoflagellate cysts, Pliocene, Belgium, North Sea.

### 1. Introduction

The subsurface Pliocene of northern Belgium was deposited in a shallow marine environment at the southern margin of the North Sea Basin. Lithostratigraphic studies of Neogene sequences in temporary quarries in the Antwerp area were first undertaken by Dumont (1839). For more than a century, studies were limited to incomplete Pliocene successions in temporary outcrops. Only with the major expansion of Antwerp harbour in the 1950s and 1960s did more complete Pliocene sections become accessible (de Heinzelin, 1950a,b, 1952, 1955a,b; P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972). Basal gravel lags, rapid facies changes and characteristic lithologies permitted a robust lithostratigraphic subdivision (De Meuter & Laga, 1976; Laga, Louwye & Geets, 2001), but many questions remained. The construction of a biostratigraphic framework, notably with planktonic foraminifera and calcareous nannoplankton, was seriously hampered by the boreal nature of the calcareous fossils, rendering a correlation with the standard biozones, defined in lower latitudes, difficult.

† Author for correspondence: mh300@cam.ac.uk § Present address: Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK.

Integration within a sequence chronostratigraphic framework (Hardenbol *et al.* 1998; Vandenberghe *et al.* 1998) thus remained incomplete.

Two large Pliocene outcrops recently became accessible during the construction of two new docks, the Deurganck and Verrebroek docks, at Doel (Figs 1, 2). These outcrops have been sampled for palynological analysis. Dinoflagellate cysts are used frequently to reconstruct Neogene and Quaternary palaeoenvironments (e.g. de Vernal, Turon & Guiot, 1994; Head, 1996, 1997, 1998a; Versteegh & Zonneveld, 1994; Zevenboom, Brinkhuis & Visscher, 1994) and for unravelling the stratigraphic relationships of shallow marine deposits in the North Sea Basin and North Atlantic realm (e.g. de Verteuil & Norris, 1996; Head, 1998b; Louwye, De Coninck & Verniers, 1999, 2000). This paper details the biostratigraphic and palaeoecological significance of dinoflagellate cysts and other palynomorphs from the Pliocene of the Verrebroek and Deurganck dock outcrops at Doel, and contains the first published report of Pliocene dinoflagellate cysts from the Antwerp harbour in northern Belgium.

# 2. The Verrebroek and Deurganck dock localities

An overview and discussion of the lithostratigraphic history of the Pliocene Kattendijk and Lillo formations

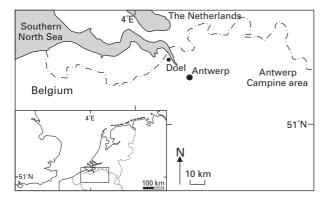


Figure 1. Map of northern Belgium and location of the area studied near Antwerp. Inset: southern North Sea Basin.

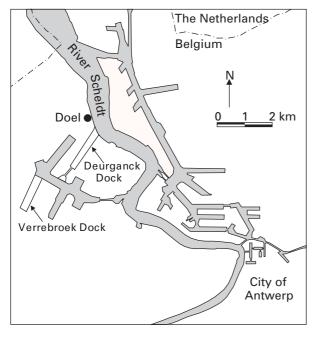


Figure 2. Location of the sections studied in the Verrebroek and Deurganck docks near Doel.

was given by De Meuter & Laga (1976). The Kattendijk and Lillo formations (Figs 3, 4) are exposed in both outcrops. The base of the Kattendijk Formation in the Verrebroek Dock is not exposed, but boreholes confirm that the unit rests unconformably on the Lower Oligocene Boom Clay Formation and locally on Miocene deposits (P. Laga, pers. comm.). A basal gravel of rounded quartz, flints, phosphate nodules and rounded bones is present at the base of the unit in the type locality at Kattendijk (Cogels, 1874; de Heinzelin, 1955c; De Meuter & Laga, 1976). The lithology of the Kattendijk Formation in both outcrops compares well to the formal lithostratigraphic description of De Meuter & Laga (1976), and consists of dark grey to greengrey medium-grained sands with dispersed shells and locally abundant fossils of the polychaete *Ditrupa* sp.

Weak cross-stratification characterizes the upper part of the formation. The boundary with the overlying Lillo Formation is unconformable.

The Luchtbal Sands Member is the lowermost member of the Lillo Formation and is a light browngrey to whitish, very shelly, glauconitic sand (Leriche, 1912; de Heinzelin, 1955c; De Meuter & Laga, 1976). The geographical distribution of this member is patchy in the Antwerp harbour area. It is suspected that the Luchtbal Sands Member is not present in our sections, but a shelly interval of similar lithology is present at the base of the Lillo Formation. At the Deurganck Dock outcrop, this interval is 1.4 m thick and comprises a lower part containing only fine shell debris and upper part consisting mainly of densely packed entire shells. A gravel layer occurs at the base of the interval in the Deurganck Dock section. In the Verrebroek Dock section, only the upper part of the interval (densely packed entire shells) is represented and has a thickness of about 40 cm. We refer to this shelly interval as the 'Basal Shelly Unit' (Fig. 4).

A gravel bed, suggesting a sequence boundary, has been observed at the boundary between the Luchtbal Sands and Oorderen Sands members in the Antwerp Harbour area (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972; Vandenberghe et al. 1998, p. 149). The boundary between our Basal Shelly Unit and the superjacent Oorderen Sands Member is rather distinct in our sections, but we did not observe a continuous erosion surface or a gravel bed at the boundary (Fig. 4). Consequently, although we regard the Basal Shelly Unit as a distinct lithofacies, it probably belongs to the same sedimentary sequence as the Oorderen Sands Member. Indeed, a shelly facies has been observed in the lowest part of the Oorderen Sands Member at the Tunnel Canal Dock, which is just 4 km east of the Deurganck Dock (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972, figs 1, 2).

According to Vandenberghe *et al.* (1998, p. 149), the Oorderen Sands Member is distinctly transgressive with respect to the Luchtbal Sands Member. The Oorderen Sands Member in the Verrebroek and Deurganck dock outcrops is lithologically more heterogeneous than the underlying Basal Shelly Unit, and compares well with the lithostratigraphic definition by De Meuter & Laga (1976). The base consists of glauconitic fine-grained sand with three compact shell layers, predominantly consisting of fragile and partly decalcified specimens of the bivalve genus *Atrina*. Weak cross-stratification was observed in the lower sandy part of the Oorderen Sands Member. The upper part is dark greyish, and contains more clay and shells and even a few shell layers (Fig. 4).

The Kruisschans Sands Member was originally described by de Heinzelin (1955*a*,*c*) and later formally defined by De Meuter & Laga (1976, p. 139) as a 'grey-green fine to medium fine, but locally even coarse

Age	Formation	Microfossil group	Ве	Benthic forams		Planktonic forams	Ostracods	Benthic molluscs	Planktonic molluscs	Gaedidae otoliths	Bolbo- forma	Dinofla cy:	
(De Meuter & Laga, 1976)	(De Meuter & Laga, 1976)	Biozones	De Meuter & Laga (1976)	IGCP 124 Working Group (1988)	Doppert, Laga & De Meuter (1979)	Spiegler et al. (1988)	Gramann & Uffenorde (1988)	Hinsch (1988)	Janssen & King (1988)	Gaemers (1988)	Spiegler (2001)	Powell (1992)	Manum et al. (1989)
		Kruisschans Sands	Elphidiella hannai	B12		/		BM22C	/	Zone	/	Mch Biozone	
Late	Oord	Oorderen Sands	Cribro- nounion excavatum Zone	Willems et al. (1988)	BFN6	/	Loxo- concha bitruncata	BM22B	Pteropod Zone	19	upper Bolbo- forma costair- regularis Zone	Louwye & Laga (1998)	/
		Luchtbal Sands	Cibicides lobatulus Zone	B11 Willems et al. (1988)	BFN5	/	Muellerina lacunosa Zone	BM22A	22	Zone 18	/	/	/
Early Pliocene	Kattendijk Formation		Mons- peliensis pseudo- tepida  Florilus boueanus Zone	B10 Willems et al. (1988)	BFN4	NPF16 Neoglobo- quadrina atlantica Zone Hooyberghs & Moorkens (1988)		BM21C	Pteropod Zone 21	Zone 17	lower Bolbo- forma costair- regularis Zone	Mch Biozone Louwye & Laga (1998)	A. anda- lousiensis Zone Louwye & Laga (1998)

Figure 3. Biozones recognized in the Kattendijk and Lillo formations.

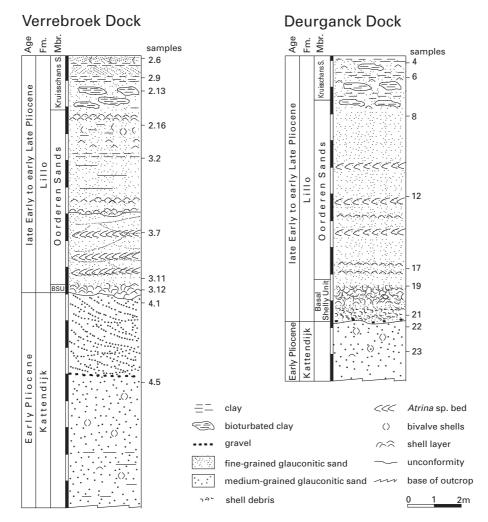


Figure 4. The Verrebroek and Deurganck dock outcrops with sample position. Fm = formation, Mbr = member, BSU = Basal Shelly Unit.

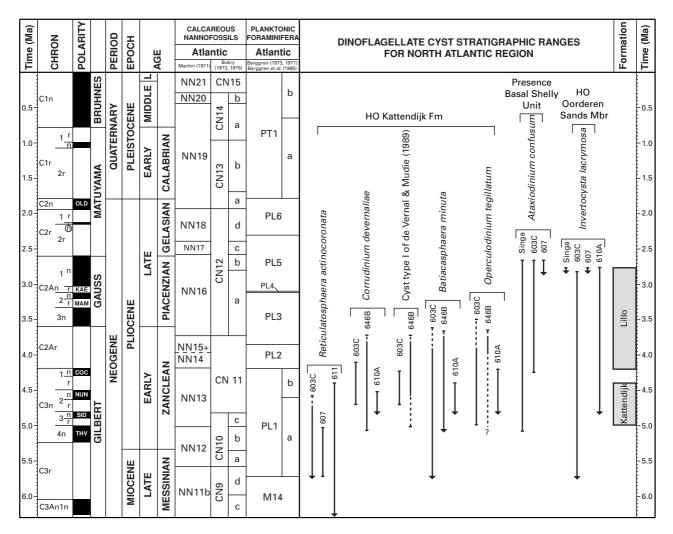


Figure 5. Stratigraphic ranges of selected dinoflagellate cyst species for the North Atlantic region calibrated to the standard time scale of Berggren *et al.* (1995). Based on: DSDP Hole 603C, western North Atlantic (Head & Norris, 2003; M. J. H., unpub. data); ODP Hole 646B, Labrador Sea (de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989); DSDP Site 607, central North Atlantic (Mudie, 1987; Versteegh, 1997); DSDP Hole 610A, eastern North Atlantic (S. D. S. and M. J. H., unpub. data); and the Singa section in Italy (Versteegh & Zevenboom, 1995; Versteegh, 1997). A dashed line indicates uncertainty in the stratigraphic range. The ages of the Kattendijk and Lillo formations are based on the present study.

glauconiferous sand with fine shell remains and many small shells, many lenses and layers of pure dark grey clay, mainly 1 to 1.5 cm thick, but locally up to 10– 15 cm'. A distinctive basal gravel was observed by de Heinzelin (1952, 1955a,c) at the type locality in the Antwerp harbour, and this may be a sequence boundary. However, De Meuter & Laga (1976) stressed the absence of a distinct boundary with the underlying Oorderen Sands Member, and our observations of the Verrebroek and Deurganck dock sections indicate a gradual transition between the Oorderen Sands and Kruisschans Sands members (Fig. 4), which implies that they belong to the same depositional sequence. We presently accept that the interval with heavily and extensively bioturbated clay in the uppermost part of our sections indeed represents the Kruisschans Sands Member because it is identical in appearance to the type area; this is an assumption, however, that requires testing.

# 3. Biostratigraphic and palaeoecological data on the Belgian Pliocene

Within the Belgian Pliocene sequence, the highest biostratigraphic resolution has been obtained using benthic foraminifers (De Meuter & Laga, 1976) and benthic molluscs (Hinsch, 1988), because calcareous planktonic microfossils have limited utility in these deposits (Fig. 3).

Hooyberghs & Moorkens (1988) recognized the planktonic foraminiferal zone NPF 16 of Spiegler, Gramann & Von Daniels (1988) in the Kattendijk Formation. This zone is identical to zone NSP 15 of King (1983) and equates approximately to zones N18 to N19 of Blow (1979), which are themselves equivalent to Zone PL1 of Berggren *et al.* (1995; Hardenbol *et al.* 1998) (Fig. 5). Zone NPF 16 together with the benthic foraminiferal zone B10, benthic mollusc zone BM21C, otolith zone 17, and pteropod zone 21 (Fig. 3) together

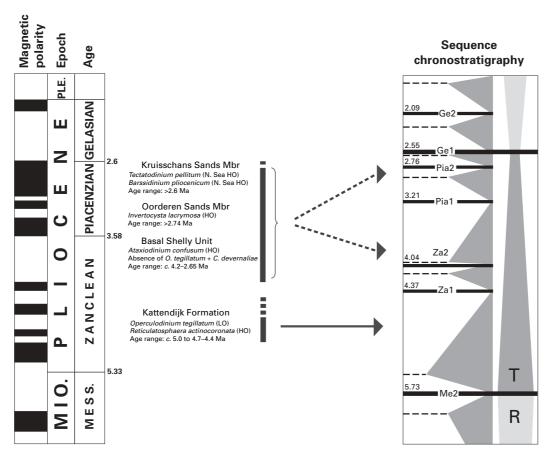


Figure 6. Sequence stratigraphic interpretation of the Verrebroek and Deurganck dock sections based on dinoflagellate cyst stratigraphy (this study). Ages of lithostratigraphic units are constrained by vertical lines (solid = firmly constrained, dashed = tentatively constrained). Units are correlated with the depositional sequence chronostratigraphy of Hardenbol *et al.* (1998): a solid arrow indicates a confirmed correlation, and dashed arrows indicate tentative correlations. The Basal Shelly Unit, Orderen Sands Member and Kruisschans Sands Member apparently all belong to the same stratigraphic sequence in our sections, but two alternative correlations are given. T and R = transgressive and regressive facies cycles. The standard time scale of Berggren *et al.* (1995) is used.

indicate an early Zanclean age for the Kattendijk Formation. The oldest inferred age for the Kattendijk Formation was assigned by Janssen & King (1988) who placed their Pteropod Zone 21 at the Miocene—Pliocene transition. The calcareous nannofossil *Reticulofenestra minutula* from the Kattendijk Formation indicates only an age younger than Late Miocene (Verbeek, Steurbaut & Moorkens, 1988).

The Luchtbal Sands Member, which is probably not represented in the Verrebroek and Deurganck dock sections (Figs 4, 6), contains the benthic foraminiferal zone B11, benthic mollusc zone BM22A, and otolith zone 18, all of which indicate a late Zanclean age.

Benthic foraminiferal zone B12 and otolith zone 19 were recognized in the Oorderen Sands and Kruisschans Sands members and point to an early Late Pliocene age. The upper Zanclean–lower Piacenzian benthic mollusc zone BM22B was recognized in the Oorderen Sands Member, while the Kruisschans Sands Member contains the Upper Pliocene BM22C zone. Pteropod zone 22, recognized in the Lillo Formation, spans the upper Lower Pliocene and Upper Pliocene. The oldest age proposed for the Oorderen Sands Member is late Early Pliocene (Spiegler, 2001).

Gramann & Uffenorde (1988) recognized only one ostracod biozone, the *Loxoconcha bitruncata–Muellerina lacunosa* Zone, in the Pliocene succession. The Zanclean (pars) to Lower Pleistocene dinoflagellate cyst biozone Mch (*Melitasphaeridium choanophorum*) of Powell (1992) was identified in the Kattendijk and Lillo formations by Louwye & Laga (1998), who also identified the Upper Miocene–Pliocene *Achomosphaera andalousiensis* Biozone of Manum *et al.* (1989) in the Kattendijk Formation.

The planktonic foraminifers of the Kattendijk Formation reflect cool-temperate sea-surface conditions (April temperatures of less than 7.2 °C) and deposition in a near coastal environment with normal salinity and no fluviatile influence (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972). Pyrite in the foraminiferal chambers indicates anaerobic intrasedimentary conditions. A water depth of 30–50 m is inferred from lithological, sedimentological and palaeontological (otolith) evidence (Gaemers, 1988).

Bryozoans and benthic foraminifers from the Luchtbal Sands Member reflect deposition in a clear water, high energy, open-marine environment shallower than wave base and of normal salinity (P. Laga, unpub.

Table 1. Distribution of marine and terrestrial palynomorphs from the Verrebroek Dock section

Lithological unit		ndijk Fm	BSU			en Sands Member			schans Sa	ınds Mbı
Sample no.	4.5	4.1	3.12	3.11	3.7	3.2	2.16	2.13	2.9	2.6
Dinoflagellate cysts (raw counts)										
Operculodinium? sp. 1	1									
Trinovantedinium ferugnomatum	+	+								
Impagidinium pallidum	+	+				(1)				
Batiacasphaera minuta Corrudinium devernaliae	1 1	19 +				(+)				
Operculodinium tegillatum	12	33	(+)							
Reticulatosphaera actinocoronata	13	3	(+)			(1)		(1)		
Corrudinium? labradori		+	( )					( )		
Selenopemphix armageddonensis		2								
Achomosphaera andalousiensis suttonensis			+							
Capisocysta lyelii			+	_						
Hystrichokolpoma rigaudiae rigaudiae		+	+	2						
cf. Alexandrium tamarense-type cysts of				1						
Rochon et al. (1999) Barssidinium graminosum	1	1	4		1	+				
Invertocysta lacrymosa	15	2	2	1	3	+				
Tuberculodinium vancampoae	13	2	_	1	3	+				
Pyxidinopsis sp. 1			+		3	+				
Impagidinium sp. indet.		1					1			
Melitasphaeridium choanophorum	+	2		1	2		+	+		
Spiniferites mirabilis	3	4	5	+	1	2	2	+		
Selenopemphix spp. indet.		1						1		
Spiniferites sp. 1			+			++	+	+		
Lejeunecysta cf. fallax Dapsilidinium pseudocolligerum	+		+			+		1 +	+	
Selenopemphix nephroides	+		'				1	'	+	
Lejeunecysta catomus		2		2	+	1	1	1	1	
Lejeunecysta marieae		-		2 +		4	2	3	2	
cf. Brigantedinium sp. of Head et al. (1989)						7	+	+	10	
Polykrikos kofoidii cysts						+			+	
Geonettia waltonensis									+	
Lejeunecysta hatterasensis									3	
Spiniferites elongatus									+	
Trinovantedinium cf. sterthensis Achomosphaera andalousiensis andalousiensis	6	5	4	3	4	+	4	+	+	1
Achomosphaera/Spiniferites spp. indet.	112	93	58	37	70	57	103	98	120	104
Amiculosphaera umbraculum	3	7	2	31	1	3	3	70	+	+
Ataxiodinium zevenboomii	1	+	2	+	3	+	+			1
Barssidinium pliocenicum	1	17	4	14	2	15	7	6	5	6
Bitectatodinium raedwaldii	15	6	33	49	17	31	5	11	4	14
Brigantedinium spp. indet.	4	14	1	32	5	49	23	35	9	6
Echinidinium euaxum	+	+		-	4.0	1	2	+	7	12
Heteraulacacysta sp. A of	+		43	6	19	45	26	19	20	43
Costa & Downie (1979)	+			5			2		1	
Lejeunecysta spp. indet. Lingulodinium machaerophorum	+	8	6	3	94	+	2 +	+ 11	1 +	11
machaerophorum	'	O	O		74	'	'	11	'	11
Operculodinium centrocarpum sensu	41	3	35	24	18	11	22	19	22	41
Wall & Dale (1966)										
Operculodinium? eirikianum	15	12					2			1
Pentapharsodinium dalei cysts	+								+	1
Selenopemphix brevispinosa	4	2			1		1	2		1
Selenopemphix dionaeacysta	1	4		1	5	5	+		+	1
Tectatodinium pellitum	+	+		+	++	3	+		2	1
Ataxiodinium cf. choane Lejeunecysta fallax		+ +			+		+		+	1 2
Dejeunecysia janax Operculodinium israelianum		2	19	3	+	8	41	29	84	42
Organic membrane of calcareous cyst		1	+	3	+	+	1	3	2	2
Selenopemphix quanta		+	2	1			2	5	11	5
Trinovantedinium glorianum		4	1	6	1	4	+	+	2	2
Forma D of Wrenn & Kokinos (1986)			4	4		+	+	+	+	1
Habibacysta tectata			21	56		+				1
Spiniferites falcipedius			+	1				+	4	3
Spiniferites membranaceus			4			1	+		1	1
Trinovantedinium variabile			+	++						+
Bitectatodinium tepikiense Brigantedinium cariacoense				+		+	+	+	3	1 +
Бriganteatnium cartacoense Filisphaera filifera filifera						+	F		3	+
ruispnaera uutera uutera						,	+	4	3	+

Table 1. Continued.

Lithological unit	Katte	ndijk Fm	BSU	Oc	orderen S	ands Mer	Kruisschans Sands Mbr			
Sample no.	4.5	4.1	3.12	3.11	3.7	3.2	2.16	2.13	2.9	2.6
Quinquecuspis concreta Selenopemphix conspicua stat. nov. Nematosphaeropsis labyrinthus Achomosphaera sp. cf. A. andalousiensis of Head (1993)							+ +	+	1 6 6	3 1 2 4
Selenoewsta psuchra Selenopemphix? sp. 1 Trinovantedinium spp. indet. Spiniferites bentorii									1 5 +	+ 4 + 5
Total in-situ dinoflagellates Estimated total in-situ dinoflagellates per gram dry weight	250 593	250 1405	250 3236	249 308	250 791	247 985	250 2543	249 7091	335 5962	324 982
Reworked dinoflagellates (unidentified)	19	8	4	7	3	7	13	21	141	99
Green algae Tasmanites Pediastrum boryanum Botryococcus cf. braunii	1 1	1		5		2	1 1	1 1	1	1 1
Marine algae incertae sedis Acritarch sp. 1 of Head et al. (1989) Paleostomocystis globosa Cymatiosphaera? invaginata Cyclopsiella elliptica	1 2	4 +		+	1					
Micrhystridium sp. 2 of Head (1993) Small spiny acritarchs Halodinium majus	2	5			2 26	10	2		2	
Cyclopsiella? trematophora Nannobarbophora walldalei	1	3 +	16	118	9	37	9 +	9	10 3	15 2
Incertae sedis 1 Paralecaniella indentata (reworked?)			2	5	2	1 2	1	2 1	11 +	2
Other marine palynomorphs Invertebrate remains Foraminiferal linings	5	6		11	17	9	1 7	1 13	3 25	10
Terrestrial palynomorphs Non-bisaccate pollen and spores Bisaccate pollen	3 127	7 124	3 38	8 123	20 47	15 136	20 294	2 291	58 898	66 705
Sample data Sample dry weight (in grams) Quantity of <i>Lycopodium clavatum</i> tablets Quantity of <i>Lycopodium clavatum</i> spores counted	100 1 45	100 1 19	75 1 11	75 1 116	75 1 45	75 1 36	75 1 14	75 1 5	75 1 8	75 1 47

Raw counts are given. A '+' indicates a taxon present but recorded outside the routine count. Parentheses () indicate presumed reworking. BSU – Basal Shelly Unit. The Basal Shelly Unit, Oorderen Sands Member and Kruisschans Sands Member all belong to the Lillo Formation. Sample positions are shown in Figure 4.

Ph.D. thesis, Katholieke Universiteit Leuven, 1972). Abundant shell debris in the Luchtbal Sands Member formed an ideal substrate for the benthic foraminifer *Cibicides*, which occurs in high numbers. Biological productivity was high, sedimentation rates were low, and the depositional environment was shallower than for the Kattendijk Formation. The Luchtbal Sands Member is probably not represented in our sections.

Benthic foraminifers from the superjacent Oorderen Sands Member clearly point to a brackish influence. The presence of near-coastal influences is corroborated by a reduction in the abundance and species diversity of planktonic foraminifers (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972). The lithological homogeneity of the sediments was probably caused by bioturbation, which in turn indicates slow sedimentation rates. This is confirmed by the presence of the bivalve *Atrina fragilis* in the lower sandy part of the

Oorderen Sands Member. *Atrina fragilis* prefers a quiet, clear-water environment with slow sedimentation rates and is absent from the upper, more clay-rich part of the Oorderen Sands Member where more turbid and higher energy conditions prevailed during deposition. The otolith association suggests a water depth between 10 and 20 m (Gaemers, 1988).

Higher numbers of benthic foraminifers of the genera *Elphidiella* and *Cribrononion* in the Kruisschans Sands Member point to deposition in shallow and turbulent waters, where high sedimentation rates prevailed (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972). Bioturbation is less intense than in underlying units. Molluscs from the Kruisschans Sands Member indicate cooling (Marquet, 1993), and Elasmobranchidae fish remains in this member also indicate cool waters (Vandenberghe *et al.* 2002). A possible correlative of the Kruisschans Sands Member

Table 2. Distribution of marine and terrestrial palynomorphs from the Deurganck Dock section

Lithological unit	Katten	dijk Fm	BS	SU	Oorderen Sands Member			Kruisschans Sands Mbr	
Sample no.	23	22	21	19	17	12	8	6	4
Dinoflagellate cysts (raw counts)									
Batiacasphaera minuta	6	2					(+)		
Corrudinium devernaliae	1	5			(1)				
Operculodinium tegillatum	16	29	(+)						
Reticulatosphaera actinocoronata	7	4	(1)						
Corrudinium? labradori Spiniferites elongatus		+ 1							
Spinijerites etongatus Filisphaera filifera	1	3	30						
Bitectatodinium? serratum	•	5	1						
Hystrichokolpoma rigaudiae rigaudiae		+	+						
Filisphaera microornata			+						
Ataxiodinium confusum s.s.				+					
Operculodinium? sp. 1	2	1	1	1	1				
Invertocysta lacrymosa	2 1	1	+		3 1	++			
Trinovantedinium glorianum Tuberculodinium vancampoae	1	1			1	3			
Ataxiodinium choane		1		+		1			
Brigantedinium cariacoense						+			
Selenopemphix conspicua stat. nov.						1			
Trinovantedinium sterthense						1			
Achomosphaera andalousiensis	3	2	7	8	2		1		
andalousiensis	2	1		2	2		22		
Lingulodinium machaerophorum machaerophorum	2	1	+	3	2		22		
Operculodinium? eirikianum	1	7	32	+		2	4		
Selenopemphix brevispinosa	6	1	32	·		1	+		
Achomosphaera andalousiensis suttonensis			4	3		8	+		
Lejeunecysta catomus						+	1		
Trinovantedinium variabile						+	2		
Lejeunecysta psuchra							1		
Trinovantedinium sp. cf. T. applanatum	2	1	1				1	2	
Amiculosphaera umbraculum Habibacysta tectata	2 3	1	1	24	1	+ 2	2	3 4	
Lejeunecysta fallax	1	+		24	+	2		1	
Selenopemphix spp. indet.	4	'		+	2	7	3	3	
Spiniferites mirabilis	•	2			_	•	-	+	
Pyxidinopsis sp. 1			3	3	3	3	1	3	
Melitasphaeridium choanophorum								1	
Operculodinium giganteum		2		•				2	
Ataxiodinium zevenboomii	1	3 2	+ 2	2 2	1 2		+	+	2 2
Barssidinium graminosum Barssidinium pliocenicum	3 19	2	2	9	11	+	2	3	13
Bitectatodinium raedwaldii	16	12	+	54	44	15	10	4	8
Brigantedinium spp. indet.	12			5	7	17	36	14	36
Dapsilidinium pseudocolligerum	1	1	2	+	2	+	+	+	1
Operculodinium centrocarpum sensu	22	9	13	50	59	8	35	33	5
Wall & Dale (1966)									
Operculodinium israelianum	7	8	2	1		11	2	37	26
Selenopemphix dionaeacysta	3 5			+		+	7		1
Selenopemphix nephroides Selenopemphix quanta	2			+	++	1 5	2	+ 1	2
Achomosphaera/Spiniferites spp. indet.	90	117	145	75	50	128	86	112	91
Spiniferites falcipedius	4	2	1	73	50	120	1	2	1
Spiniferites hyperacanthus	4	10	+	1	10	6	7	3	8
Tectatodinium pellitum	4		1	+	2	1	1	4	2
Heteraulacacysta sp. A of Costa &		15	+	4	32	22		14	18
Downie (1979)									
Impagidinium sp. indet.		+	1			+			1
Spiniferites membranaceus Echinidinium euaxum		4	4	++	+ 6	2 3	9	++	3 2
Forma D of Wrenn & Kokinos (1986)				2	3	3	7	1	+
Organic membrane of calcareous cyst				1	3	1	3	2	14
Lejeunecysta spp. indet.				+	1	+	5	1	3
Selenopemphix? sp.2 of Head (1993)				1			5	2	7
Stelladinium? sp. 1						+	+	+	+
Lejeunecysta marieae							1		+
cf. Brigantedinium sp. of Head et al. (1989)									1
Geonettia waltonensis Trinovantedinium spp. indet.									1
11 movameamum Spp. muct.	249	250	249	249	248	249	245	250	250

Table 2. Continued.

Lithological unit	Kattendijk Fm		BSU		Oorderen Sands Member			Kruisschans Sands Mbr	
Sample no.	23	22	21	19	17	12	8	6	4
Estimated total in-situ dinoflagellates per gram dry weight	913	603	1364	791	160	678	424	1483	3747
Reworked dinoflagellates (unidentified)	7	17	7	8	16	15	22	19	36
Green algae									
Tasmanites	1			+		+		1	1
Marine algae incertae sedis Algal cyst sp. 1 of Head (1996) Cyst type I of de Vernal & Mudie (1989) Paralecaniella indentata (reworked?)		+ + 2 1							
Pterospermella sp. indet. Incertae sedis 1	1	1					5	+	
Cymatiosphaera spp.	1			3	7		1	1	
Cyclopsiella spp. indet.	7		+	1	3	9	14	4	4
Nannobarbophora walldalei	+			+		1	1	+	3
Small spiny acritarchs	6	9	1		2	2	3	2	5
Cyclopsiella? trematophora		+	+	6	22	5	26		5
Other marine palynomorphs Foraminiferal linings	40		+	2	17	3	31	9	36
Terrestrial palynomorphs									
Non-bisaccate pollen and spores	9	5	6	10	15	24	29	26	34
Bisaccate pollen	78	8	0	66	91	72	159	131	512
Sample data									
Sample dry weight (in grams)	75	75	75	75	75	75	75	75	75
Quantity of <i>Lycopodium clavatum</i> tablets	2	2	2	2	2	2	2	2	2
Quantity of Lycopodium clavatum spores counted	78	118	52	90	441	105	168	48	19

Raw counts are given. A '+' indicates a taxon present but recorded outside the routine count. Parentheses () indicate presumed reworking. BSU – Basal Shelly Unit. The Basal Shelly Unit, Oorderen Sands Member and Kruisschans Sands Member all belong to the Lillo Formation. Sample positions are shown in Figure 4.

at Grobbendonk in the Antwerp–Campine area of northern Belgium has yielded pollen indicative of a cold climate (Vandenberghe *et al.* 2002).

#### 4. Materials and methods

Ten samples from the Verrebroek Dock outcrop and nine samples from the Deurganck Dock outcrop were examined in detail for organic-walled dinoflagellate cysts, acritarchs and other marine palynomorphs (Tables 1, 2). Seventy-five or 100 grams of dry sediment were processed for each sample (Tables 1, 2). Standard maceration techniques were used, involving removal of carbonates with hot 10 % HCl followed by digestion for 6 hours in hot 38 % HF. After rinsing to neutrality, samples were gently stirred and decanted several times in order to remove all organic matter from the remaining mineral fraction, which was then discarded. The organic residues were given ultrasound for about 15 seconds, then sieved on a 20 μm Nytal nylon screen, stained with Safranin-O and mounted on microscope slides using glycerine jelly. Neither oxidation nor alkali treatments were applied to the material.

About 250 dinoflagellate cysts were counted at  $\times$  400 magnification for each sample, and the rest of the slide was then searched for rare specimens. The numbers of acritarchs, Chlorophyta, foraminiferal linings, invertebrate remains, pollen and spores were also noted during the count of 250 dinoflagellate

cysts. Pollen and other terrestrial palynomorphs were studied in detail from the two uppermost samples of the Verrebroek Dock outcrop (VBD 2.9 and VBD 2.6) using those slides prepared for dinoflagellate cyst analysis. The diversity and concentration of pollen in underlying samples were too low to facilitate detailed study. Lycopodium clavatum tablets (batch no. 938934, X = 10679,  $s = \pm 426$  per tablet; obtained from the Subdepartment of Quaternary Sciences, Department of Geology, Lund University, Sweden) were added to help calculate the concentration of dinoflagellate cysts.

Dinoflagellate cysts are moderately to exceptionally well preserved. A preservational bias by oxidation seems unlikely since protoperidiniacean species are well preserved and well represented throughout the Verrebroek and Deurganck dock outcrops. Reworking of pre-Neogene dinoflagellate cysts is relatively unimportant (<12.6 % of total cysts counted), except in the uppermost two samples of the Verrebroek Dock, VBD 2.9 and 2.6, where up to 30 % were counted. Reworked dinoflagellate cysts are mainly Palaeogene species, although a few Mesozoic species were also noted. Photomicrographs were taken with a Leica DC3 digital camera mounted on a Leica DMR microscope (Figs 7-12) and on a JEOL 6400 SEM (Fig. 13). The nomenclature follows Williams, Lentin & Fensome (1998), Louwye (1999), Head (2000, 2003) and Head & Norris (2003). Selected taxa are discussed in the Appendix. This paper uses the time scale of Berggren

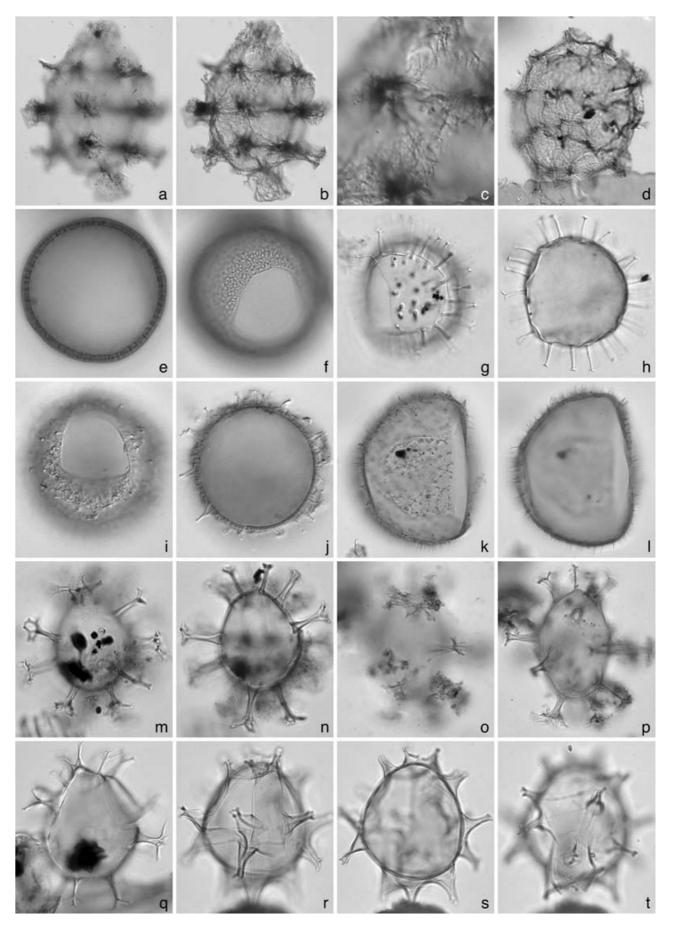


Figure 7. For legend see facing page.

et al. (1995). All slides are housed in the Palaeontology Research Unit, Ghent University.

### 5. Results from dinoflagellate cyst analysis

A total of 76 species of dinoflagellate cyst have been recorded in the present study (Tables 1, 2), of which the following are documented for the first time from the Pliocene of the southern North Sea Basin: Barssidinium graminosum, cf. Alexandrium tamarense-type cysts of Rochon et al. 1999, Corrudinium devernaliae, Corrudinium? labradori, Echinidinium euaxum, Lejeunecysta fallax, Lejeunecysta hatterasensis, Lejeunecysta psuchra, organic linings of calcareous cysts, Pentapharsodinium dalei cysts, Polykrikos kofoidii cysts, Pyxidinopsis sp. 1, Quinquecuspis concreta, Selenopemphix conspicua stat. nov., Selenopemphix sp. 1, Spiniferites bentorii, Spiniferites sp. 1, Trinovantedinium sterthense and Trinovantedinium variabile. The following acritarchs were also recorded for the first time: Acritarch sp. 1 of Head, Norris & Mudie (1989), Cyclopsiella elliptica, Cyst type I of de Vernal & Mudie (1989), Halodinium majus, and Incertae sedis 1. Most of these species are illustrated (Figs 7-13).

# 6. Stratigraphic significance of the dinoflagellate cysts

The stratigraphic ranges of dinoflagellate cyst species recorded in the present study are based on a number of sites including DSDP Hole 603C, western North Atlantic (Head & Norris, 2003; M. J. H., unpub. data); ODP Hole 646B, Labrador Sea (de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989); DSDP Site 607, central North Atlantic (Mudie, 1987; Versteegh, 1997); DSDP Hole 610A, eastern North Atlantic (S. D. S. and M. J. H., unpub. data); and the Singa section in Italy (Versteegh & Zevenboom, 1995; Versteegh, 1997). Most of these sites have magnetostratigraphic and/or oxygen isotope control, although ODP Hole 646B in the Labrador Sea is constrained primarily

by calcareous nannofossil datums (Knüttel, Russell & Firth, 1989) which may be diachronous at these high latitudes. Dinoflagellate ranges for ODP Hole 646B must therefore be regarded as approximate. The stratigraphic ranges of selected species are given in Figure 5.

#### 6.a. Kattendijk Formation

Few species have their highest occurrence (HO) in the Kattendijk Formation. Batiacasphaera minuta (Fig. 8g-i) is present in the Kattendijk Formation and has its HO in Subchron C2Ar (3.6-4.2 Ma) in DSDP Hole 603C in the western North Atlantic, with occurrences younger than about 3.9 Ma possibly representing reworking (M. J. H., unpub. data). In DSDP Hole 610A, eastern North Atlantic, it has a highest persistent occurrence in Subchron C3n1r (c. 4.4 Ma; S. D. S. and M. J. H., unpub. data). In ODP Hole 646B, Labrador Sea, this species has a highest common and persistent occurrence close to the calcareous nannofossil zone NN15/NN16 boundary (c. 3.8 Ma; as Batiacasphaera sphaerica, in de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989), with sporadic higher occurrences through zone NN16 probably representing reworking. Accordingly we place the HO of B. minuta in the North Atlantic within the range of c. 4.4 and 3.6 Ma, but probably no younger than c. 3.8 Ma (Fig. 5).

Operculodinium tegillatum (Fig. 7i, j) is restricted to the Kattendijk Formation, the only other published records being from the Coralline Crag Formation in eastern England (Head, 1997). In DSDP Hole 603C, western North Atlantic, O. tegillatum has a range base at c. 5.0 Ma and a HO at c. 3.5 Ma (near the Early—Late Pliocene boundary), but with occurrences younger than about 3.9 Ma possibly representing reworking (M. J. H., unpub. data). In DSDP Hole 610A, eastern North Atlantic, it has a highest persistent occurrence in Subchron C3n1n (c. 4.2 Ma; S. D. S. and M. J. H., unpub. data), with sporadic higher occurrences considered to represent reworking. This species has a comparable HO close to the calcareous nannofossil

Figure 7. Dinoflagellate cysts from the Verrebroek Dock (VBD) and Deurganck Dock (DGD) sections. Various magnifications. Max. dia. = Maximum diameter. (a–d) Cysts of *Polykrikos kofoidii* Chatton. (a–c) lateral view of (a) upper surface, (b) mid focus, and (c) close-up of upper surface showing fibrous wall; length including processes, 101 μm; sample VBD 2.9 p1, R19/3. (d) lateral view of upper surface; length including processes, 64 μm; sample VBD 2.9 p1, M28/2. (e, f) *Habibacysta tectata* Head, Norris & Mudie. Dorsal view at (e) mid focus and (f) upper surface; max. dia., 38 μm; sample VBD 3.12 p2, R18/2. (g, h) *Operculodinium centrocarpum sensu* Wall & Dale, 1966. Right lateral? view of (g) upper surface, and (h) mid focus. This specimen has an almost smooth wall surface. Central body max. dia., 32 μm; sample VBD 2.6 p1, R33/4. (i, j) *Operculodinium tegillatum* Head. Dorsal view of (i) dorsal view, and (j) mid focus; central body length, 32 μm; sample VBD 4.5 p2, S22/4. (k, l) *Operculodinium israelianum* (Rossignol). View uncertain of (k) upper surface, and (l) mid focus; note spongy-fibrous wall surface; central body max. dia., 92 μm; sample VBD 2.6 p1, Q28/4. (m, n) *Achomosphaera andalousiensis* subsp. *andalousiensis* (autonym). Ventral view of (m) ventral surface, and (n) mid focus; central body length, 36 μm; sample VBD 2.6 p1, P29/1. (o, p) *Achomosphaera andalousiensis* subsp. *suttonensis* Head. Ventral view at (o) high focus, and (p) mid focus; central body length, 51 μm; sample DGD 19, Y40/3. (q) *Spiniferites bentorii* (Rossignol). Left lateral view at mid focus; central body length, 53 μm; sample VBD 2.6 p1, W40/0. (r–t) *Spiniferites* sp. 1. Dorsal view of (r) dorsal surface, (s) mid focus, and (t) ventral surface, showing characteristic broad-based processes with weakly-developed terminations; central body length, 40 μm; sample VBD 3.12 p2, M27/0.

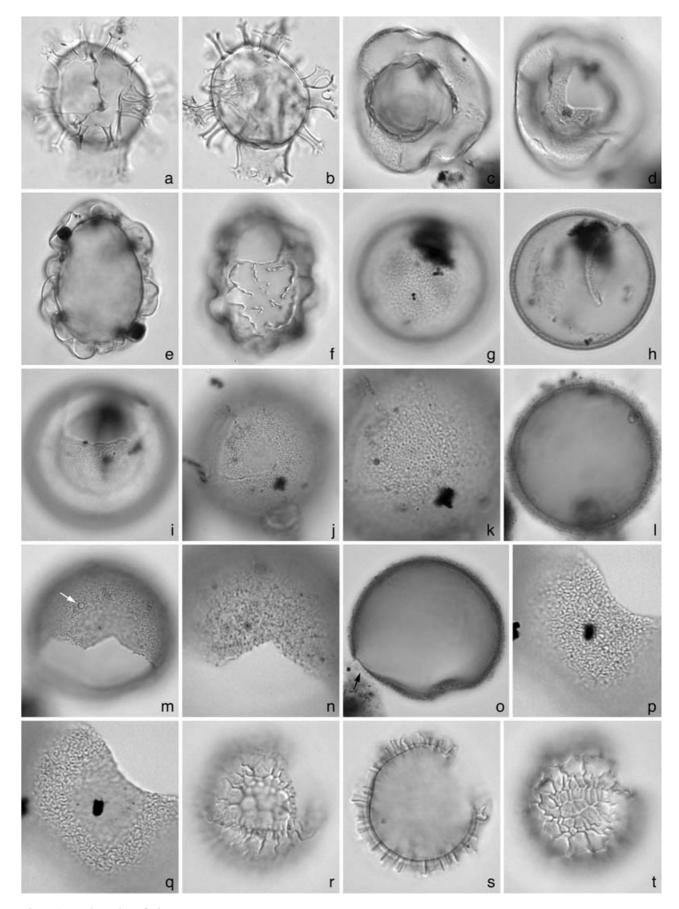


Figure 8. For legend see facing page.

zone NN15/NN16 boundary (c. 3.8 Ma) in ODP Hole 646B in the Labrador Sea (as *Operculodinium crassum*, in de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989) (Fig. 5).

Corrudinium devernaliae (Fig. 9a-c) is restricted to the Kattendijk Formation, since we assume that a single specimen recorded from the Oorderen Sands Member of the Deurganck Dock is reworked. This species has a well-delimited Early Pliocene range in DSDP Hole 603C, western North Atlantic, extending from Subchron C3n2r (4.7 Ma) into the early part of Subchron C2Ar (c. 4.1 Ma) (Head & Norris, 2003). In ODP Hole 646B, Labrador Sea, it ranges from the top of the Lower Pliocene calcareous nannofossil zones NN12 through NN15 (c. 5.1–3.8 Ma) (as Corrudinium sp. I, in de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989). Corrudinium devernaliae has a HO in the Early Pliocene Nunivak Subchron (C3n2n, c. 4.5 Ma) of DSDP Hole 610A in the eastern North Atlantic (S. D. S. and M. J. H., unpub. data), and a specimen was illustrated from the Lower Pliocene calcareous nannofossil zone NN15 of DSDP Site 611 in the northern North Atlantic (as Corrudinium harlandii, in Mudie, 1987) (Fig. 5).

A single well-preserved specimen of Cyst type I of de Vernal & Mudie, 1989 (Fig. 12e, f) was found in the Kattendijk Formation at the Deurganck Dock. This acritarch has a narrow range within the Lower Pliocene of the Labrador Sea (undifferentiated nannofossil zones NN13–14 through NN15: de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989), and has a similarly narrow range, between subchrons C3n2r and C3n1n (c. 4.7 and 4.2 Ma), in the western North Atlantic DSDP Hole 603C (M. J. H., unpub. data) (Fig. 5).

Reticulatosphaera actinocoronata (Fig. 9k) is most frequent in the Kattendijk Formation, and rare specimens higher in the Deurganck and Verrebroek dock sequences are considered reworked. The HO of this species in the North Atlantic region lies within the Early Pliocene (Head, Norris & Mudie, 1989, p. 439). In particular, R. actinocoronata has a HO at Subchron C3n4n (Thyera Subchron, c. 5.0 Ma) in DSDP Site

607, central North Atlantic, and at Subchron C3n1r (c. 4.4 Ma) in DSDP Site 611, northern North Atlantic (as Cannosphaeropsis sp. 1 and ?Cannosphaeropsis sp. 1, respectively, in Mudie, 1987; Baldauf et al. 1987). Because species ranges are indicated only by presence/absence data in Mudie (1987), it is not possible to judge whether reworking may account for the highest occurrences. In the western North Atlantic, DSDP Site 603C, this species has a highest common occurrence at Subchron C3n2r (c. 4.7 Ma), although rare but persistent occurrences extend into Subchron C2Ar (c. 4.0 Ma) and it is not clear if these occurrences represent reworking (M. J. H., unpub. data). In summary, R. actinocoronata ranges no higher than about 4.4 Ma (early Zanclean) in the North Atlantic region, and this figure might be closer to c. 4.7 Ma based on data from DSDP Site 603C (Fig. 5).

Cysts of *Pentapharsodinium dalei* (Fig. 10e, f) are found in both the Kattendijk Formation and the Kruisschans Sands Member of the Verrebroek Dock section. The lowest previous record of this species was from the Lower Pleistocene Marine Isotope Stage (MIS) 27 of the Labrador Sea (de Vernal *et al.* 1992), although *Pentapharsodinium* cf. *dalei* was recorded from the Upper Pliocene of the Arctic Sea (Matthiessen & Brenner, 1996). The presence of this species in the Verrebroek Dock sequence extends its stratigraphic range back to the Early Pliocene.

## 6.b. Basal Shelly Unit, Lillo Formation

A single specimen of *O. tegillatum* in the Basal Shelly Unit at the base of the Lillo Formation is probably reworked. Forma D of Wrenn & Kokinos (1986) (Fig. 9l) occurs regularly in the Basal Shelly Unit and the Oorderen Sands Member. This species has its lowest occurrence (LO) in the Lower Pliocene, foraminiferal zone 19 (Blow, 1979) of the De Soto Canyon, Mexico (Wrenn & Kokinos, 1986). A single specimen of *Ataxiodinium confusum sensu stricto* (Fig. 8c, d) is recorded in the Basal Shelly Unit of the Deurganck Dock. This species has a stratigraphic base within the

Figure 8. Dinoflagellate cysts from the Verrebroek Dock (VBD) and Deurganck Dock (DGD) sections. Various magnifications. Max. dia. = Maximum diameter. (a, b) *Spiniferites falcipedius* Warny & Wrenn. Dorsal view of (a) dorsal surface, and (b) mid focus; central body length 52 μm; sample VBD 3.12 p2, R13/2. (c, d) *Ataxiodinium confusum sensu stricto* Versteegh & Zevenboom. Ventral view at (c) mid focus, and (d) ventral surface; periblast length, 38 μm; sample DGD 19, F48/0. (e, f) *Ataxiodinium zevenboomii* Head. Ventral view at (e) mid focus, and (f) dorsal surface; endoblast length, 37 μm; sample VBD 4.5 p2, N40/0. (g–i) *Batiacasphaera minuta* (Matsuoka). Antapical view of (g) antapical surface, showing finely microreticulate surface, (h) mid focus, and (i) apical surface; max. dia., 28 μm; sample DGD 23, Q37/0. (j–o) *Bitectatodinium raedwaldii* Head. (j–l) Dorsal view of (j) dorsal surface showing opercular plate 4" in place, (k) close-up of dorsal surface, and (l) mid focus; length including luxuria, 43 μm; sample DGD 17, H22/0. (m–o) Apical view of (m) apical surface showing archeopyle formed by loss of plates 3" and 4", and arrow indicating circular mark at apex, (n) close-up showing fibrous luxuria, and (o) mid focus with arrow indicating erect and suberect pili of luxuria; central body width, excluding luxuria, 45 μm; sample VBD 4.5 p2, L25/0. (p, q) *Bitectatodinium tepikiense* Wilson. External view of torn fragment, showing characteristic vermiculate pattern of luxuria in plan view; (p) upper focus, (q) slightly lower focus; width of photo (p), 27 μm; sample VBD 2.6 p1, R39/3. (r–t) *Corrudinium? labradori* Head, Norris & Mudie. Left lateral view at upper, mid and lower foci. Note 2P archeopyle and prominent crest around cingulum. Central body length, 24 μm; sample VBD 4.1 p2, E31/3.

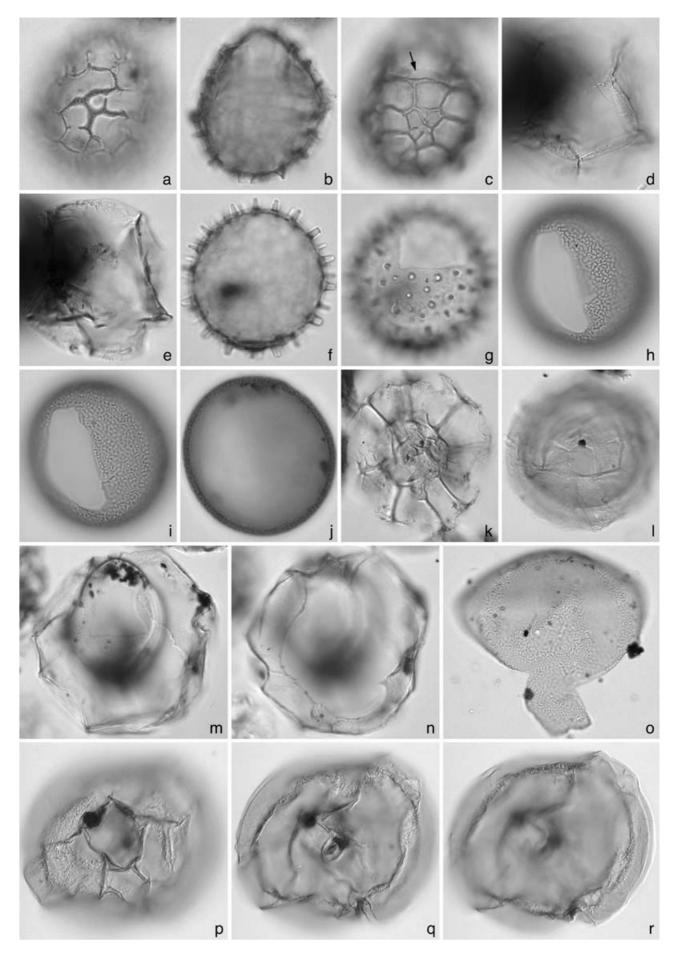


Figure 9. For legend see facing page.

lower Zanclean (top of the calcareous nannofossil zone NN12) in the Singa section of southern Italy, and it has a HO in both the Singa section and central North Atlantic DSDP Site 607 at 2.65 Ma, hence corresponding to a range of about 5.1–2.65 Ma (Versteegh & Zevenboom, 1995; Versteegh, 1997). In DSDP Hole 603C, eastern North Atlantic, *Ataxiodinium confusum* has a HO near the top of Subchron C2An1n (c. 2.7–2.6 Ma; M. J. H., unpub. data) (Fig. 5). Head (1997) encountered A. confusum in the Ramsholt Member of the Coralline Crag Formation of eastern England. Achomosphaera andalousiensis subsp. suttonensis (Fig. 70, p) has its LO in the Basal Shelly Unit, but this subspecies has a poorly known stratigraphic range, having been reported elsewhere from the Lower and Upper Pliocene of England (Head, 1997). Capisocysta lyelii (Fig. 90) appears to be restricted to the Basal Shelly Unit of the Verrebroek Dock. This species has been reported previously only from the Lower Pliocene Ramsholt Member of the Coralline Crag Formation in eastern England (Head, 1998b,c).

## 6.c. Oorderen Sands Member, Lillo Formation

Invertocysta lacrymosa (Fig. 9m, n) has a range top in the upper part of the Oorderen Sands Member. According to Versteegh (1995, 1997), this species has a well-defined highest occurrence at 2.75 Ma in both the Upper Pliocene Singa section of southern Italy and the North Atlantic ODP Site 607, and in higher latitudes at 2.8 Ma in ODP Hole 646B, Labrador Sea (de Vernal & Mudie, 1989) and at 2.84 Ma in DSDP 400A, Bay of Biscay (as Thalassiphora delicata in Harland, 1979). In DSDP Hole 610A, eastern North Atlantic, it has a highest occurrence at c. 2.74 Ma (S. D. S. & M. J. H., unpub. data) (Fig. 5). Its highest known occurrence in the North Sea Basin is from the mid-Pliocene Sudbourne Member of the Coralline Crag Formation of eastern England (Head, 1997).

#### 6.d. Kruisschans Sands Member, Lillo Formation

Geonettia waltonensis occurs in the Kruisschans Sands Member. This species has a presently known

stratigraphic range of Early Pliocene (eastern England, possibly 3.8–3.6 Ma and certainly no older than 4.6 Ma) to Late Pliocene (c. 2.1 Ma, DSDP Hole 603C) (Head, 2000).

Cysts of *Polykrikos kofoidii* (Fig. 7a–d) were found in a single sample from the Kruisschans Sands Member of the Verrebroek Dock. Although recorded sporadically in studies of the Quaternary, we know of no previous pre-Quaternary occurrence of this species, with the exception of questionably identified specimens from the Middle Miocene through Pleistocene of offshore New Jersey (as *Polykrikos kofoidii*?, unillustrated, in de Verteuil, 1996).

#### 7. Palaeoenvironment

Assemblages from both the Deurganck and Verrebroek docks reflect a neritic depositional environment in a temperate to cool climate. Differences between adjacent samples and sites can be explained by changing climate and sea level, and the unstable and localized nature of an inner shelf environment. Despite this complex interplay of influences, and our limited understanding of Pliocene dinoflagellate ecology (most of the taxa in our samples are extinct), it is nevertheless possible to draw inferences from our assemblages using the abundances of indicator species.

The Kattendijk Formation contains several known thermophilic taxa including *Tectatodinium pellitum* (Fig. 13a–d) and sporadically high abundances of the genus *Barssidinium*. Also present are significant numbers of species, including *Batiacasphaera minuta* and *Reticulatosphaera actinocoronata*, for which we have little palaeo-autecological data, as well as rare occurrences of the cold-tolerant species *Impagidinium pallidum* (Fig. 9d, e). Presence of the outer neritic to oceanic species *Invertocysta lacrymosa* (Fig. 9m, n) and *Impagidinium pallidum* indicates open-water conditions (Wrenn & Kokinos, 1986; Rochon *et al.* 1999), an interpretation supported by the rarity of *Operculodinium israelianum* which is associated with shallow water.

The Basal Shelly Unit unconformably overlying the Kattendijk Formation shows conspicuous evidence

Figure 9. Dinoflagellate cysts from the Verrebroek Dock (VBD) and Deurganck Dock (DGD) sections. Various magnifications. Max. dia. = Maximum diameter. (a–c) *Corrudinium devernaliae* Head & Norris. Ventral view of (a) ventral surface showing vesicular base of crests, (b) mid focus, and (c) dorsal surface, arrow showing wide unornamented margin of archeopyle; length including crests, 38 μm; sample DGD 22, O31/0. (d, e) *Impagidinium pallidum* Bujak. Uncertain view of (d) upper surface, and (e) mid focus; max. dia. including crests, 53 μm; sample VBD 4.5 p2, S37/4. (f, g) *Operculodinium*? sp. 1. Ventral view at (f) mid focus showing solid hyaline processes, and (g) dorsal surface; central body length, 35 μm; sample VBD 4.5 p2, S23/2. (h–j) *Pyxidinopsis* sp. 1. Dorsal view of (h) dorsal surface showing detail of microreticulation, (i) slightly lower focus, and (j) mid focus; max. dia., 40 μm; sample VBD 3.12 p2, N19/4. (k) *Reticulatosphaera actinocoronata* (Benedek). Uncertain view of upper surface; central body max. dia., 29 μm; sample VBD 4.1 p2, Q41/0. (l) Forma D of Wrenn & Kokinos, 1986. Mid focus showing archeopyle with opercular plates slightly displaced; max. dia., 82 μm; sample DGD 4, L19/3. (m, n) *Invertocysta lacrymosa* Edwards. Ventral view of (m) dorsal surface of endoblast, and (n) lower focus on dorsal surface of periblast; periblast length, 67 μm; sample VBD 3.2 p2, R17/2. (o) *Capisocysta lyelii* Head. Internal view of epicyst showing incompletely microreticulate wall ornament; width, 60 μm; sample VBD 3.12 p2, S23/0. (p–r) *Heteraulacacysta* sp. A of Costa & Downie, 1979. Antapical view of (p) antapical surface, (q) apical surface, and (r) slightly lower focus; max. width, 82 μm; sample VBD 3.12 p2, R18/0.

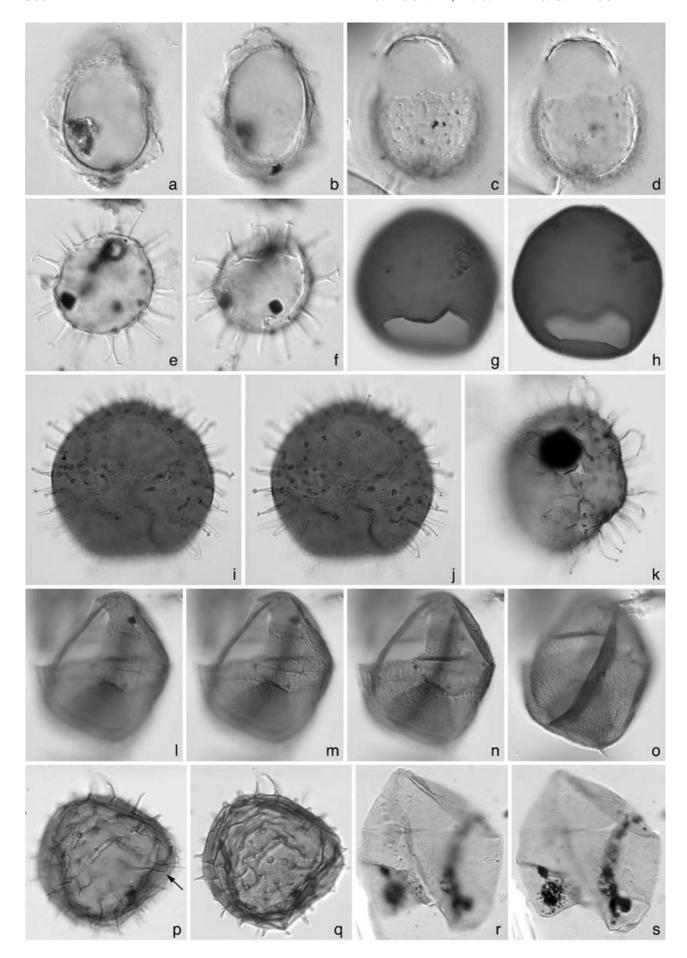


Figure 10. For legend see facing page.

of cooling based on high abundances of *Filisphaera* filifera and *Habibacysta tectata* (Fig. 7e, f), which are both cool-tolerant species (Head, 1994, 1996; Versteegh, 1995). In the Verrebroek Dock section, abundant *Habibacysta tectata* in sample VBD 3.11 indicates similar cool conditions in the lower part of the Oorderen Sands Member, although warmer temperatures returned during later deposition of this member.

A shallowing trend is noted in the upper part of the Oorderen Sands Member and the Kruisschans Sands Member. This trend is indicated by increasing abundance of *Operculodinium israelianum* (Fig. 7k, l), a species associated with shallow depths and particularly estuaries today (Head, 1996), and by increasing proportions of pollen and spores, particularly in the Kruisschans Sands Member.

Dinoflagellate cysts of the Kruisschans Sands Member reflect warm marine conditions, and are characterized by high species richness and many thermophilic species, including *Barssidinium pliocenicum* (Fig. 10i, j), *Tectatodinium pellitum*, and *Lingulodinium machaerophorum* which persist to the top of our sections. The increased abundance of *Operculodinium israelianum* is probably explained by shallowing conditions. This species occurs in warm regions today, but is also associated with cooler intervals of the Late Pliocene in eastern England (Head, 1998b). There is no indication otherwise from the dinoflagellate cysts of cooling in the Kruisschans Sands Member.

Pollen analysis of two samples (VBD 2.6 and 2.9) from the Kruisschans Sands Member at the Verrebroek Dock has yielded the following taxa: *Pinus* (85–86 %), *Tsuga* (4.6–4.8 %), *Cedrus* (3.3–3.8 %), *Sciadopitys* (2.0–3.2 %), *Picea* (1.3 %), *Abies* (0.6–1.6 %), *Sequoia* (0.6 %), fern spores (0.6 %), *Juniperus*-type (0.3 %), *Taxodium*-type (0.3 %), and Gramineae (0.3 %). These results are not directly comparable with other pollen records in the region because the residues were sieved at 20 μm, presumably causing the loss of smaller angiosperm pollen. Nonetheless, the presence

of temperate taxa, particularly *Sciadopitys, Taxodium*-type and *Sequoia*, indicates that these samples are probably no younger than the Reuverian pollen stage of the Netherlands (Zagwijn, 1960; van der Hammen, Wijmstra & Zagwijn, 1971). In spite of the dominance of *Pinus*, which is typically over-represented in marine deposits, the pollen confirms a temperate terrestrial climate in which the frost-sensitive conifer *Sciadopitys* clearly thrived.

#### 8. Discussion and conclusions

The Kattendijk Formation in our sections is no older than c. 5.0 Ma, based on the LO of *Operculodinium tegillatum* in DSDP Hole 603C (M. J. H., unpub. data). This is supported by the LO of *Corrudinium devernaliae* at c. 5.1 Ma in DSDP Hole 646B (de Vernal & Mudie, 1989; Knüttel, Russell & Firth, 1989). Indeed, it might not be older than c. 4.7 Ma, based on the LO of Cyst type I of de Vernal & Mudie (1989) in DSDP Hole 603C (M. J. H., unpub. data).

The Kattendijk Formation is no younger than about 4.4 Ma based on the HO of Reticulatosphaera actinocoronata, and this datum may be closer to c. 4.7 Ma, depending on the possibility of reworking in North Atlantic records. Other notable species having HOs in the Kattendijk Formation are *Batiacasphaera* minuta (North Atlantic HO at between 4.4 and 3.6 Ma, but probably no younger than c. 3.8 Ma) and Operculodinium tegillatum (North Atlantic HO at 4.2–3.5 Ma, possibly about 3.9 Ma) and Corrudinium devernaliae (North Atlantic HO at c. 3.8 Ma). We therefore interpret the age of the Kattendijk Formation at between about 5.0 and 4.4 Ma, which supports the early Zanclean age based on other fossil groups. If range data only from the eastern North Atlantic (DSDP Hole 610A) are used, then the Kattendijk Formation is no younger than 4.5 Ma, based on the HO of Corrudinium devernaliae in DSDP Hole 610A.

Vandenberghe et al. (1998) proposed a correlation of the Kattendijk Formation with standard sequence

Figure 10. Dinoflagellate cysts from the Verrebroek Dock (VBD) and Deurganck Dock (DGD) sections. Various magnifications. Max. dia. = Maximum diameter. (a, b) cf. *Alexandrium tamarense*-type cysts of Rochon *et al.* 1999. Equatorial view at (a) upper focus, and (b) lower focus; central body length, 31 μm; sample VBD 3.11 p2, X33/0. (c, d) Organic membrane of calcareous cyst. Equatorial view of (c) upper surface showing zigzag archeopyle margin, and (d) slightly lower focus; length excluding ornament, 43 μm; sample VBD 2.9 p1, V37/2. (e, f) Cyst of *Pentapharsodinium dalei* Indelicato & Loeblich III. Uncertain view at (e) mid focus, and (f) lower focus; central body max. dia., 25 μm; sample VBD 4.5 p2, K31/4. (g, h) *Brigantedinium cariacoense* (Wall). Apical view of (g) apical surface, and (h) mid focus; max. dia., 41 μm; sample VBD 3.2 p2, H38/0. (i, j) *Barssidinium pliocenicum* Head. Ventral view of (i) dorsal surface, and (j) slightly lower focus, showing tabulation in the form of lines of thinning around the archeopyle; central body length, 83 μm; sample DGD 4, R58/3. (k) *Barssidinium graminosum* Lentin, Fensome & Williams. Dorsal view at mid focus, showing slender processes about 2.0 μm diameter near base and up to 20 μm long; central body length, 72 μm; sample 4.5 p2, W41/2. (l–o) *Lejeunecysta hatterasensis* Head & Norris. Right lateral view of (l–n) upper surface at successively lower foci, and (o) lower surface showing one of two antapical horns; length, 56 μm; sample VBD 2.9 p1, W37/3. (p, q) *Echinidinium euaxum* Head. Uncertain view of (p) upper surface, with arrow showing expanded process tip, and (q) slightly lower focus; central body max. dia., 42 μm; sample VBD 2.9 p1, E39/1. (r, s) *Lejeunecysta psuchra* Matsuoka. Dorsal view at (r) upper focus, and (s) lower focus; note large archeopyle that extends to apex; length 81 μm; sample VBD 2.9 p1, U32/0.

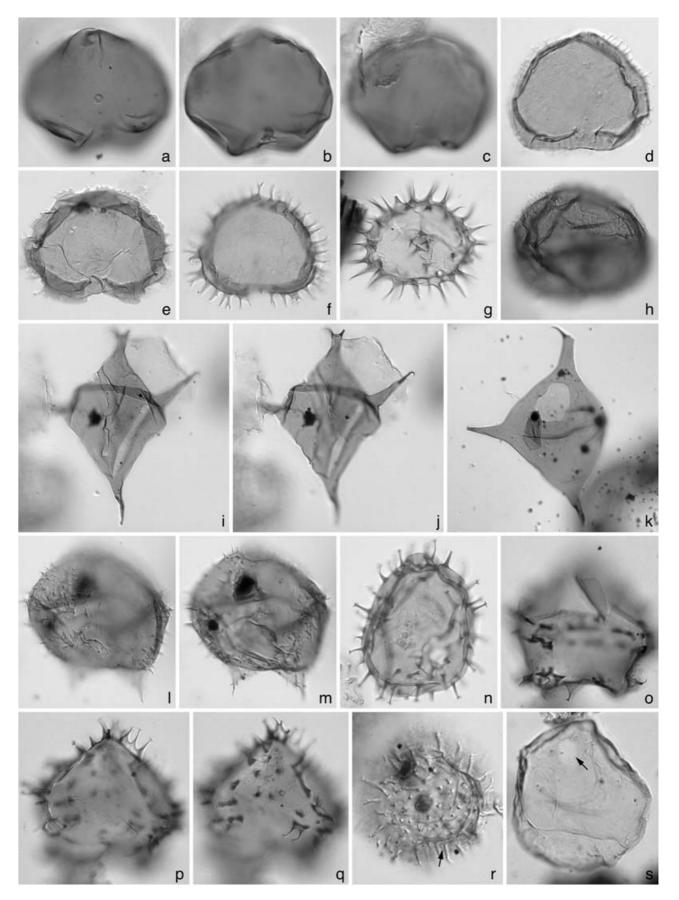


Figure 11. For legend see facing page.

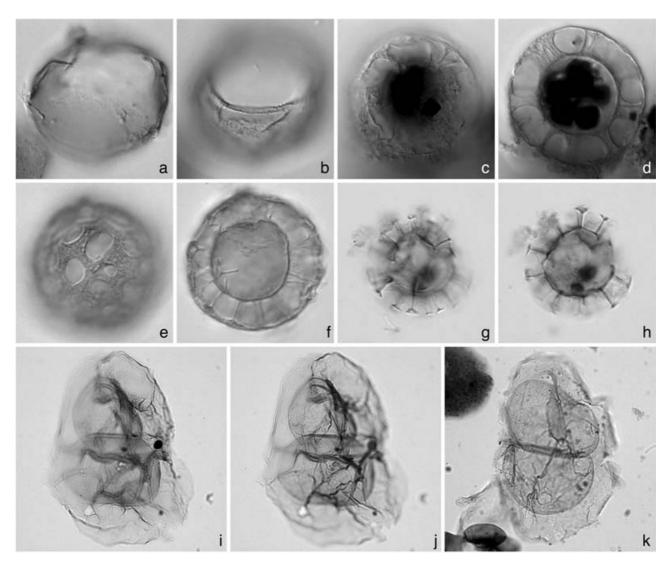


Figure 12. Acritarchs (r, s) from the Verrebroek Dock (VBD) and Deurganck Dock (DGD) sections. Various magnifications. Max. dia. = Maximum diameter. (a, b) *Paleostomocystis globosa* Louwye. Antapertural view at (a) mid focus, and (b) apertural surface; max. dia., 39 μm; sample VBD 4.5 p2, X48/0. (c, d) Acritarch sp. 1 of Head, Norris & Mudie (1989). (c) upper surface, and (d) mid focus; overall max. dia., 33 μm; sample VBD 4.5 p2, Q33/0. (e, f) Cyst type 1 of de Vernal & Mudie (1989). (e) upper surface, and (f) mid focus; overall max. dia., 30 μm; sample DGD 22, G30/0. (g, h) Algal cyst sp. 1 of Head (1996). (g) upper surface, (h) mid focus; central body max. dia., 17 μm; sample DGD 22, L52/3. (i–k) Incertae sedis 1. (i, j) upper and mid foci respectively; max. length, 167 μm; sample VBD 2.6 p1, X19/2. (k) mid focus; max. length, 120 μm; sample DGD 8, V44/2.

Figure 11. Dinoflagellate cysts (a-q) and acritarchs (r, s) from the Verrebroek Dock (VBD) section. Various magnifications. Max. dia. = Maximum diameter. (a-c) Quinquecuspis concreta (Reid). Ventral view of (a) ventral surface, (b) mid focus, and (c) slightly lower focus; width, 68 µm; sample VBD 2.9 p1, P17/3. (d) Selenopemphix brevispinosa Head, Norris & Mudie. Antapical view at mid focus, with archeopyle offset strongly to left of dorsoventral midline; central body width, 52 μm; sample VBD 2.6 p1, B14/0. (e) Selenopemphix conspicua (de Verteuil & Norris) stat. nov. Apical view at mid focus, showing archeopyle offset strongly to left of dorsoventral midline; width including crests, 52 μm; sample VBD 2.6 p1, B14/0. (f) Selenopemphix dionaeacysta Head, Norris & Mudie. Apical view at mid focus; central body width, 40 µm; sample VBD 2.6 p1, A33/3. (g) Selenopemphix quanta (Bradford). Apical? view of upper surface; central body width, 45 µm; sample VBD 2.9 p1, X39/2. (h) Selenopemphix? sp. 1. Apical view of apical surface, showing thin cingular flange; central body width, 60 µm; sample VBD 2.9 p1, P25/1. (i-k) Stelladinium? sp. 1. (i–j) dorso-ventral view of (i) upper surface showing long tear in hypocyst, and (j) lower surface; length, 96 μm; sample VBD 2.9 p1, N24/4. (k) Dorsal view of dorsal surface, with right lateral horn and right apical process both missing due to breakage; length, 101 µm; sample VBD 2.9 p1, K41/4. (l, m) Trinovantedinium glorianum (Head, Norris & Mudie). Dorsal view of (l) dorsal surface, and (m) mid focus. Note granulation on surface of central body (between spinules) that does not extend to antapical horns; length, 57 µm; sample VBD 2.9 p1, M32/2. (n) Trinovantedinium variabile (Bujak). Equatorial? view of upper surface, showing multifurcate process tips; central body max. dia., 50 μm; sample VBD 2.6 p1, T34/4. (o-q) Trinovantedinium ferugnomatum de Verteuil & Norris. Dorsal view of (o) dorsal surface, (p) mid focus, and (q) ventral surface; length excluding processes, 42 μm; sample VBD 4.5 p2, K35/0. (r) Nannobarbophora walldalei Head. Upper surface, showing solid processes with arrow indicating rootlike process base; central body max. dia., 31 µm; sample VBD 2.9 p1, V38/3. (s) Cyclopsiella? trematophora (Cookson & Eisenack). Mid focus, with subcircular pylome indicated by arrow; length, 60 µm; sample VBD 2.9 p1, W19/2.

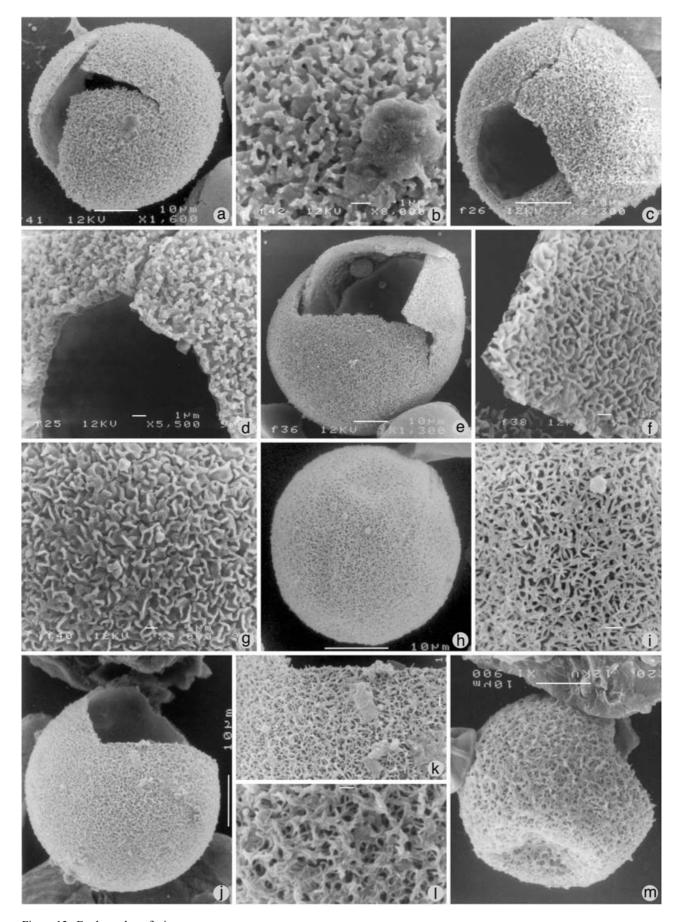


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3.4, and the base of this formation with the sequence boundary at 5.5 Ma (Haq, Hardenbol & Vail, 1987) which is now regarded as sequence boundary Me2 at 5.73 Ma of Hardenbol *et al.* (1998). Our study confirms correlation of the Kattendijk Formation with standard sequence 3.4 (5.73–4.37 Ma; Fig. 6), although we were not able to date the base of this formation as it was not exposed in our section. Assemblages show a distinctly open-water influence that is not seen higher in our sections.

The basal gravel of the Luchtbal Sands Member in the type area can be regarded as a sequence boundary, and Vandenberghe *et al.* (1998) have correlated it with Za1 at 4.37 Ma (Hardenbol *et al.* 1998). The Luchtbal Sands Member is probably missing from the Deurganck and Verrebroek dock sections.

It may be noted that the lowest (Ramsholt) member of the Coralline Crag Formation in eastern England has been correlated with the Luchtbal Sands Member using benthic foraminifera (P. Laga, unpub. Ph.D. thesis, Katholieke Universiteit Leuven, 1972; Doppert, Laga & De Meuter, 1979; Doppert, 1985; Hodgson & Funnell, 1987). Ostracods (Wilkinson, 1980) and molluscs (Cambridge, 1977) have also been used to correlate the Coralline Crag Formation with the Luchtbal Sands Member, although a more recent study of the molluscs by Marquet (1998) has led to a correlation with both the Luchtbal Sands Member (Lillo Formation) and the Kattendijk Formation. Our own evidence from the dinoflagellate cysts suggests that the lowest (Ramsholt) member of the Coralline Crag Formation is younger than the Kattendijk Formation, based on the absence of Reticulatosphaera actinocoronata and Corrudinium devernaliae (Head, 1997) from the Coralline Crag deposits.

The Basal Shelly Unit at the base of the Lillo Formation in our sections contains few age diagnostic dinoflagellate cyst species. It is assumed that rare specimens of *O. tegillatum* and *B. minuta* are reworked because these species are typically common in the Lower Pliocene of the North Atlantic region. The Basal Shelly Unit may therefore post-date the highest common and/or persistent occurrence of *O. tegillatum* which occurs at between about 4.2 and 3.7 Ma in the North Atlantic. *Ataxiodinium confusum sensu stricto*, although rare in the Basal Shelly Unit, is not considered reworked because (1) it does not occur in the subjacent

Kattendijk Formation, and (2) elsewhere it always occurs in low abundances, so that reworked specimens have a low probability of being recovered. This species has a range top at about 2.7–2.6 Ma in DSDP Hole 603C, western North Atlantic (M. J. H., unpub. data), and a similar HO of 2.65 Ma in both the Mediterranean region and central North Atlantic (Versteegh, 1997). The above data tentatively constrain the Basal Shelly Unit at between c. 4.2 and 2.65 Ma (late Zanclean or Piacenzian) and suggest a hiatus as would be expected from its unconformable contact with the underlying Kattendijk Formation.

The base of our Basal Shelly Unit appears to correlate either with Za2 at 4.04 Ma or Pia1 at 3.21 Ma (Hardenbol *et al.* 1998). If the correlation with Za2 at 4.04 Ma is correct, it would coincide with MIS Gi16, a pronounced cold stage at about 4.0 Ma (Shackleton, Hall & Pate, 1995), which would be consistent with the cool-water dinoflagellate flora seen in both the Basal Shelly Unit and the lower part of the Oorderen Sands Member.

The Oorderen Sands Member is a transgressive unit unconformably overlying the Luchtbal Sands Member in the type area, and its base represents a sequence boundary (Vandenberghe et al. 1998, p. 149). In our sections, the Oorderen Sands Member appears to be a transgressive continuation of the Basal Shelly Unit, and the presence of cool-water dinoflagellate species in both the Basal Shelly Unit and the lower part of the Oorderen Sands Member is consistent with this interpretation. The HO of Invertocysta lacrymosa near the top of the sandy part of the Oorderen Sands Member indicates that deposition of this unit was completed not later than 2.74 Ma. Indeed, the disappearance of *I. lacrymosa* may have been ecologically suppressed because the environment was shallowing during deposition of the upper part of the Oorderen Sands Member, and this species has outer neritic to oceanic affinities (Wrenn & Kokinos, 1986). The cooling observed in the Basal Shelly Unit continues into the lower part of the Oorderen Sands Member, as indicated by high numbers of Habibacysta tectata in the Verrebroek Dock section. Higher within the Oorderen Sands, palaeotemperatures become warmer.

The Kruisschans Sands and Oorderen Sands members belong to the same depositional sequence,

Figure 13. Dinoflagellate cysts from the Verrebroek Dock (VBD) section. All SEM illustrations. Scale bars are 10 μm on portraits, and 1 μm on close-up views. (a, b) *Tectatodinium pellitum* Wall. Dorsal view of (a) portrait, and (b) close-up showing surface of the distally-open spongy luxuria; sample VBD 2.13b. (c, d) *Tectatodinium pellitum* Wall. Dorsal view of (c) portrait, and (d) close-up showing surface and irregular archeopyle margin; sample VBD 2.9b. (e–g) *Bitectatodinium tepikiense* Wilson. Dorsal view of (e) portrait, and (f, g) close-up of wall structure showing vermiculate pattern formed by erect and suberect lamellae; sample VBD 2.13a. (h, i) *Bitectatodinium raedwaldii* Head. Presumed ventral view of (h) portrait, and (i) close-up of distally-fused surface fibres; sample VBD 2.13d. (j, k) *Bitectatodinium raedwaldii* Head. Left-lateral view of (j) portrait, and (k) close-up of distally-fused surface fibres; sample VBD 2.9a. (l, m) *Bitectatodinium raedwaldii* Head. Antapical view of specimen with particularly thick luxuria, showing (m) portrait, and (k) close-up of distally-fused surface fibres; sample VBD 3.11.

and it is therefore likely that they both pre-date 2.74 Ma based on the HO of I. lacrymosa in the Oorderen Sands Member. The cold-sensitive species Barssidinium pliocenicum, Bitectatodinium raedwaldii and Tectatodinium pellitum present in the Kruisschans Sands Member are consistent with this likelihood. These species do not apparently reappear in the Pliocene of the southern North Sea Basin after about 2.6 Ma, owing to the onset of less equable climatic conditions caused by Northern Hemisphere cooling at this time (Head, 1998a,b, 2000; Leroy, Wrenn & Suc, 1999). Deposition hence took place under warm- to mild-temperate conditions in a shallowing environment. Pollen from the Kruisschans Sands Member reflect a temperate vegetation and appear consistent with a Reuverian (c. 3.5–2.6 Ma) pollen stage assignment.

The Lillo Formation in our sections (Basal Shelly Unit, Oorderen Sands Member and Kruisschans Sands Member) apparently belongs entirely to a single depositional cycle that pre-dates the sequence boundary Pia2 (2.76 Ma). We suggest a correlation either with the sequence bounded by Pia1 and Pia2 (3.21–2.76 Ma; Hardenbol *et al.* 1998) or that bounded by Za2 and Pia1 (4.04–3.21 Ma; Hardenbol *et al.* 1998) (Fig. 6). This leaves open the possibility that the Luchtbal Sands Member represents either the sequence bounded by Za1 and Za2 or that by Za2 and Pia1. Future palynological investigations of the Luchtbal Sands, Oorderen Sands, and Kruisschans Sands members at their type localities may clarify these uncertainties.

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# Appendix. Taxonomic notes on selected dinoflagellate cysts and acritarchs

Ataxiodinium confusum Versteegh & Zevenboom, 1995 sensu stricto (Fig. 8c, d). A single specimen, recorded from sample DGD 19, compares with the holotype of A. confusum (Versteegh & Zevenboom, 1995, pl. 1, figs 1, 4, 7) in having wall layers fully appressed in mid-dorsal and mid-ventral areas. The paratypes of A. confusum, and also a specimen from eastern England (Head, 1997, fig. 6.17–6.20), show small blister-like separations of wall layers within the mid-dorsal and mid-ventral areas.

Achomosphaera andalousiensis subspecies andalousiensis (autonym) (Fig. 7m, n) and suttonensis Head, 1997 (Fig. 7o, p). Specimens that could not be assigned at subspecific level were counted as Achomosphaera/Spiniferites indeterminate. Obscuring debris has meant that this species is therefore underrepresented in the counts. In sample DGD 21, for example, A. andalousiensis (undifferentiated) may account for as many as 16 percent of specimens presently assigned to Achomosphaera/Spiniferites indeterminate.

Bitectatodinium raedwaldii Head, 1997 (Figs 8j–o, 13h–m). Specimens have adjacent pili that are not conspicuously fused distally when seen under light microscopy (Fig. 8j–o), unlike the type material from the mid-Pliocene of eastern England (Head, 1997). Although distal fusion is clearly evident in our material under SEM (Fig. 13h–m), the pattern is more variable than shown for the type material. Allowing for this wider range in variability, we now consider 'Bitectatodinium tepikiense (columellate luxuria)' of Head (1998a), illustrated from the Upper Pliocene of eastern England, to be conspecific with Bitectatodinium raedwaldii. All these specimens clearly lack the erect lamellae that characterize Bitectatodinium tepikiense Wilson (Head, 1994) (Figs 8p, q; 13e–g).

Capisocysta lyelii Head, 1998c (Fig. 90). Several specimens representing isolated epicysts were recorded in a single sample from the Basal Shelly Unit in the Verrebroek Dock section. Although it was not possible to discern the hypocystal tabulation, specimens have a pronounced incompletely microreticulate ornament that distinguishes C. lyelii from C. lata. This is the first record of C. lyelii beyond its type stratum of the Ramsholt Member of the Coralline Crag Formation, eastern England (Head, 1998c).

Heteraulacacysta sp. A of Costa & Downie, 1979 (Fig. 9p–r). This distinctive species is well known from the Eocene through Middle Miocene of the North Atlantic region (Head, 1993), and has been accepted as occurring in situ in the Upper Miocene of the eastern USA. (as Heteraulacacysta campanula in de Verteuil & Norris, 1996). Specimens recorded as in situ from the uppermost Pliocene

St Erth Beds of southwestern England (Head, 1993) were later considered by Head (1999) as reworked on account of their rarity at St Erth and the absence of Pliocene records elsewhere. This view must now be reconsidered in view of the large numbers and good preservation of this distinctive species in our material from Belgium which cannot be explained easily by reworking.

Organic membranes of calcareous dinoflagellate cysts (Fig. 10c, d). Specimens are present throughout the Deurganck and Verrebroek dock sequences. They have a spheroidal to broadly ovoidal shape, incomplete reticulum and zigzag principal archeopyle suture. Crests are most pronounced at junctions where they may be up to 3 µm high. This group presumably represents the organic membranes of several species of calcareous dinoflagellate cysts, judging from their strong similarity with a specimen incubated from modern sediments of northern Norway (Dale, 1983, figs 27, 28). Kallosphaeridium sp. of Head & Westphal (1999) from the upper Lower Pliocene (3.6-4.1 Ma) of the Bahamas is similar to some of our specimens and we presume it also represents the organic membrane of a calcareous dinoflagellate cyst. This morphotype ranges from the uppermost Miocene through Lower Pleistocene of the western North Atlantic, DSDP Hole 603C (M. J. H., unpub. data).

Quinquecuspis concreta (Reid, 1977) (Fig. 11a–c). Specimens compare well with the overall morphology described for this species, and some have longitudinal striations found in some modern specimens (Rochon *et al.* 1999).

Selenopemphix conspicua (de Verteuil & Norris, 1992) stat. nov. (Fig. 11e). Basionym = Selenopemphix brevispinosa conspicua de Verteuil & Norris, 1992, p. 399–401, pl. 2, figs 2–8, pl. 10, figs 1–4, pl. 11, figs 1–2, text-fig. 5. Conspicuous and consistent differences between this species and Selenopemphix brevispinosa Head, Norris & Mudie, 1989 warrant its elevation to species status.

Spiniferites falcipedius Warny & Wrenn, 1997 (Fig. 8a, b). This species, described from the Upper Miocene and Lower Pliocene of Morocco by Warny & Wrenn (1997), has also been recorded from the mid Pliocene of eastern England (as *Achomosphaera* sp. in Head, 1997) and uppermost Pliocene (Antian Stage) of eastern England (as *Spiniferites mirabilis* in Head, 1996, fig. 14.6 only; and in Head, 1999, pl. 3, fig. 8). Warny & Wrenn (1997) suggested that *Spiniferites falcipedius* and *Spiniferites mirabilis* are closely related.