

DINOFLAGELLATE CYSTS FROM THE MIDDLE EOCENE TO ?LOWERMOST OLIGOCENE SUCCESSION IN THE KYSSING RESEARCH BOREHOLE, CENTRAL DANISH BASIN

CLAUS HEILMANN-CLAUSEN

Department of Earth Sciences

Aarhus University

DK-8000 Århus C

Denmark

e-mail: claus.heilmann@geo.au.dk

STEFAN VAN SIMAEYS

Historical Geology

University of Leuven

Redingenstraat 16

B-3000 Leuven

Belgium

e-mail: stefaan.vansimaey@geo.kuleuven.ac.be

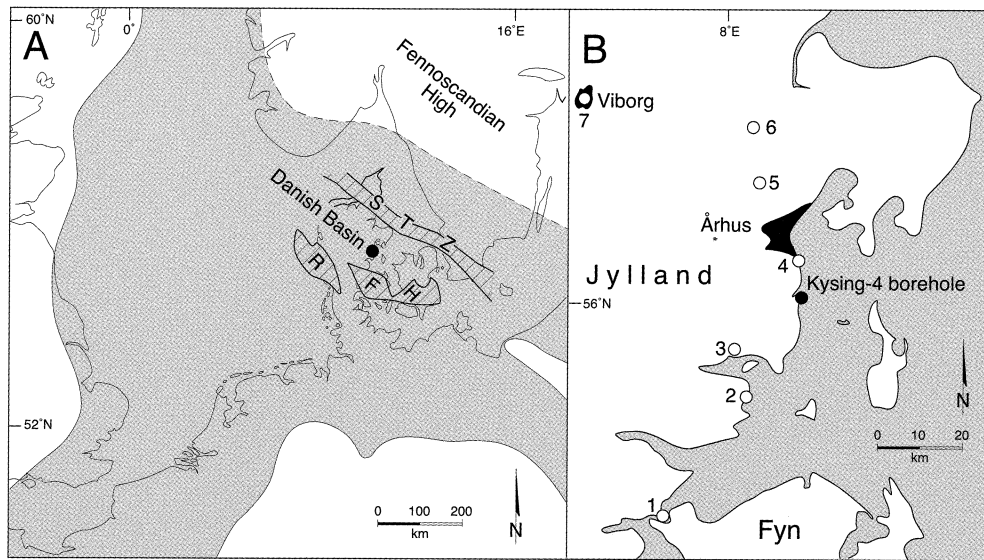
Abstract

Rich and well-preserved assemblages of organic walled dinoflagellate cysts in 50 samples from a 154 m thick and almost complete, Middle Eocene to ?lowermost Oligocene section from the Kysing Research Borehole in eastern Jylland, Denmark are systematically described. One genus *Costacysta* gen. nov., and twelve species *Chiropteridium eocaenicum* sp. nov., *Costacysta bucina* gen. et sp. nov., *Distatodinium pilosum* sp. nov., *Echinidinium? lucidum* sp. nov., *Hapsocysta kysingensis* sp. nov., *Horologinella? pentagonalis* sp. nov., *Operculodinium eisenackii* sp. nov., *Phthanoperidinium cornutum* sp. nov., *Selenopemphix septum* sp. nov., *Svalbardella partimtabulata* sp. nov., *Thalassiphora gracilis* sp. nov. and *Thalassiphora microperforata* sp. nov. are formally described. The genus *Hapsocysta* is emended, and is considered to be a senior synonym of *Piccoladinium*. The gradual change of the dinoflagellate cyst assemblages in this section demonstrates that sedimentation was almost continuous during the time span of ca. 12 Ma. The biostratigraphic resolution based on dinoflagellate cyst events is generally finer than the calcareous nannofossil NP biozonation. A comparison with published dinoflagellate cyst data from the Norwegian–Greenland Sea shows that several important events are mainly synchronous throughout the region, suggesting a general similarity of the water masses. An isolated occurrence of *Svalbardella* suggests a short cooling event during early Bartonian times. The palynofacies in most of the section is almost purely of pelagic type. A more proximal, mid shelf palynofacies and a distinctive episode of reworking coincide with the Upper Eocene Moesgaard Clay and indicate a brief, but rather large sea level fall during the deposition of this unit. The Eocene/Oligocene boundary is tentatively identified near the base of the Viborg Formation, and approximately coincides with increased reworking of dinoflagellate cysts and a strong increase in bisaccate pollen, indicating more proximal conditions and possibly also a climatic cooling.

INTRODUCTION

A cored research borehole, spanning the Middle Eocene to probably lowermost Oligocene, was recently drilled at Kysing, Denmark (Text-Figure 1). The borehole was drilled to provide a suitable North Sea Basin section for integrated stratigraphy at a site where seismic observations had indicated the presence of thick Eocene strata (Andersen and Tychsen, 1977). The section recovered is stratigraphically almost complete and represents the most continuous record of open marine environments from this time interval known

in northwest Europe (Text-Figure 2). The purpose of this paper is to provide a detailed systematic and stratigraphic description of the rich and well-preserved assemblages of dinoflagellate cysts in this important section. Brief comparisons of main dinoflagellate cyst events are made with previous studies in the region. It is the first of several multidisciplinary studies of the Kysing section (Heilmann-Clausen et al. 2001). The Kysing section is located near the Eocene depocenter of the Danish Basin. This subbasin of the North Sea Basin is situated between the Ringkøbing-Fyn High to the south and the Fennoscandian Border Zone



Text-Figure 1. A. Map of the North Sea region showing the location of the Kysing-4 Borehole (black dot). The presumed Middle-Late Eocene extent of the North Sea is also illustrated (gray shade). The border of the Eocene North Sea towards the Fennoscandian High is uncertain (dashed line), due to late Cenozoic uplift and erosion of the High. For the Danish area, the main structural elements are also shown. STZ = Sorgenfrei-Tornquist Zone, RFH = Ringkøbing-Fyn High. The paleogeography is modified from Kockel (1988) and Ziegler (1990). B. Central east Jylland with location of the Kysing-4 Borehole (UTM coordinates 578650 m E, 626850 m N), and other sections mentioned in the text. 1 = LB-38 Borehole, 2 = Pøt Strand, 3 = Søvind, 4 = Moesgaard Strand, 5 = Grundfjør, 6 = Ølst/Hinge, 7 = Viborg-1 Borehole.

in the northeast (Text-Figure 1). During the Mid and Late Eocene, the subs basin was in an offshore position within the paleo-North Sea. The depositional setting was bathyal-outer neritic (Heilmann-Clausen et al., 1985), but in contrast to the central North Sea Basin a calcareous nannofossil ooze, the Søvind Marl Formation, rich in planktonic and benthic foraminifera accumulated here (Dinesen et al., 1977; Thiede et al., 1980) (Text-Figure 3). Almost no information has previously been published on dinoflagellate cysts from this ooze.

PREVIOUS DINOFLAGELLATE CYST RESEARCH

The literature on dinoflagellate cysts from the Middle Eocene to Lower Oligocene in Denmark is limited. An informal zonation of the Eocene to lowermost Oligocene (Heilmann-Clausen, 1988) was based on several unspecified sections, but few details of these sections were given. The Upper Lutetian to Priabonian was subdivided into three zones, ranges of selected species within the zones were indicated, and a calibration was made with the calcareous nannofossil zonation, based on the Viborg-1 Borehole. Köthe (1990), Heilmann-Clausen and Costa (1989) and Heilmann-Clausen (1993; 1995a) provided

few additional data. An unpublished report (Heilmann-Clausen, 1995b) described the distribution of dinoflagellate cysts in the Paleogene from a borehole in western Jylland.

EOCENE SEDIMENTS AND STRATIGRAPHY IN THE DANISH BASIN

Paleocene and Eocene sediments in the Danish Basin were deposited in an upper bathyal to outer neritic environment, comparable to that of the central North Sea (Heilmann-Clausen et al., 1985). It is generally believed that these deposits were subsequently deeply buried by Neogene sediments. The Neogene strata were, however, eroded during the Late Neogene to Quaternary as a result of a major regional uplift of the eastern part of the Basin, which brought the Paleogene succession to the surface (Jensen and Schmidt, 1992; Japsen and Chalmers, 2000). Eocene and Oligocene deposits are therefore accessible in several outcrops and shallow boreholes in Eastern Jylland.

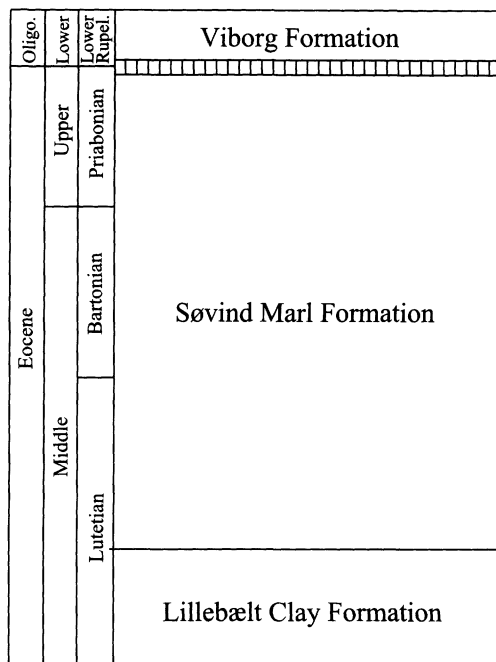
The stratigraphy was described by Dinesen et al. (1977) and Heilmann-Clausen et al. (1985); the latter authors formalized the lithostratigraphic units. Michelsen et al. (1998) subsequently correlated these deposits in Denmark

Legend:

- Marl
- Clayey marl or clay/marl interbedding
- Clay
- Laminated clay
- G Glaucinite

Depth (m)	Sample	Lithology	Lithostratigraphy	Preliminary NP Zonation	Chronostratigraphy
0-10	1776, 1775, 1774, 1773, 1771, 1768	Marl	Vi Fm	21	Rup.?, L.O.?
10-20	1932, 1930, 1928, 1926, 1922, 1919, 1916, 1906, 2668	Clayey marl or clay/marl interbedding	Moesg. Clay	19/20	Priabonian, Upper Eocene
20-30	2667, 2666, 2665, 2664	Clayey marl or clay/marl interbedding	Søvind Marl Formation	18	Upper Eocene
30-40	2663, 2662, 2661	Clayey marl or clay/marl interbedding	Søvind Marl Formation	17	Middle Eocene
40-50	2660, 2659, 2658, 2657	Clayey marl or clay/marl interbedding	Søvind Marl Formation	15	Middle Eocene
50-60	2656, 2655, 2654, 2653	Clayey marl or clay/marl interbedding	Søvind Marl Formation	?	Middle Eocene
60-70	2652	Clayey marl or clay/marl interbedding	Søvind Marl Formation	?	Middle Eocene
80-90	2651, 2650, 2649, 2648, 2647, 2646, 2645, 2644, 2643, 2642, 2641	Clayey marl or clay/marl interbedding	Søvind Marl Formation	16	Middle Eocene
90-100	2640, 2639, 2638, 2637, 2636, 2635, 2634	Clayey marl or clay/marl interbedding	Søvind Marl Formation	15	Middle Eocene
100-110	2633	Clayey marl or clay/marl interbedding	Søvind Marl Formation	L.C.?	Middle Eocene

Text-Figure 2. The Kysing-4 Borehole section with positions of samples studied. Samples from the Moesgaard Clay and above were taken at outcrop and shallow boreholes at the same locality. On the basis of identical detailed lithology, the position of these samples have been projected into the Kysing-4 section as shown. Samples 1906–1932 are from the Kysing-3 Borehole, samples 1768–1776 are from the coastal cliff and boreholes 1 and 2. The unpublished NP zonation (calcareous nannoplankton) is also shown (courtesy of E. Thomsen). Question marks indicate intervals that have not been referred to an NP biozone. Abbreviations: L.C. = Lillebælt Clay Formation, Moesg. = Moesgaard, Kys. = Kysing, Vi Fm. = Viborg Formation.



Text-Figure 3. Middle Eocene to lowermost Oligocene stratigraphy in the central part of the Danish Basin (Viborg-1 Borehole). From Heilmann-Clausen et al. (1985).

with a sequence stratigraphic subdivision of the Cenozoic in the North Sea. The succession (Text-Figure 3) includes, in ascending order, the uppermost Ypresian–Lutetian Lillebælt Clay Formation, which is an up to 50 m thick unit of mainly non-calcareous, hemipelagic clay beds. This unit passes gradually upwards into Lutetian to Priabonian hemipelagic marls referred to the Søvind Marl Formation, which is up to 50 m thick in previously studied sections, but approximately 125 m thick at Kysing. The Søvind Marl Formation was deposited in a bathyal environment (King, 2001) and the water masses were open marine. Separated by an important regional unconformity (Dinesen, 1972), the Eocene hemipelagic strata are overlain by clays and muds referred to the Oligocene. The oldest unit above this unconformity is the Viborg Formation. It was initially deposited in an outer shelf environment, but water depth gradually shallowed. The extremely rare planktonic foraminifera indicate that the water mass was no longer open marine (Ulleberg, 1974). The Viborg Formation is part of depositional sequence 4.1a described from the eastern North Sea and northwest Jylland by Danielsen et al. (1997). They showed that the sequence prograded from the north, and that thick proximal sandy deposits of the sequence occur in the easternmost North Sea, approximately 200 km northwest of Kysing.

Previously, the most complete succession across the Eocene–Oligocene unconformity is from the Viborg-1 Borehole in the central part of the basin (Dinesen et al., 1977; Thiede et al., 1980). There the Søvind Marl Formation reaches 50 m in thickness and includes strata referred to biozones NP19/20 to NP21 (Thiede et al., 1980; Thomsen, 1995). The overlying Viborg Formation is 85 m thick. The calcareous lower and middle parts are referred to biozone NP21 (Mikkelsen, 1975; Thiede et al., 1980; Thomsen, 1995). The entire formation includes *in-situ* *Areosphaeridium diktyoplokum*, and can be referred to the German dinoflagellate cyst subzone D12nc (Köthe 1990; Heilmann-Clausen, 1995a, b). The micro- and nannoplankton biostratigraphy of the Viborg Formation thus points to an age close to the Eocene–Oligocene boundary, either earliest Rupelian or latest Priabonian (Heilmann-Clausen, 1995b). The Viborg Formation is traditionally considered to be of Oligocene age (Ulleberg, 1987). The base Viborg Formation unconformity in the Viborg-1 Borehole is indicated by a glauconitic horizon and a lithofacies break. It has not been recognized biostratigraphically, and the duration of the hiatus appears to have been short. A virtually complete stratigraphic record across the Eocene–Oligocene transition is likewise known from small temporary outcrops in the cliffs along the east coast of Jylland between Århus and Kysing (Text-Figure 1) (Thomsen 1995; Heilmann-Clausen, 1995a). Seismic studies indicate thick Eocene strata in this area, and apparently the depocenter of the Danish Basin was situated close to Kysing during the Eocene (Andersen and Tychsøn, 1977; Heilmann-Clausen et al., 2001).

MATERIAL AND METHODS

The Section Studied

The Kysing Research Borehole was drilled by Aarhus University in 1999 at Kysing, approximately 15 km south of Århus (Text-Figure 1). Its formal name is Kysing-4. At the drilling site, transitional Eocene–Oligocene strata are exposed in the foot of the coastal cliff. The borehole was completely cored with almost 100% recovery, and the succession drilled is illustrated in Text-Figure 2. Preliminary results were briefly reported by Heilmann-Clausen et al. (2001). The section spans the thickest Lutetian to ?lowermost Rupelian sediments known in Denmark, and the lithologies are more heterogeneous than in other sections. The strata are provisionally referred to the Søvind Marl Formation, two new informal units (the Moesgaard Clay and the Kysing Marl) and the Viborg Formation. The lowermost few meters possibly belong to the Lillebælt

Clay Formation. Preliminary studies of foraminifera (King, 2001) suggest that the Kysing section is chronostratigraphically more complete than the Viborg-1 Borehole, previously taken as the reference section for this interval. The unpublished calcareous nannofossil stratigraphy allows identification of all NP Biozones between NP15 and NP21 (E. Thomsen, personal communication; Text-Figure 2). The glauconite-rich level above Biozone NP18 (Text-Figure 2) probably indicates a hiatus because only the lowermost part of NP18 appears to be present (E. Thomsen, personal communication). The thick succession assigned to the Søvind Marl Formation (approximately 125 m) includes several less calcareous to non-calcareous clay intervals. Some intervals exhibit regular clay/marl cyclicity, probably representing Milankovitch cycles. The uppermost part is an off-white, highly calcareous marl. The overlying 10 m thick Moesgaard Clay is a dark clay unit. Its lower part, and the underlying Søvind Marl Formation, is occasionally exposed in the coastal cliff at Moesgaard Strand (Text-Figure 1). The lower and upper boundaries of the Moesgaard Clay are sharp and indicate breaks in the depositional process, during which pronounced shifts of the paleoenvironment took place. The Kysing Marl is a highly glauconitic, light grey marl, resembling the Søvind Marl Formation. The Viborg Formation is a moderately calcareous, greenish-grey, finely micaceous clay with glauconite at the base; the lower boundary appears to be sharp.

Samples, Preparation and Analysis

The stratigraphic positions of the 50 samples in this study are shown in Text-Figure 2. Thirty-six samples (samples 2633 to 2668) are from cores of the Kysing-4 Borehole. The 14 samples from the Moesgaard Clay and above were taken from outcrop and shallow boreholes numbers 1 to 3, drilled at the same locality and processed prior to the drilling of Kysing-4. Samples 1906 to 1932 are from borehole number 3, and samples 1768 to 1776 are from the coastal cliff and boreholes numbers 1 and 2. Identical lithologic details in the sections allowed all the samples to be projected into the Kysing-4 Borehole, as shown in Text-Figure 2. The uppermost sample of the Søvind Marl Formation (number 2668) included approximately 1% burrows extending from the overlying Moesgaard Clay.

The samples were processed using standard techniques. After careful cleaning of sample surfaces, especially the removal of the outermost part of core samples and the avoiding of occasional sheared core fragments, carbonates were removed with HCl. After centrifugation, the silicates were removed with HF. After cold HF treatment

for a minimum of four days, the samples were again centrifuged. Excess HF and silicofluorides were removed by boiling the sample in 18% HCl for 30 minutes. Occasionally, this boiling was repeated in order to dissolve gel-like silicofluorides. Finally, the samples were washed twice with demineralized water. The acid-treated material was sieved on 20 µm nylon filters and inspected. Most samples of the Søvind Marl Formation were then ready for mounting on slides for light microscopy. A few samples of the Søvind Marl Formation with abundant mineral grains were centrifuged using ZnCl₂ in dilute HCl with a specific gravity of 2.0. A few of the Søvind Marl Formation samples and almost all the overlying samples, were oxidized using cold 65% HNO₃ for 5 or 10 minutes. Sample residues were mounted in gelatine–glycerine except for numbers 1928 to 1932, which were mounted in silicone oil. The palynological analysis comprised counts of 100 to 300 specimens of organic-walled microplankton using a plain transmitted light microscope. The large number of dinoflagellate cysts present in all the samples allowed an additional search for rare species in the remaining material. In most of the samples, the analysis also included a visual estimate of the relative proportions of main types of organic particles greater than 20 µm in diameter, i.e., palynomorphs, phytoclasts and amorphous aggregates (Tyson, 1995). Photomicrography used black and white film, which was subsequently digitized. Selected cysts were drawn with drawing apparatus.

Type depository

The types of the new taxa are lodged in the type collection of the Geological Museum, Øster Voldgade 5–7, DK-1350 Copenhagen, Denmark. They are identified by their individual ‘MGUH’ number. The position of the respective specimen in the slide is identified using ‘England Finder’ coordinates. The top of the slides should be aligned with the edge of the ‘England Finder’ marked ‘left’.

SYSTEMATIC PALEONTOLOGY

The organic-walled microplankton assemblages in the material studied are dominated by dinoflagellate cysts. A full list of taxa is given in Table 1, which also gives their stratigraphic distributions. Names of dinoflagellate cyst taxa generally follow Fensome and Williams (2004). In this section, new taxa and taxa in open nomenclature are described. Comments are given on various established taxa where appropriate, as well as on informal groups that

Table 1. Distribution of organic-walled microplankton (mainly dinoflagellate cysts) in the Kysing-4 borehole. The figures are percentages of total microplankton; 0 = presence outside of count; ? = uncertain record; cf = atypical but possibly within the circumscription of taxon; aff = compared with, but different from taxon. The group 'other microplankton' mainly includes *Spirinferties* spp. Abbreviations: DeC = De Coninck, H-C&C = Heilmann-Clausen and Costa.

CHRONOSTRATIGRAPHY	LITHOSTRATIGRAPHY	SAMPLES	UPPER EOCENE		MIDDLE EOCENE		LUTETIAN	
			LOW. OLIG. RUPELIAN	UPPER EOCENE	MIDDLE EOCENE	LUTETIAN		
	Viborg Formation		Kysing Marl	PRIABONIAN	BARTONIAN	Savind Marl Formation		
<i>Achilleodinium bifurcoides</i>	1776	-	0	1926	2668	-	2633	-
<i>Achnosphaera alicornu</i>	1775	-	1	1922	2667	0	2634	-
<i>Achnosphaera expansa</i>	1774	-	2	1919	2666	0	2635	-
<i>Adnatosphaeridium multispinosum</i>	1773	0	0	1916	2665	0	2636	-
<i>Amphorosphaeridium ? multispinosum</i>	1771	1	-	1906	2664	0	2637	-
<i>Araeosphaera araneosa</i>		-	-		2663	0	2638	-
<i>Areoligera senonensis</i>		-	-		2662	1	2639	-
<i>Areoligera sentosa - fauloma Group</i>		-	-		2661	0	2640	-
<i>cf. Areoligera sentosa in H-C&C 89</i>		-	-		2660	1	2641	-
<i>Areoligera undulata</i>		-	-		2659	0	2642	-
<i>Areosphaeridium diktyoplokom</i>		2	7		2658	1	2643	-
<i>Areosphaeridium ebdonii</i>		-	0		2657	0	2644	-
<i>Areosphaeridium michoudii</i>		-	2		2656	0	2645	-
<i>Batiacasphaera baculata</i>		-	1		2655	0	2646	-
<i>Batiacasphaera compta</i>		-	0		2654	1	2647	-
<i>Batiacasphaera explanata</i>		-	3		2653	0	2648	-
<i>Callogodinium arniculum</i>		0	5		2652	0	2649	-
<i>Cerebrosysta bartonenis s. str.</i>		-	0		2651	0	2650	-
<i>Cerod. barton. - Corrud. incompos. transitional</i>		-	4		2650	1	2651	-
<i>Cerebrosysta magna</i>		-	0		2649	0	2652	-
<i>Ceroadnium depressum</i>		-	1		2648	0	2653	-
<i>C. coleothrypta rotundata s. Dec 86</i>		0	1		2647	0	2654	-
<i>Charlesdowniea coleothrypta var. 1 H-C&C 89</i>		-	0		2646	1	2655	-
<i>Charlesdowniea tenuivirgula</i>		-	?		2645	0	2656	-
<i>Chiropteridium cf. dispersum in Eaton 76</i>		-	-		2644	0	2657	-
<i>Chiropteridium eocaenicum</i>		-	0		2643	0	2658	-
<i>Cleistosphaeridium diversispinosum</i>		1	0		2642	0	2659	-
<i>Cordosphaeridium biarmatum</i>		-	1		2641	0	2660	-
<i>Cordosphaeridium aff. callosum</i>		1	1		2640	0	2661	-
<i>Cordosphaeridium cantharellus</i>		-	2		2639	0	2662	-
<i>Cordosphaeridium funiculatum</i>		0	0		2638	0	2663	-
<i>Cordosphaeridium gracile</i>		-	2		2637	0	2664	-
<i>Cordosphaeridium inodes</i>		-	0		2636	0	2665	-
<i>Cordosphaeridium minimum</i>		-	1		2635	0	2666	-
<i>Corrudinium incompositum s. str.</i>		4	0		2634	0	2667	-
<i>Corrudinium sp. 1</i>		-	2		2633	0	2668	-
<i>Costacysta bucina</i>		-	3		2632	0	2669	-
<i>Cribroperidinium tenuitubulatum</i>		3	0		2631	0	2670	-
<i>Dapsilidinium pseudocolligerum</i>		-	2		2630	0	2671	-
<i>Deflandrea denticulata</i>		0	1		2629	0	2672	-
<i>Deflandrea tetraphylla</i>		1	1		2628	0	2673	-
<i>Deflandrea phosphorica</i>		-	0		2627	0	2674	-
<i>Desmidiaceae zygote? sp. indet. in DeC 01</i>		-	2		2626	0	2675	-
<i>Dinopterygium cf. cladoides</i>		-	1		2625	0	2676	-
<i>Diphyes colligerum</i>		-	3		2624	0	2677	-

Table 1 (continued).

CHRONOSTRATIGRAPHY	LOW. OLIG.		UPPER EOCENE		MIDDLE EOCENE		LITHOSTRATIGRAPHY	SAMPLES
	RUPELIAN		PRIABONIAN		BARTONIAN			
	Viborg Formation		Moesgaard Clay		Søviind Marl Formation			
	1776	1775	1768	1926	2668	2667	cf. <i>Kalliosphaeridium capulatum</i>	
	1774	1773	1932	1922	2667	2666	<i>Lanternosphaeridium lanosum</i>	
	1773	1771	1930	1919	2666	2665	<i>Lanternosphaeridium</i> sp. 1	
	1771		1928	1916	2664	2664	<i>Lejeunecysta hyalina</i>	
				1906	2663	2662	<i>Lentina serrata</i>	
					2662	2661	<i>Lingulodinium machaerophorum</i>	
					2661	2660	<i>Liosphaeridium ? mamellatum</i>	
					2660	2659	<i>Lophocysta sulcolimbata</i>	
					2659	2658	<i>Melittasphaeridium pseudorecurvatum</i>	
					2658	2657	<i>Melittasphaeridium asterium</i>	
					2657	2656	<i>Membranophoridium aspinatum</i>	
					2656	2655	<i>Microdinium reticulatum</i>	
					2655	2654	<i>Muratodinium fimbriatum</i>	
					2654	2653	<i>Nematosphaeropsis</i> spp.	
					2653	2652	<i>Oligosphaeridium</i> sp. A in DeC 86	
					2652	2651	<i>Oligosphaeridium ? cf. H. rigaudae</i> in DeC 86	
					2651	2650	<i>Operculodinium divergens</i> Group	
					2650	2649	<i>Operculodinium eisenackii</i>	
					2649	2648	<i>Operculodinium microtriatinum</i>	
					2648	2647	<i>Operculodinium nanaconulum-placitum</i> Group	
					2647	2646	<i>Palaeocystodinium cf. goizowense</i>	
					2646	2645	<i>Palambages ? sp. 1</i>	
					2645	2644	<i>Palambages</i> sp.	
					2644	2643	<i>"Palmnickia lobifera"</i>	
					2643	2642	<i>Paralecaniella indentata</i>	
					2642	2641	<i>Paucilobomorpha tiraditla</i>	
					2641	2640	<i>Paucisphaeridium inversibuccinum</i>	
					2640	2639	<i>Pentadinium goniferum</i>	
					2639	2638	<i>Pentadinium laticinctum</i>	
					2638	2637	<i>Pentadinium cf. lophophorum</i>	
					2637	2636	<i>Pentad. cf. taeniagerum</i> in DeC 85	
					2636	2635	<i>Planzhenhaeren Eisenack 54</i>	
					2635	2634	<i>Phtharoperidium comutum</i>	
					2634	2633	<i>Phtharoperidium clithridium</i>	
							<i>Phtharoperidium cornutum</i>	
							<i>Phtharoperidium distinctum</i>	
							<i>Phtharoperidium geminatum</i>	
							<i>Phtharoperidium levinum</i>	
							<i>Phtharoperidium powellii</i>	
							<i>Phtharoperidium regalis</i>	
							<i>Phtharoperidium</i> spp.	
							<i>Polysphaeridium zoharyi</i>	
							<i>Problematicum III in Manum 76</i>	
							<i>Pyxidella ? scrobiculata</i>	
							<i>Pyxidopsis densepunctata</i>	
							<i>Reticulatosphaera acinocoronata</i>	
							<i>Reticulatosphaera ? sp. A in DeC 95</i>	
							<i>Rhombodinium draco</i>	
							<i>Rhombodinium longimanum</i>	

have been used in this study. Open nomenclature is used in cases where it is uncertain if the specimens fall outside the morphological variation of the existing taxa, or the numbers of specimens were not large enough to formally describe a new taxon. Four informal groups of closely related species are established. The stratigraphic distributions of these groups are easy to delineate, as opposed to the individual species that are often difficult to separate. The morphologic terminology of the dinoflagellate cysts mainly follows Fensome, Riding and Taylor (1996). For convenience, the dinoflagellate cyst species are listed in alphabetic order after genera in the text and as far as possible in Plates 1 to 15. For classification above the generic level, see Fensome et al. (1993). One green alga and one acritarch are described at the end of this section. Lists of synonymy are given where considered to be appropriate.

Division DINOFLAGELLATA (Bütschli 1885)
Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Genus *Areoligera* Lejeune-Carpentier 1938
Areoligera sentosa–*Areoligera tauloma* Group
Plate 1, figs. 1, 2

Remarks. Some specimens in this group are typical representatives of *Areoligera sentosa* Eaton 1976. Others have 'T'-shaped endings on the majority of spines as in *Areoligera tauloma* Eaton 1976, although their membranes are not as deeply incised as is typical for that species.

Genus *Cerebrocysta* Bujak in Bujak et al. 1980
Cerebrocysta bartonensis–*Corrudinium incompositum*
transitional forms
Plate 2, fig. 10

Remarks. Typical forms of *Cerebrocysta bartonensis* Bujak in Bujak et al. 1980 (Plate 2, figs. 6, 7) and *Corrudinium incompositum* (Drugg 1970) Stover & Evitt 1978 (Plate 2, fig. 11) are common in the material. In addition to the typical forms, we recorded intermediate morphologies in many samples from the middle and upper part of the section. The continuous intergradation between the two species in these samples hampers separation of the two taxa, and also documents their close biological affinity. Because typical specimens of these two species differ so markedly, we have, nonetheless, tried to distinguish them separately, rather than treating them as a single group. This revealed different ranges, with typical *Cerebrocysta bartonensis* being restricted to, and common in, the lower to middle part of the section.

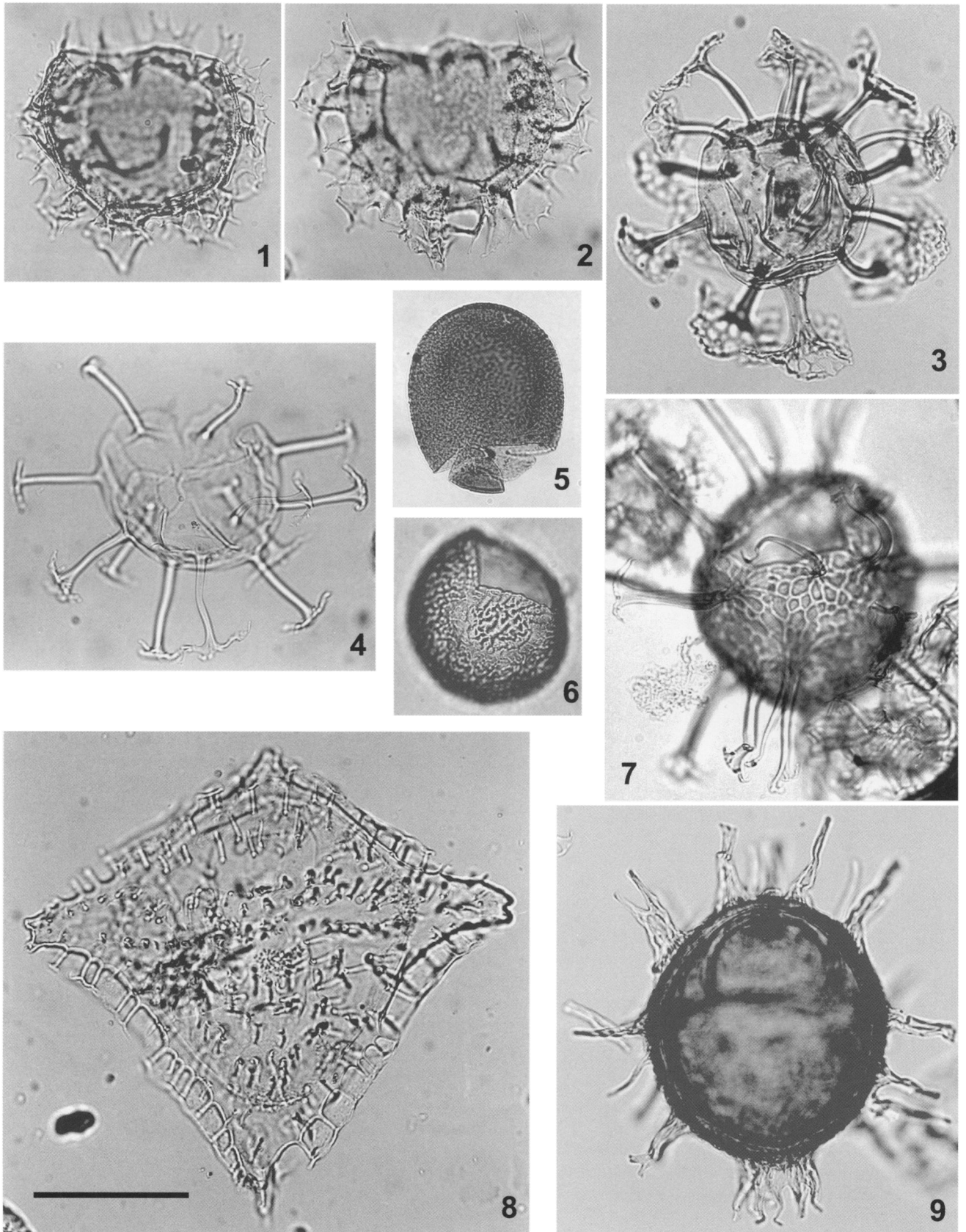
Genus *Charlesdowniea* Lentin & Vozzhennikova 1989
Charlesdowniea coleothrypta subsp. *rotundata*
sensu De Coninck 1986
Plate 1, fig. 8

Remarks. These specimens are close to the specimen figured by De Coninck (1986, pl. 5, figs. 24, 25, as *Kisselovia coleothrypta* subsp. *rotundata*) from the Upper Eocene of the southern Netherlands. In particular, they share an almost rhombic outline, bear fine, numerous processes and their ectocoel is narrow. Both the Netherlands and Danish specimens differ, however, from *Charlesdowniea coleothrypta* subsp. *rotundata* (Châteauneuf & Gruas Cavagnetto 1978) Lentin & Vozzhennikova 1989. The latter subspecies, described from the Lower Eocene of France, bears fewer, more robust processes and its ectocoel is wider. Our specimens resemble the Upper Eocene *Charlesdowniea clathrata* subsp. *angulosa* (Châteauneuf & Gruas Cavagnetto 1978) Lentin & Vozzhennikova 1989, which also bears fine, numerous processes and has a narrow ectocoel, although the cyst outline is pentagonal.

PLATE 1

Bar scale in Fig. 8 = 50 µm applies to all specimens.

- | | | | |
|------|--|---|---|
| 1, 2 | <i>Areoligera sentosa</i> – <i>A. tauloma</i> Group. 1: Sample 2654.
2: Sample 2652. | 6 | <i>Cerebrocysta magna</i> Bujak 1994. Sample 1930. |
| 3 | <i>Areosphaeridium diktyoplokum</i> (Klumpp 1953) Eaton
1971. Sample 2650. | 7 | <i>Cordosphaeridium funiculatum</i> Morgenroth 1966.
Sample 2667. |
| 4 | <i>Areosphaeridium michoudii</i> Bujak 1994. Sample 2634. | 8 | <i>Charlesdowniea coleothrypta</i> subsp. <i>rotundata sensu</i>
De Coninck (1986). Sample 1768. |
| 5 | <i>Caligodinium amiculum</i> Drugg 1970. Specimen showing
relatively coarse ornamentation. Manum and Wil-
liams (1995) interpreted the archeopyle as hypocystal.
Sample 2658. | 9 | <i>Cordosphaeridium biarmatum</i> Morgenroth 1966.
Sample 2640. |



Genus *Chiropteridium* Gocht, 1960
Chiropteridium eoceanicum sp. nov.
 Plate 2, figs. 1–5

Description. Marginate, cavate, skolochorate cysts. The granulate endocyst is dorsoventrally flattened and lenticular. The periphragm completely encloses the endophragm, and is smooth with very small perforations. Both phragma are mid-dorsally and mid-ventrally appressed. Well-developed pericoels are present at the lateral margins of the ventral surface of the cyst. The two pericoels extend to a lesser degree to the lateral margins of the dorsal surface. These two mainly lateral lobes extend from the apical to the antapical region and form antapical lobes of the same length. At some places within these lobes, the periphragm is supported by columellae. The lobes bear smooth, slender projections with bifurcate distal endings. Solid processes, which may branch distally, occur on the dorsal surface adjacent to the lobes and the archeopyle margin. No paratabulation is indicated, except for the archeopyle. The archeopyle is apical (Type tA), and exhibits a markedly angular suture. The parasulcal notch is distinctly offset. The operculum bears one large, transverse lobe with slender bifurcate projections.

Derivation of name. From the Eocene.

Designation of holotype. Plate 2, figs. 1 and 2. Slide 2658 G6, England Finder coordinates J53/1. MGUH 27762. Kysing-4 borehole, sample 2658, Middle Eocene. Specimen dimensions: Pericyst length (excysted) 87 µm; pericyst breadth 96 µm; endocyst length (excysted) 57 µm; endocyst breadth 63 µm.

Designation of paratype. Paratype 1: Plate 2, fig. 3, Slide 2658 G5, England Finder coordinates D31/4. MGUH

27763. Kysing-4 borehole, sample 2658, Middle Eocene. Paratype 2: Plate 2, figs. 4 and 5, Slide 2658 G5, England Finder coordinates O23. MGUH 27764. Kysing-4 borehole, sample 2658, Middle Eocene.

Dimensions of measured specimens. Pericyst length (excysted) 66 (91) 107 µm. Pericyst breadth 83 (94) 109 µm. Endocyst length (excysted) 45 (60) 71 µm. Endocyst breadth 55 (63) 76 µm. (28 specimens measured).

Comparison. *Chiropteridium eoceanicum* sp. nov. differs from all other species of *Chiropteridium* in having two lateral pericoels extending continuously from the apical to antapical region. *Chiropteridium eoceanicum* sp. nov. therefore lacks the highly irregular and often jagged outline typical for the genus. *Chiropteridium eoceanicum* sp. nov. resembles *Membranophoridium aspinatum* Gerlach 1961, but differs by having projections on the lobes and on the lateral margins of the dorsal surface. It is concluded that *Chiropteridium eoceanicum* sp. nov. has a morphological position between *Chiropteridium* and *Membranophoridium*. The presence of two pericoels is also shared with *Palynodinium*. However, in *Palynodinium* the pericoels are ventrolateral in position, not lateral as in *Chiropteridium eoceanicum* sp. nov. Furthermore, in *Palynodinium* the position of the paracingulum is clearly reflected by aligned processes on the dorsal surface, and the central body is spherical, not lenticular.

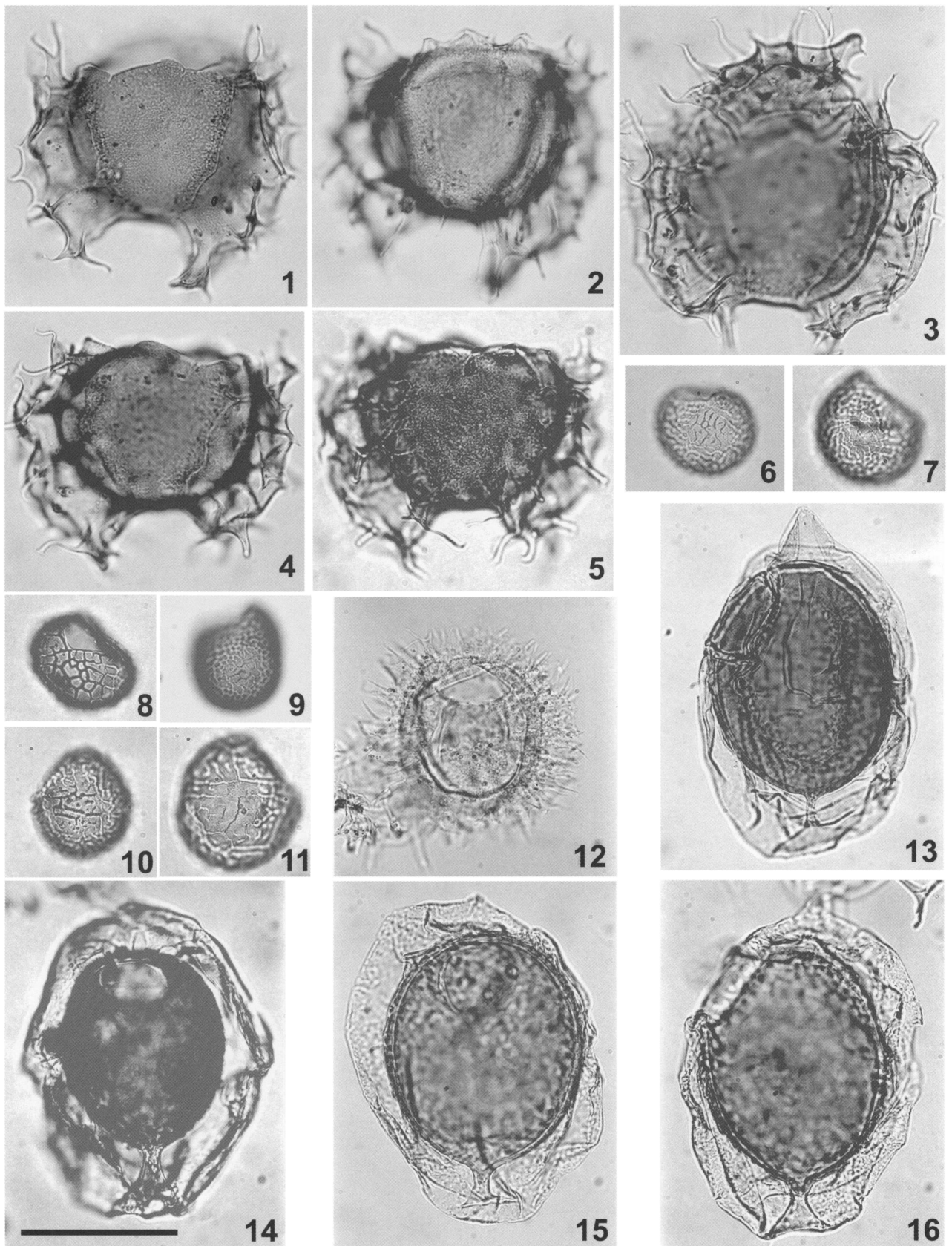
Genus *Cleistosphaeridium* Davey et al. 1966
Cleistosphaeridium diversispinosum Davey et al. 1966

Systematophora placacantha (Deflandre & Cookson 1955)
 Davey et al. 1969; Heilmann-Clausen and Costa, 1989, pl. 13, figs. 4, 5, 7; Köthe, 1990, pl. 15, fig. 6.

PLATE 2

Bar scale in Fig. 14 = 50 µm applies to all specimens.

- | | | | |
|------|---|-------|---|
| 1, 2 | <i>Chiropteridium eoceanicum</i> sp. nov. Holotype. 1: Exterior view of ventral surface. 2: Interior view of dorsal surface. Sample 2658. | 11 | <i>Corrudinium incompositum</i> (Drugg 1970) Stover & Evitt 1978. Sample 2649. |
| 3 | <i>Chiropteridium eoceanicum</i> sp. nov. Paratype 1. Sample 2658. | 12 | <i>Cordosphaeridium</i> aff. <i>callosum</i> Morgenroth 1966. Sample 2649. |
| 4, 5 | <i>Chiropteridium eoceanicum</i> , sp. nov. Paratype 2. 4: Interior view of ventral surface. 5: Exterior view of dorsal surface. Sample 2658. | 13–16 | <i>Costacysta bucina</i> sp. nov. 13: Paratype 3, lateral view. A ring-structure (?flagellar scar) in midventral surface is seen to the right. Pøt Strand Borehole, sample 1805. 14: Paratype 2. Holes in the periphragm anterior to the archeopyle margin are visible. LB-38 Borehole, sample 482. 15: Holotype. Sample 2653. 16: Paratype 1. Sample 2653. |
| 6, 7 | <i>Cerebrocysta bartonensis</i> Bujak in Bujak et al. 1980. Two specimens from sample 2649. | | |
| 8, 9 | <i>Corrudinium</i> sp. 1. 8: Sample 2643. 9: Sample 2665. | | |
| 10 | <i>Cerodinium bartonensis</i> Bujak in Bujak et al. 1980 – <i>Corrudinium incompositum</i> (Drugg 1970) Stover & Evitt 1978 transitional form. Sample 2649. | | |



Remarks. Eaton et al. (2001) emended *Cleistosphaeridium diversispinosum* to include a morphologic continuum observed among cysts from the type stratum. These cysts exhibit a morphologic variation, ranging from specimens with a nontabular, or indistinctly penitabular, process distribution as in the holotype of *Cleistosphaeridium diversispinosum*, to specimens with a more clear penitabular distribution of the processes. The latter forms display some development of basal ridges between adjacent processes. The abundant specimens of *Cleistosphaeridium diversispinosum* observed in the present study clearly fall within this morphologic spectrum. The Miocene holotype of the closely related species *Cleistosphaeridium placacanthum* (Deflandre & Cookson 1955) Eaton et al. 2001, differs by showing a more distinct penitabular process distribution, due to more well developed annular ridges at the base of the process groups. Abundant *Cleistosphaeridium placacanthum*, as *Systematophora placacantha* (Deflandre & Cookson 1955) Davey et al. 1969, was previously recorded and illustrated from the Eocene of northern Germany (Heilmann-Clausen & Costa, 1989; Köthe, 1990). These records may be included in *Cleistosphaeridium diversispinosum* as emended by Eaton et al. (2001). Abundant *Systematophora placacantha* was likewise recorded, and used for biozonation, in the Eocene of the North Sea by Bujak and Mudge (1994). No specimens were illustrated by these authors, but there is little doubt that these cysts from coeval strata can also be included in *Cleistosphaeridium diversispinosum*.

Genus *Cordosphaeridium* Eisenack 1963

Tityrosphaeridium Sarjeant, 1981, p. 120 (junior synonym)

Remarks. *Tityrosphaeridium* was established by Sarjeant (1981) for species with paracingular processes formerly placed in *Cordosphaeridium*. According to Sarjeant (1981), paracingular processes are absent in the type of the genus,

Cordosphaeridium inodes. This interpretation of processes in *Cordosphaeridium inodes* was, however, rejected by Lentin and Williams (1985), who mentioned the presence of paracingular processes in the holotype. Lentin and Williams (1985) therefore considered *Tityrosphaeridium* to be a junior synonym of *Cordosphaeridium*. This view was also held by Stover and Williams (1987), who commented in detail on the morphology and distribution of processes on the holotype of *Cordosphaeridium inodes*. They stated: "...the drawings of the holotype (Sarjeant 1981, text-fig. 1) clearly show two, distinctive, dorsal taeniate processes immediately posterior to and slightly to the left and right of the archeopyle's longitudinal midline. These two processes (labelled 2" and 3") are in the customary position, relative to 3", of processes reflecting paraplates 3c and 4c, respectively, on typical gonyaulacacean cysts." Quattrocchio and Sarjeant (1996) maintained Sarjeant's (1981) interpretation that *Cordosphaeridium* lacks paracingular processes. They did not comment specifically on the two taeniate processes immediately posterior to the archeopyle that were interpreted as paracingular in position by Stover and Williams (1987). Conflicting interpretations of the morphology of the holotype of *Cordosphaeridium inodes* therefore exist, in spite of it being well illustrated by Klumpp (1953) and Sarjeant (1981). The interpretation of Stover and Williams (1987) is adopted herein, and hence the genus *Tityrosphaeridium* is interpreted as being a junior synonym of *Cordosphaeridium*.

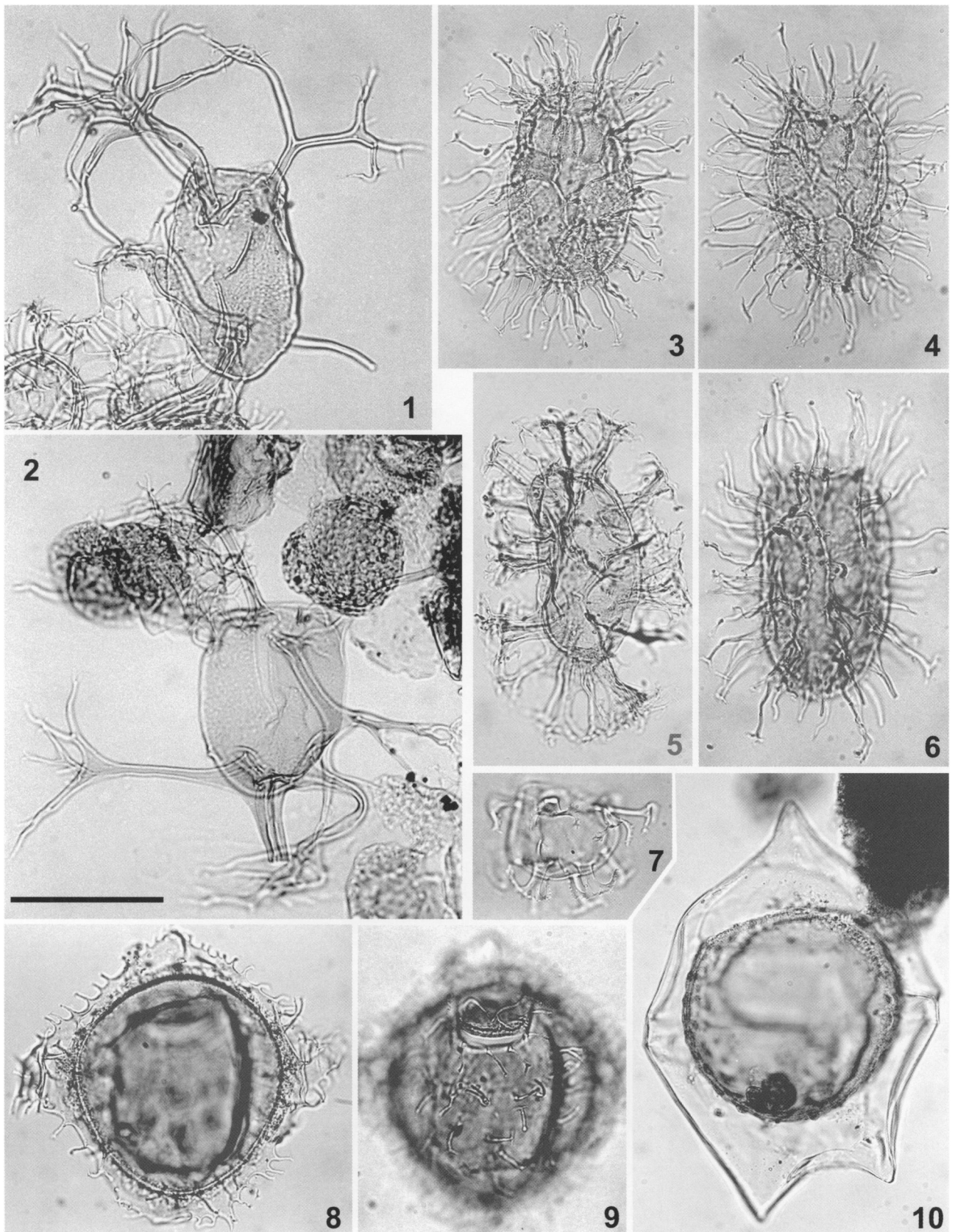
Cordosphaeridium aff. *callosum* Morgenroth 1966
Plate 2, fig. 12

Description. These forms are similar to *Cordosphaeridium callosum*, especially due to the presence of a thick cloudy-fibrous outer layer of the central body, from which the processes arise. However, the dimensions differ markedly. *Cordosphaeridium callosum* is much smaller, with a central body diameter varying between 17 and 22

PLATE 3

Bar scale in Fig. 2 = 50 µm applies to all specimens.

- | | | | |
|---------|---|------|---|
| 1, 2 | <i>Distatodinium biffii</i> Brinkhuis et al. 1992. Two specimens from sample 1905 (same stratigraphic level as sample 2668). | 7 | <i>Enneadocysta arcuata</i> (Eaton 1971) Stover & Williams 1995. Sample 2641. |
| 3, 4, 6 | <i>Distatodinium pilosum</i> sp. nov. 3: Holotype, with operculum <i>in-situ</i> . Sample 2654. 4: Paratype 1. Sample 2654. 6: Paratype 2. Sample 2654. | 8, 9 | <i>Dracodinium</i> aff. <i>varielongitudum</i> (Williams & Downie 1966) Costa & Downie 1979. 7: Optical section. 8: Exterior view of dorsal surface. Sample 2648. |
| 5 | <i>Distatodinium ellipticum</i> (Cookson 1965) Eaton 1976. Sample 2666. | 10 | <i>Deflandrea heterophlycta</i> Deflandre & Cookson 1955. Sample 1928. |



µm. Furthermore, these specimens have more numerous processes. *Exochosphaeridium? solaster* (Morgenroth 1966) Stover & Evitt 1978, differs by lacking the thick, cloudy outer layer of the central body.

Dimensions of measured specimens. Total cyst diameter 72 (79) 99 µm. Central body diameter 54 (60) 72 µm. (7 specimens measured).

Cordosphaeridium cantharellus (Brosius 1963)

Gocht 1969

Plate 14, fig. 1

Remarks. In addition to the more typical forms, we have included specimens with continuous ectophragm and specimens with shorter processes within this species.

Genus *Corrudinium* Stover & Evitt 1978

Corrudinium sp. 1

Plate 2, figs. 8, 9

Description. *Corrudinium* sp. 1 is a small proximate cyst ornamented by polygonal fields delineated by low septa or ridges and covering the entire cyst surface. The polygonal fields are much smaller and more numerous than normal gonyaulacacean thecal plates, and do not therefore represent a paratabulation. Paratabulation is only indicated by the archeopyle, which is precingular, Type P (3" only).

Comparison. *Corrudinium* sp. 1 is related to *Corrudinium incompositum* (Drugg 1970) Stover & Evitt 1978, but differs from the typical morphology of this species by nearly all the polygonal fields being complete, in contrast to the many incomplete polygonal fields in *Corrudinium incompositum*.

Genus *Costacysta* gen. nov.

Description. A gonyaulacacean, holocavate dinoflagellate cyst with an ellipsoidal endocyst enclosed in a larger, thinner walled pericyst. The two phragma are connected by a prominent process or columella arising from the antapex of the endocyst. The columella is narrow and massive at the base, and situated on top of a minute horn of the endocyst. The main part of the columella is hollow and the columella expands strongly towards the distal end, attaining the shape of a funnel. The distal end of the columella is continuous with the periphragm. The two phragma are furthermore connected by a crater-like or funnel-shaped ring structure situated on the midventral surface, and probably representing a flagellar scar. The archeopyle is precingular (Type P, 3" only). Apart from the archeopyle, no paratabulation is clearly indicated, although folds and wrinkles of the periphragm may be present and loosely form a partial paracingulum and a few other parasutures.

Derivation of name. For the palynologist Lucy I. Costa.

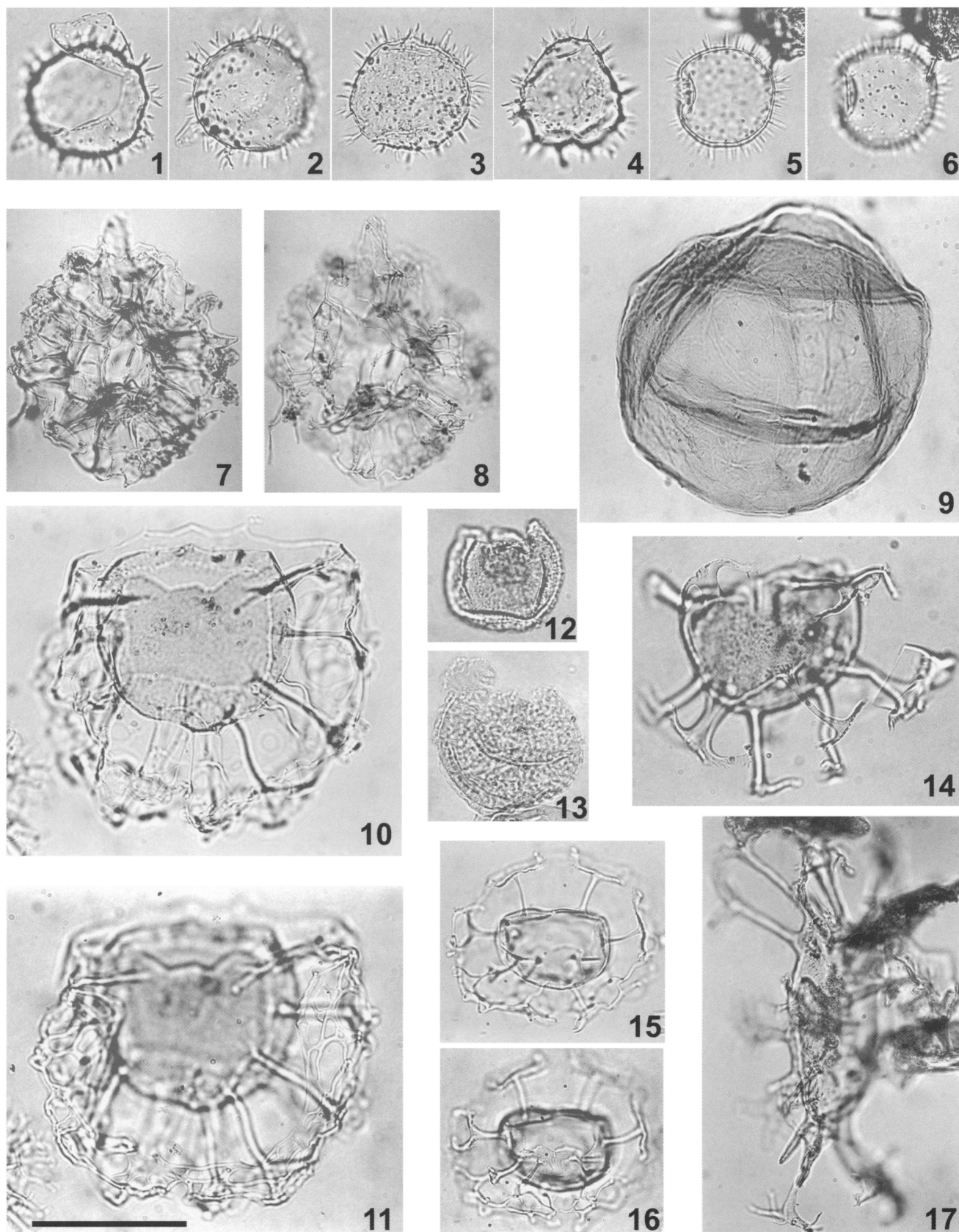
Type species. *Costacysta bucina* gen. et sp. nov., Lutetian, upper part of Lillebælt Clay Formation and lower part of Søvind Marl Formation, Denmark.

Comparison. No previously described genera are morphologically close to *Costacysta* gen. nov. Two cavate gonyaulacoid genera with a prominent columella are known, *Amiculospaera* Harland 1979 and *Wilsonisphaera* Slimani 1994. In *Amiculospaera* the columella is at the apex, and furthermore no cavity is present in the hypocyst where the phragma are appressed. According to Schiøler and Wilson (1994), who described *Wilsonisphaera* as its junior synonym *Glaphyrosphaera*, this taxon has a prominent columella in the parasulcal area. It further differs from *Costacysta* by the presence of parasutural ridges on the periphragm.

PLATE 4

Bar scale in Fig. 11 = 50 µm applies to all specimens.

- | | | | |
|------|--|--------|---|
| 1, 2 | <i>Echinidinium? lucidum</i> sp. nov. Holotype, with adnate operculum. Sample 1930. | 10, 11 | <i>Glaphyrocysta semitecta</i> (Bujak in Bujak et al. 1980) Lentin & Williams 1981. 10: Dorsal surface. 11: Ventral surface. Sample 2668. |
| 3 | <i>Echinidinium? lucidum</i> sp. nov. Paratype. Sample 1928. | 12, 13 | <i>Elytrocysta brevis</i> Stover & Hardenbol 1994. 12: Sample 1774. 13: Sample 1773. |
| 4 | <i>Echinidinium? lucidum</i> sp. nov. Sample 1930. | 14 | <i>Enneadocysta arcuata</i> (Eaton 1971) Stover & Williams 1995. Sample 2645. |
| 5, 6 | <i>Echinidinium? lucidum</i> sp. nov. Specimen in two different foci. Sample 1930. | 15, 16 | <i>Enneadocysta? aff. arcuata</i> (Eaton 1971) Stover & Williams 1995. Specimen in two different foci. Sample 2661. |
| 7, 8 | cf. <i>Ectosphaeropsis burdigalensis</i> Londeix & Jan Du Chêne 1988. Specimen in two different foci. Sample 2667. | 17 | <i>Distatodinium paradoxum</i> (Brosius 1963) Eaton 1976. Sample 1932. |
| 9 | Gen. et sp. indet. 1 in Heilmann-Clausen and Costa (1989). Sample 2668. | | |



Costacysta bucina sp. nov.

Plate 2, figs. 13–16

Description. As for the genus, with the following additional features. The endophragm is thick, 1 to 3 μm , and varies from almost smooth, through finely granular, to irregularly verrucate–gemmate. The periphragm is thin, less than 0.5 μm , and hyaline. The periphragm bulges inwards at the margins of the archeopyle, and is here fused to the endocyst. Holes of variable size (2 to 8 μm) are usually present in parts of the periphragm, in particular adjacent to the archeopyle margin and in parts of the ventral surface.

Derivation of name. From Latin, *bucina* meaning shepherd's horn, from the appearance of the antapical columella.

Designation of holotype. Plate 2, fig. 15, Slide 2653 H3, England Finder coordinates U56/1. MGUH 27765. Kysing-4 borehole, sample 2653, Middle Eocene. Specimen dimensions: Pericyst length 105 μm ; pericyst breadth 81 μm ; endocyst length 75 μm ; endocyst breadth 65 μm ; length of antapical columella 12 μm ; thickness of endophragm 2 μm .

Designation of paratype. Paratype 1. Plate 2, fig. 16, Slide 2653 H1, England Finder coordinates C47/2. MGUH 27766. Kysing-4 borehole, sample 2653, Middle Eocene. Specimen dimensions: Pericyst length 108 μm ; pericyst breadth 75 μm ; endocyst length 78 μm ; endocyst breadth 60 μm ; length of antapical columella 18 μm ; thickness of endophragm 2 μm . Paratype 2. Plate 2, fig. 14, Slide 482 G1, England Finder coordinates P54. MGUH 27767. LB 38 borehole, sample chc92 at 19.4 m, Søvind Marl Formation, Middle Eocene. Paratype 3. Plate 2, fig. 13, Slide 1805 G2, England Finder coordinates L40. MGUH 27768. Pøt Strand borehole 1991, sample at 7.8–8.0 m, Søvind Marl Formation, Middle Eocene.

Dimensions of measured specimens. Pericyst length 84 (100) 114 μm . Pericyst breadth 64 (79) 90 μm . Endocyst length 62 (71) 78 μm . Endocyst breadth 49 (59) 67 μm . Length of antapical columella 11 (16) 26 μm . Thickness of endophragm 1.5–3 μm . (18 specimens measured).

Variation. The crater-like ring structure on the ventral surface of the endocyst may be small and nearly invisible, or larger, approaching the shape and size of the antapical columella.

Genus *Dinopterygium* Deflandre 1935*Dinopterygium* cf. *cladooides* Deflandre 1935

?*Dinopterygium cladooides* Deflandre, 1935, p. 131, pl. 8, fig. 6; Morgenroth, 1966, p. 12, pl. 2, fig. 11.

?*Heteraulacacysta pustulata* Jan Du Chêne & Adediran, 1985, p. 15, pl. 19, fig. 1.

Dinopterygium cladooides sensu Morgenroth 1966; Heilmann-Clausen and Costa, 1989, pl. 10, fig. 10.

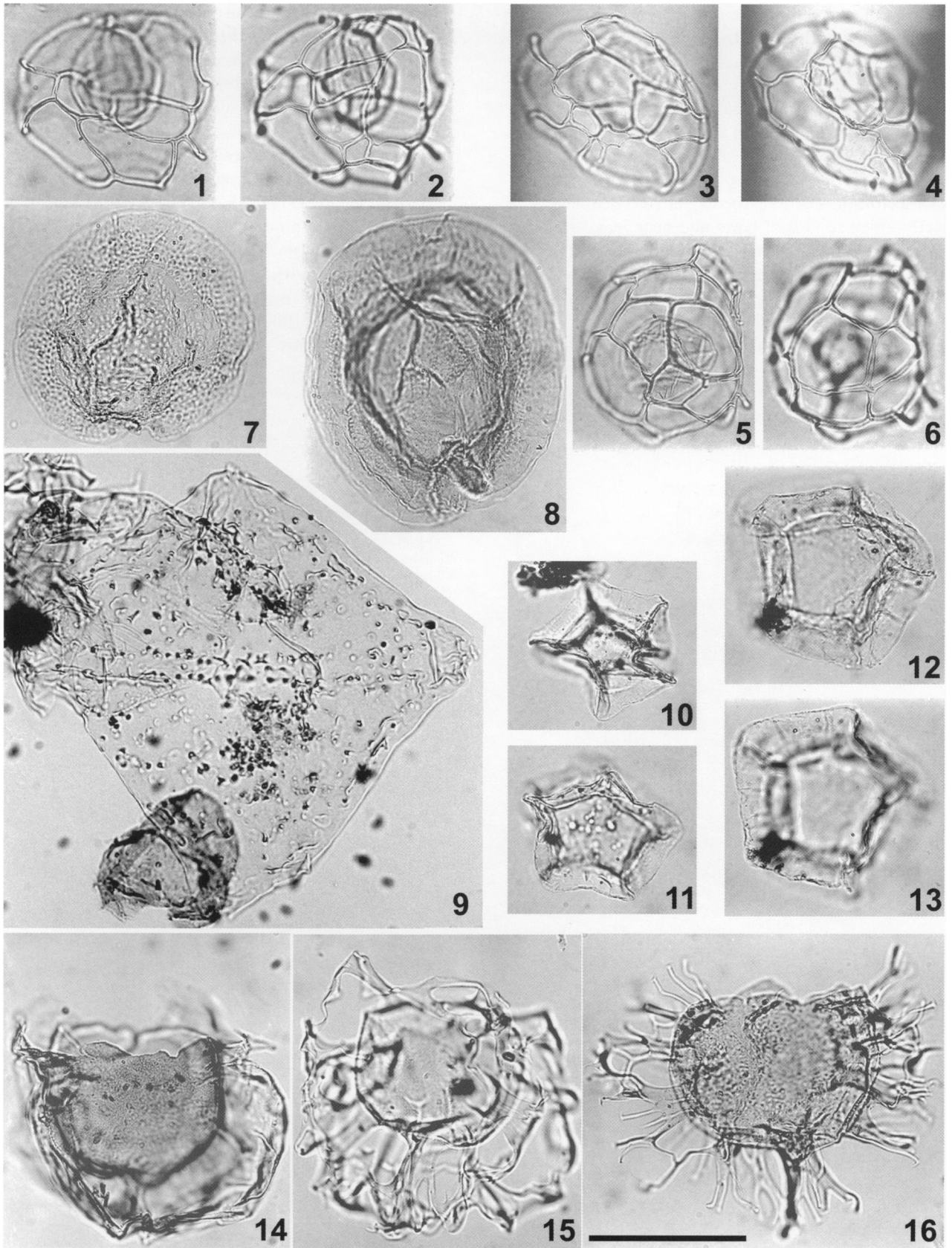
Description. The specimens of this form exhibit intratabular sculpture of massive or hollow, short tubercles that are cylindrical or distally expanded. Occasionally the tubercles may support a thin outer periphragm that may be observed in optical section. In these cases, the wall is tectate with intramural columellae, instead of autophragm with external tubercles. The tubercles/columellae are probably infillings of trichocyst pores in the theca of the motile cell (Evitt, 1985, text-fig. 4.2J). These pore-casts are absent in the pandasutural bands, which are usually free of ornament but sometimes may exhibit large round holes.

Comparison. Usually the specimens have small tubercles, for example the specimen figured by Heilmann-Clausen and Costa (1989). The form figured by Morgenroth (1966) has larger tubercles. Some authors classify speci-

PLATE 5

Bar scale in Fig. 16 = 50 μm applies to all specimens.

- | | | | |
|------|--|--------|---|
| 1, 2 | <i>Hapsocysta kysingensis</i> sp. nov. Holotype. 1: Upper surface. 2: Interior view of lower surface. Sample 2666. | 11 | <i>Horologinella? pentagonalis</i> sp. nov. Paratype 2. Sample 1928. |
| 3, 4 | <i>Hapsocysta kysingensis</i> sp. nov. Paratype 2. 3: Upper surface. 4: Interior view of lower surface. Sample 2666. | 12, 13 | <i>Horologinella? pentagonalis</i> sp. nov. Paratype 1. 12: Upper surface. 13: Interior view of lower surface. Sample 1930. |
| 5, 6 | <i>Hapsocysta kysingensis</i> sp. nov. Paratype 1. 5: Upper surface. 6: Interior view of lower surface. Sample 2666. | 14 | <i>Glaphyrocysta? vicina</i> (Eaton 1976) Stover & Evitt 1978. Sample 2650. |
| 7 | <i>Heteraulacacysta porosa</i> Bujak in Bujak et al. 1980. Sample 2667. | 15 | <i>Glaphyrocysta? spineta</i> (Eaton 1976) Stover & Evitt 1978. Sample 2634. |
| 8 | <i>Heteraulacacysta? leptalea</i> Eaton 1976. Sample 2652. | 16 | <i>Glaphyrocysta ordinata</i> (Williams & Downie 1966) Stover & Evitt 1978. Sample 2650. |
| 9 | <i>Gochtodinium spinula</i> Bujak 1979. Sample 2667. | | |
| 10 | <i>Horologinella? pentagonalis</i> sp. nov. Holotype. Sample 1930. | | |



mens similar to this material in *Heteraulacacysta campanula* Drugg & Loeblich Jr. 1967.

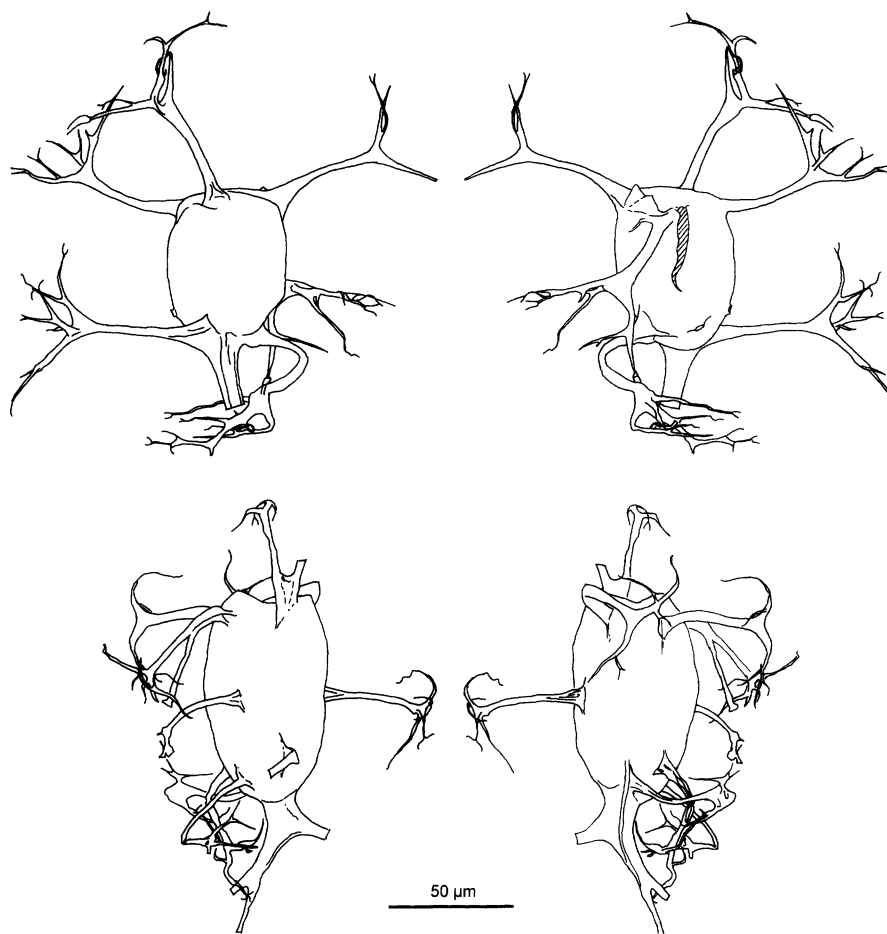
Genus *Distatodinium* Eaton 1976
Distatodinium biffii Brinkhuis et al. 1992
 Plate 3, figs. 1, 2, Text-Figure 4

Description. The four specimens recorded have a distinctly elongate central body and bear long, irregularly branched tubular or ribbon-shaped processes with slender shafts. The processes occur exclusively or mainly in the anterior and posterior parts of the cyst. In detail the distribution is as follows: at the archeopyle margin four to six ?precingular processes are present. In two specimens the basal part of a pair of these processes are fused. The equatorial zone is completely devoid of processes in two of the specimens (Plate 3, fig. 1 and the upper specimen in

Text-Figure 4), whereas the other two specimens have two ?paracingular processes (the lower specimen in Text-Figure 4). The antapical-postcingular? region bears two or three free processes, in addition to a large structure consisting of two or three proximally coalesced processes (Text-Figure 4).

Dimensions of measured specimens. Pericyst length 150 (169) 192 μm . Pericyst breadth 101 (136) 169 μm . Endocyst length 65 (78) 85 μm . Endocyst breadth 44 (48) 50 μm . Maximum process length varies between 45 μm and 105 μm . (4 specimens measured).

Comparison with type material. The holotype was stated to have 7 processes at the archeopyle margin (Brinkhuis et al., 1992); in this material the number is 4–6. This material shows variability of process development in the equatorial zone. This zone is devoid of processes in the type material, but two small (?parasulcal) processes may occur close to the equator (Brinkhuis et al. 1992, pl.



Text-Figure 4. *Distatodinium biffii* Brinkhuis et al. 1992. Two specimens from same stratigraphic level as sample 2668. The uppermost specimen is from sample 1905, slide F2, T35; also shown in Plate 3, fig. 2. The lowermost specimen is from sample 1905, slide 1912 C1, S49/3.

9, fig. 4). Other characters in these specimens, including the large dimensions of the cysts, are similar to the type material.

Wall structure. The wall is 0.5–1 μm thick and is externally smooth. In optical section internal cavities can be seen. They cause a faint to distinct punctate to pseudoreticulate appearance of the wall.

Variation. The dimensions and most morphologic features of the cysts are similar. The variable development of processes in the equatorial zone is presumably due to intraspecific variation in this assemblage that is derived from a single stratigraphic horizon.

Remarks. Previous records of *Distatodinium biffii* are from Late and “Mid” Oligocene strata, with the oldest record from the Mid Rupelian in Belgium (Van Simaëys et al., 2004). The detailed description given here is to ensure that these much older, Eocene, specimens represent the same species. *Distatodinium biffii* was recorded in two different boreholes, Kysing-3 and Kysing-4, at exactly the same stratigraphic level, in the Søvind Marl Formation immediately below the base of the Moesgaard Clay. The processing of these samples from the two boreholes was done with a gap of several years. This probably precludes the possibility of contamination.

Distatodinium pilosum sp. nov.
Plate 3, figs. 3, 4, 6

Description. A species of *Distatodinium* characterized by an oval or elongate cyst body with a finely granular surface. The processes are typically slender, solid, simple or branched. Proximally they are slightly expanded. In cross-section, the processes are usually flattened and blade-like. Distally they may be pointed or have small widenings, usually bifurcations. Small groups of processes may be connected by high septa. The processes are often aligned into rows parallel to the long axis of the cyst body, but some take a more random position, and others are arranged in arcuate complexes. The number of processes exceeds 80. The archeopyle is apical.

Derivation of name. From Latin *pilosus*, meaning with wiry hair.

Designation of holotype. Plate 3, fig. 3, Slide 2654 K5, England Finder coordinates W26. MGUH 27769. Kysing-4 borehole, sample 2654, Middle Eocene. Specimen dimensions: Total length 110 μm ; total breadth 79 μm ; central body length 66 μm ; central body breadth 42 μm ; length of processes 18–24 μm .

Designation of paratype. Paratype 1: Plate 3, fig. 4, Slide 2654 K5, England Finder coordinates B50. MGUH 27770. Kysing-4 borehole, sample 2654, Middle Eocene.

Specimen dimensions: Total length 108 μm , total breadth 82 μm ; central body length 62 μm , central body breadth 40 μm ; length of processes 20–24 μm . Paratype 2: Plate 3, fig. 6, Slide 2654 K5, England Finder coordinates S38/3. MGUH 27771. Kysing-4 borehole, sample 2654, Middle Eocene.

Dimensions of measured specimens. Total length (excysted) 63 (93) 112 μm . Total breadth 48 (73) 89 μm . Central body length (excysted) 54 (62) 67 μm . Central body breadth 31 (40) 44 μm . Length of processes 12–31 μm . (14 specimens measured).

Comparison. *Distatodinium pilosum* sp. nov. differs from all other species of the genus by the numerous solid, slender processes which have no distal expansion. *Distatodinium pilosum* sp. nov. differs from *Distatodinium virgatum* Stover 1977 by having solid processes and from *Distatodinium ellipticum* (Cookson & Eisenack) Eaton 1976 in having no distal expansion. *Distatodinium pilosum* sp. nov. differs from *Distatodinium solidum* Châteauneuf 1980 in having a much higher number of processes that are often aligned into rows parallel to the long axis of the cyst body.

Genus *Dracodinium* Gocht 1955
Dracodinium aff. *varielongitudum*
(Williams & Downie 1966) Costa & Downie 1979
Plate 3, figs. 8, 9

Description. Cysts of the subfamily Wetzelielloideae with variable development of pericoel and horns: some specimens are circumcavate with a wide pericoel, whereas others are essentially cornucavate. The lateral horns may be longer than other horns, up to 20 μm , or they may be shorter than other horns. The right antapical horn may be only slightly shorter than the left one, or it may be much reduced. The endocyst is usually thick-walled (between 0.5 and 3 μm) and expanded in dorso-ventral direction; this is typical of *Dracodinium*. Some of the processes, which may be restricted to parts of the margin, are broad-based thereby imparting a saw-toothed cyst outline. The distribution of processes is usually nontabular.

Comparison. These forms occur mainly in the uppermost Lutetian to lowermost Bartonian samples 2648 to 2651. They are close to *Dracodinium varielongitudum* and *Dracodinium solidum* Gocht 1955, but differ by the partly or wholly saw-toothed outline.

Genus *Echinidinium* Zonneveld 1997
ex Head et al. 2001
Echinidinium? *lucidum* sp. nov.
Plate 4, figs. 1–6, Text-Figure 5



Text-Figure 5. *Echinidinium? lucidum* sp. nov. Sketch of process types observed.

Description. A small, subspherical, proximochorate dinoflagellate cyst. The thin, smooth, hyaline wall and especially the numerous short processes are colorless and strongly refractive. The processes are rigid, massive, and of unequal length. The process morphology is variable (Text-Figure 5). Most processes are conical, or cylindrical with pointed tips. Some processes have a more irregular shape; they may be distally expanded and bifurcate, rarely irregularly branched. The distribution of the processes is mostly nontabular. Locally, processes may be aligned in short rows and can be fused in the lower part, forming a denticulate septum. An archeopyle is rarely visible, and its type has not been identified. It seems to be theropylic, with an operculum consisting of at least two adnate paraplates.

Derivation of name. From Latin *lucidus*, meaning sending out light, with reference to the strong refractivity of the cyst wall.

Designation of holotype. Plate 4, figs. 1, 2, Slide 1930 G2, England Finder coordinates H51. MGUH 27772. Kysing-3 borehole, sample 1930, Upper Eocene. Specimen dimensions: Total cyst diameter 51 μm ; central body diameter 37 μm .

Designation of paratype. Plate 4, fig. 3, Slide 1928 G1, England Finder coordinates P46/4-P47/3. MGUH 27773. Kysing-3 borehole, sample 1928, Upper Eocene.

Dimensions of measured specimens. Total cyst diameter 45 (49) 53 μm . Central body diameter 33 (39) 45 μm . Maximum length of spines 6 (7) 8 μm . (9 specimens measured).

Comparison. Within this genus, this species especially resembles *Echinidinium delicata* Zonneveld 1997, which

however has hollow and more uniform processes. There is also some similarity with the Recent genus *Islandinium* Head et al. 2001, especially with *Islandinium minutum* (Harland & Reid in Harland et al. 1980) Head et al. 2001. However, *Islandinium minutum* differs by having a saphopylic archeopyle, simpler processes and being pigmented. *Echinidinium? lucidum* sp. nov. differs from *Selenopemphix quanta* (Bradford 1975) Matsuoka 1985 in lacking two rows of paracingular processes, and by its more complex processes.

Remarks. The allocation of this species with the Recent genus *Echinidinium* is provisional since the archeopyle type is not well known. Furthermore, species of the genus *Echinidinium* are normally pigmented.

Genus *Ectosphaeropsis* Londeix & Jan Du Chêne 1988
cf. *Ectosphaeropsis burdigalensis*
Londeix & Jan Du Chêne 1988
Plate 4, figs. 7, 8

Remarks. A single specimen was recorded. Its size and morphology are typical of this species except for the ectophragm, which is trabeculate and not membraneous. This is an unusually early record; however rare *Ectosphaeropsis burdigalensis* has previously been recorded in two Lower Oligocene sidewall cores in the Linde-1 borehole, northwest Jylland from dinoflagellate cyst Subzone D14na of Köthe (1990) (Heilmann-Clausen 1995b). These samples were referred to biozone NP 22 by Thomsen (1995).

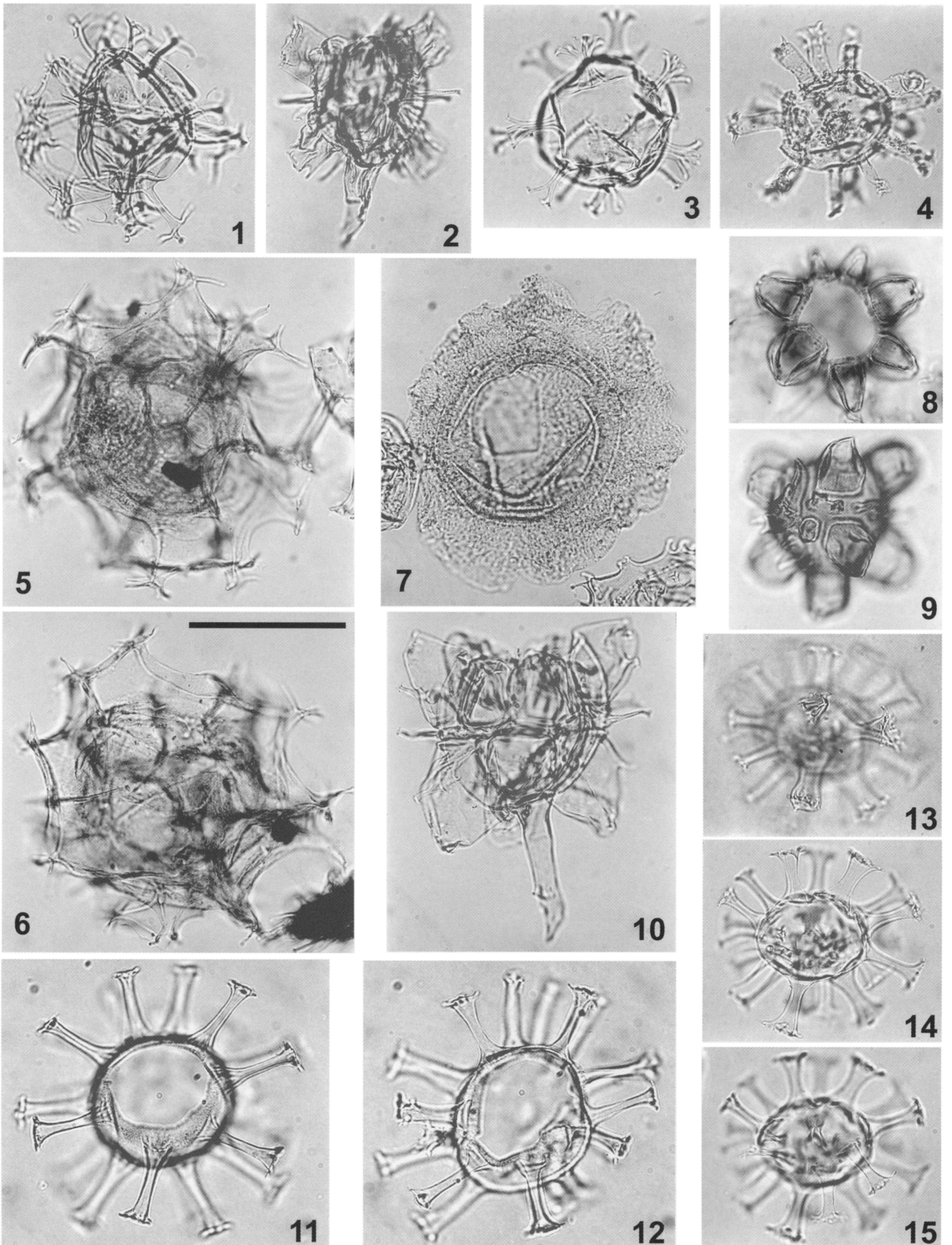
Genus *Enneadocysta* Stover & Williams 1995
Enneadocysta? aff. arcuata (Eaton 1971)
Stover & Williams 1995
Plate 4, figs. 15, 16

Remarks. This dinoflagellate cyst has denticulate, arcuate furcations at the distal end of each process, similar to

PLATE 6

Bar scale in Fig. 6 = 50 μm applies to all specimens.

- | | | | |
|------|--|--------|---|
| 1 | <i>Hystrichostrogylon</i> sp. 1. Sample 2666. | 7 | <i>Lanternosphaeridium lanosum</i> Morgenroth 1966. Sample 2652. |
| 2 | <i>Hystrichokolpoma salacia</i> Eaton 1976. Sample 2634. | 8, 9 | <i>Hystrichokolpoma globulus</i> Michoux 1985. Two specimens from sample 2662. |
| 3 | <i>Homotryblium floripes</i> (Deflandre & Cookson 1955) Stover 1975. Sample 1906. | 10 | <i>Hystrichokolpoma cinctum</i> Klumpp 1953. Sample 2638. |
| 4. | <i>Hystrichosphaeridium cylindratum</i> Morgenroth 1966. Sample 2642. | 11, 12 | <i>Hystrichokolpoma?</i> sp. 1. Two specimens from sample 1771. |
| 5, 6 | <i>Hystrichostrogylon</i> aff. <i>holohymenium</i> Islam 1983. Two specimens from sample 1930. | 13–15 | <i>Hystrichokolpoma?</i> sp. 1. A specimen in high (13), median (14) and low (15) focus. Sample 1771. |



those present in *Enneadocysta arcuata*. It resembles *Enneadocysta arcuata* in other aspects too, except for the development of a loose network of smooth trabeculae, which extend from the ends of the denticulate furcations and connect neighboring processes. This form is common in sample 2661.

Genus *Fibrocysta* Stover & Evitt 1978

Fibrocysta axialis–*Fibrocysta bipolaris* Group

Remarks. This group includes the species *Fibrocysta axialis* (Eisenack 1965) Stover & Evitt 1978 and *Fibrocysta bipolaris* (Cookson & Eisenack 1965) Stover & Evitt 1978. Due to their similar morphology, no efforts were made to distinguish the two taxa. The *Fibrocysta axialis*–*Fibrocysta bipolaris* Group differs from the *Fibrocysta radiata*–*Fibrocysta vectensis* Group by having solid, non-fibrous processes.

Fibrocysta radiata–*Fibrocysta vectensis* Group

Remarks. This group includes the species *Fibrocysta radiata* (Morgenroth 1966) Stover & Evitt 1978 and *Fibrocysta vectensis* (Eaton 1976) Stover & Evitt 1978. Due to the similar morphology, no efforts were made to distinguish the two taxa. The cysts included in this group are characterized by having fibrous processes.

Genus *Hapsocysta* Davey 1979 emend. nov.

Piccoladinium Versteegh & Zevenboom, 1995, p. 223 (junior synonym).

Emendation. Four apical paraplates are present in this genus (Text-Figure 6). These paraplates are recognized by parasutural strands similar to those present at the parasutures of the other paraplate series. Other features of the genus are as stated in the original diagnosis of Davey (1979).

Remarks. When Davey (1979) established this genus, he mentioned that the “apical areas do not appear to be defined”. The type species of the genus is *Hapsocysta peridictya* (Eisenack & Cookson 1960) Davey 1979. In Text-Figure 6, we have reproduced an illustration of the holotype of *Hapsocysta peridictya* from Eisenack and Cookson (1960). In Text-figure 6 we have also shown our interpretation of the paratabulation. Two possible scenarios are shown; both interpretations clearly show a normal gonyaulacacean apical region with four apical paraplates. The details of these interpretations are explained in the caption of Text-Figure 6. The genus *Piccoladinium* Versteegh & Zevenboom 1995 is considered to be a junior synonym of *Hapsocysta* because the generic difference was stated to be the presence of an apical paraplate series in *Piccoladinium*. The single species of *Piccoladinium*, *Piccoladinium fenestratum* Versteegh & Zevenboom 1995, is therefore transferred here to *Hapsocysta*.

Hapsocysta fenestrata (Versteegh & Zevenboom 1995)
comb. nov.

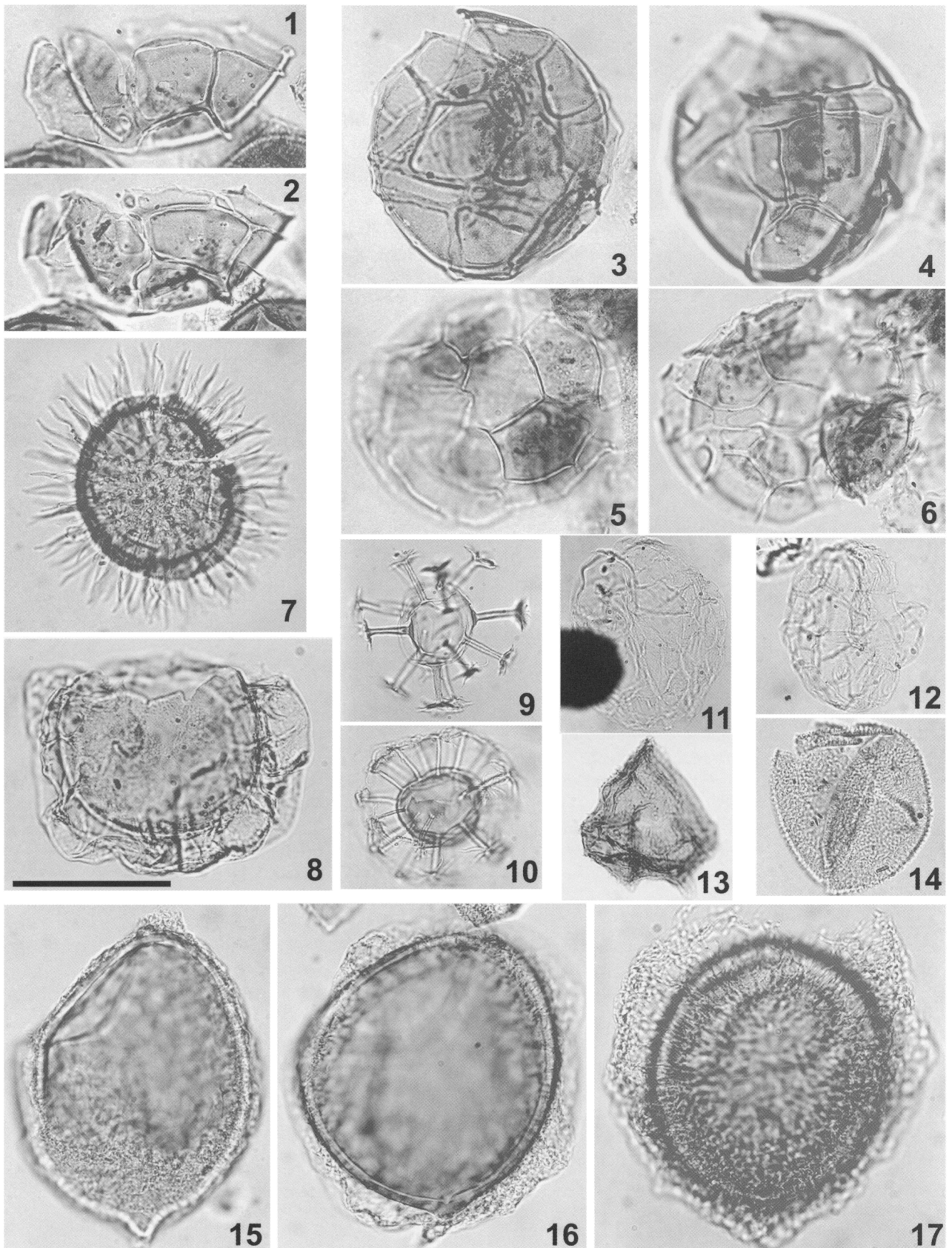
Piccoladinium fenestratum Versteegh & Zevenboom, 1995,
p. 223, pl. 4, figs 1–7 (basonym).

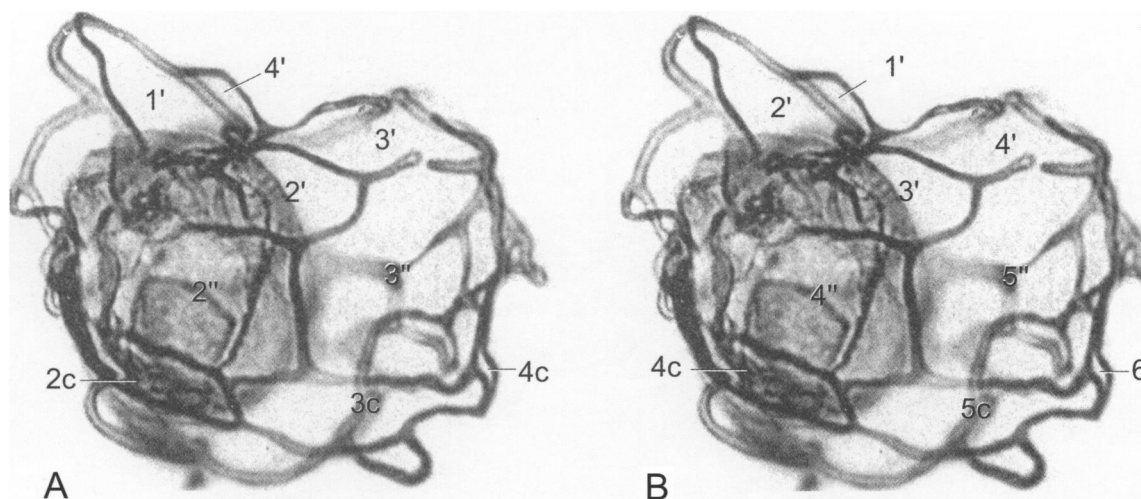
Hapsocysta kysingensis sp. nov.
Plate 5, figs. 1–6, Text-Figure 7

PLATE 7

Bar scale in Fig. 8 = 50 µm applies to all specimens.

- | | | | |
|------|--|--------|--|
| 1, 2 | <i>Impagidinium?</i> sp. 1. Hypocyst of a broken specimen, the ventral pericoel is seen at left. 1: Upper surface. 2: Interior view of lower surface. Sample 1775. | 9 | <i>Melitasphaeridium asterium</i> (Eaton 1976) Bujak et al. 1980. Sample 2668. |
| 3, 4 | <i>Impagidinium?</i> sp. 1. Lateral view of specimen showing ventral pericoel at right. 3: Upper surface. 4: Interior view of lower surface. Sample 1773. | 10 | <i>Melitasphaeridium pseudorecurvatum</i> (Morgenroth 1966) Bujak et al. 1980. Sample 2646. |
| 5, 6 | <i>Impagidinium?</i> sp. 1. Polar view of specimen showing ventral pericoel to the left. 5: Hypocyst. 6: Interior view of epicyst. Sample 1775. | 11, 12 | <i>Lophocysta sulcolimbata</i> Manum 1979. Two specimens from sample 2668. |
| 7 | <i>Lingulodinium</i> cf. <i>machaerophorum</i> (Deflandre & Cookson 1955) Wall 1967. The number of processes is larger than typical for the species. Sample 2646. | 13 | <i>Lentinia serrata</i> Bujak in Bujak et al. 1980. Sample 2666. |
| 8 | <i>Membranophoridium aspinatum</i> Gerlach 1961. Sample 2666. | 14 | cf. <i>Kallosphaeridium capulatum</i> Stover 1977. Sample 1775. |
| | | 15–17 | <i>Lanternosphaeridium</i> sp. 1. Specimens illustrating the wide variation in development of the fibrous covering. 15 and 17: Sample 2654. 16: Sample 2653. |





Text-Figure 6. The holotype of *Hapsocysta peridictya* (Eisenack & Cookson 1960) Davey 1979, reproduced from Eisenack and Cookson (1960, pl. 3, fig. 6), turned 90 degrees clockwise. Two alternative, possible paratabulations based on visible parasutural strands are shown with Kofoidian paraplata symbols. Both interpretations recognize two elongate (obviously paracingular) paraplates. Above these a four-sided precingular paraplata is seen to the left, adjacent to a five-sided paraplata on the right. It is not clear which interpretation is the correct one; however, the one shown to the right (showing paracingular paraplates 4c–6c) is the more likely solution since it involves a close dorsal contact between the network and the inner body. Both interpretations clearly show a normal gonyaulacacean apical region with the presence of four well-developed apical paraplates. An alternative interpretation that assumes the precingular paraplates to be postcingular leads to an abnormal antapical region and may therefore be rejected.

Cannosphaeropsis peridictya Eisenack & Cookson 1960;
De Coninck, 1986, pl. 1, figs. 21, 22.
?Species 1 Firth, 1966, pl. 21, figs. 1–4.

Description. A dinoflagellate cyst with a thin-walled, subspherical central body surrounded by an open network of smooth parasutural ribbons. The parasutural network is widely separated from the central body, except on the dorsal side where small parts of the sutural ribbons adhere to the central body. The parasutural ribbons are 1–2 μm wide, and are usually taeniate. Sometimes a low septum may be developed on the outer surface of some of the ribbons.

Paratabulation. The Kofoidian paratabulation formula is gonyaulacacean, 0–2 pr, 4', 6'', 6c, 2–4s, 5–6'', 1p, 1'''. This is based on three specimens (Text-Figure 7). The dorsal side shows neutral torsion, with 3'' above 4'''. The ventral organization of the cyst appears to be of S-type, with 6'' apparently subtriangular and with no, or only very little, contact between 6'' and 1'. The paratabulation pattern of the epicyst is variable. It may be insert, with all four apical homologues well developed, and in contact with the apical pore complex, or metasert, with the rudimentary first apical homologue 1' in contact with 2', but not with 3'. The four paraplates 5'', 4', as and 6'' have the 4'/6'' configuration (i.e. 4' in contact with 6'') in each of the three specimens. Paraplates 4', 1', as and 6'' have

the 4'/as configuration (Text-Figure 7B, C), or a configuration intermediate between 4'/as and 1'/6'' (Text-Figure 7A). The paratabulation pattern of the hypocyst is sexiform. The first postcingular homologue 1''' may be present (Text-Figure 7C), or incorporated into a large undivided parasulcal field (Text-Figure 7A).

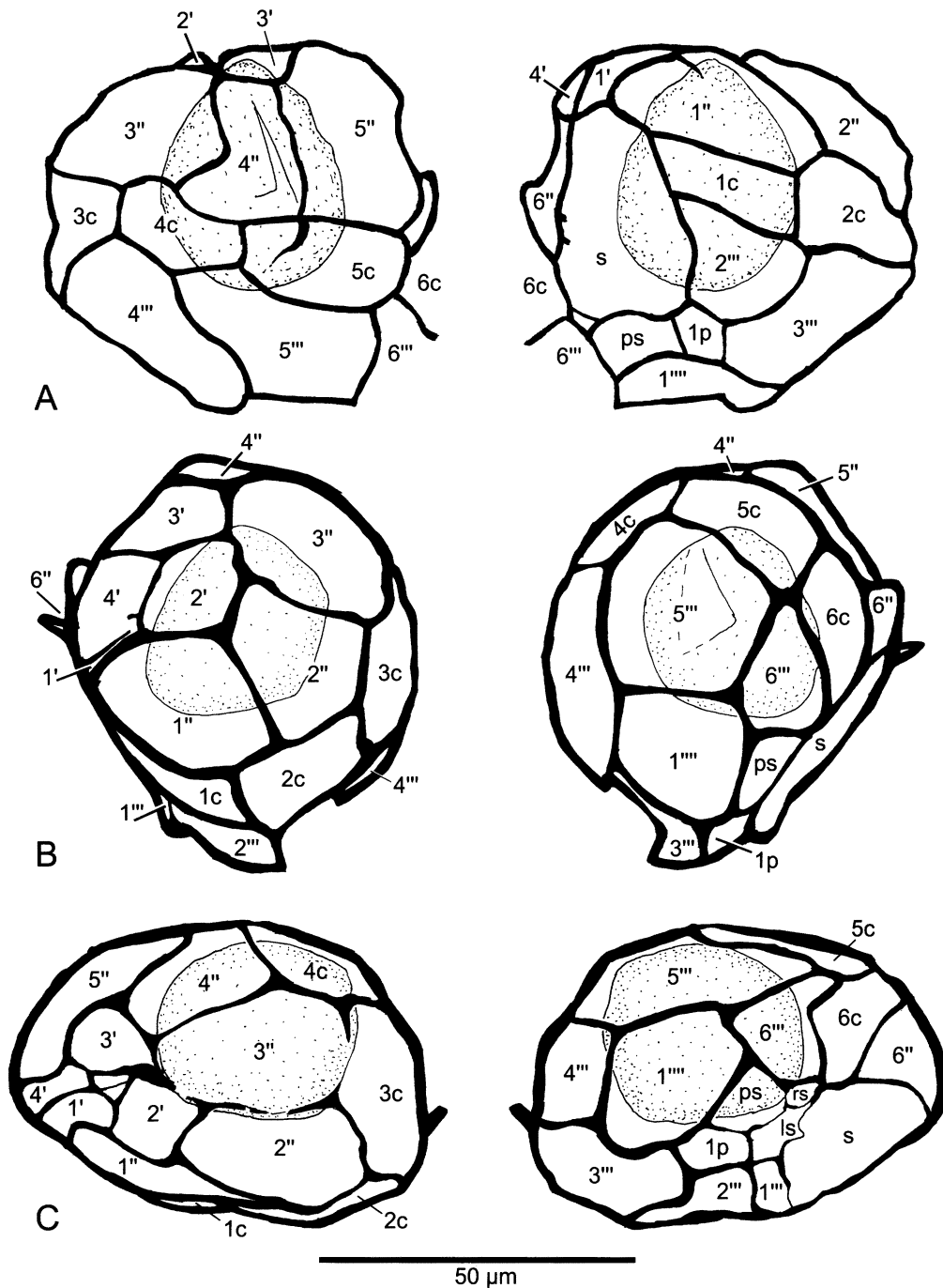
Archeopyle. Ruptures on the endocyst in some of the specimens may represent archeopyle sutures, but these are faint, and their nature could not be identified with certainty.

Derivation of name. From the type locality, Kysing.

Designation of holotype. Plate 5, figs. 1, 2 and Text-Figure 7A, Slide 2666 G4, England Finder coordinates M25/2. MGUH 27774. Kysing-4 borehole, sample 2666, Upper Eocene. Specimen dimensions: Pericyst maximum diameter 63 μm ; pericyst minimum diameter 59 μm ; endocyst maximum diameter 35 μm ; endocyst minimum diameter 30 μm

Designation of paratype. Paratype 1: Plate 5, figs. 5, 6 and Text-Figure 7B, Slide 2666 G4, England Finder coordinates T45. MGUH 27775. Kysing-4 borehole, sample 2666, Upper Eocene. Paratype 2: Plate 5, figs. 3, 4 and Text-Figure 7C, Slide 2666 G4, England Finder coordinates K41/1. MGUH 27776. Kysing-4 borehole, sample 2666, Upper Eocene.

Dimensions of measured specimens. Pericyst maximum diameter 47 (63) 77 μm . Pericyst minimum diameter



Text-Figure 7. *Hapsocysta kysingensis* sp. nov. with paratabulation indicated. Upper and lower surfaces are shown as exterior views. The specimens are also shown in Plate 5. A: Holotype. B: Paratype 1. C: Paratype 2.

44 (54) 62 µm. Endocyst maximum diameter 21 (31) 42 µm. Endocyst minimum diameter 15 (24) 30 µm. (12 specimens measured).

Comparisons. The specimens are superficially similar to two Lower Cretaceous species, *Hapsocysta peridictya*

and *Hapsocysta susanae*. However, *Hapsocysta kysingensis* sp. nov. differs from both these taxa in its reduced paratabulation of the sulcus. In *Hapsocysta peridictya* and *Hapsocysta susanae*, the tabulation of the sulcal paraplatelets is fully reflected. For *Hapsocysta peridictya*, this is illus-

trated in Davey (1979: pl. 4, figs. 2, 5). The reduction or complete absence of paraplate 1^{'''} (probably included in the functional parasulcus of the holotype, Text-Figure 7A) in *Hapsocysta kysingensis* sp. nov., marks a further difference from *Hapsocysta susanae*. Further differences are the larger size of *Hapsocysta peridictya* and the more robust parasutural strands in *Hapsocysta susanae*. Details of the paratabulation in *Hapsocysta peridictya* are not well known and this prevents further comparisons with this species. *Hapsocysta fenestrata* comb. nov. differs in having pericystical paraplates with intratabular holes, rather than parasutural ribbons. *Hapsocysta kysingensis* sp. nov. also resembles the Upper Oligocene to Lower Miocene 'cysts without walls', *Chaenosphaerula magnifica* Damassa 1997 and *Evittosphaerula paratabulata* Manum 1979, described in detail by Damassa (1997). Both differ from *Hapsocysta* by the lack of endocysts. However *Chaenosphaerula magnifica* closely resembles *Hapsocysta kysingensis* sp. nov. in paratabulation, in particular the incompletely delineated sulcal paraplates and the variable epicystical paratabulation.

Genus *Horologinella* Cookson & Eisenack 1962

Horologinella? *pentagonalis* sp. nov.

Plate 5, figs. 10–13

Description. A medium-sized palynomorph composed of a thin walled, smooth, subspherical to angular central body. The surface is subdivided into polygonal fields. Two of the fields, occurring on opposite surfaces of the central body, are regular pentagons. All fields are bordered by high, thin and flexible septa. The distal margins of the septa are smooth. A deep and narrow invagination is present in one side of the holotype, but has not been observed in the paratypes. No archeopyle or other kind of opening in the wall has been observed.

Derivation of name. From the Greek *pentagon*, with reference to the presence of the five-sided fields.

Designation of holotype. Plate 5, fig. 10, Slide 1930 G2, England Finder coordinates L34/4. MGUH 27777. Kysing-3 borehole, sample 1930, Upper Eocene. Specimen dimensions: Total diameter 42 µm; central body diameter 30 µm; maximum height of septa 6 µm.

Designation of paratype. Paratype 1: Plate 5, figs. 12, 13, Slide 1930 G1, England Finder coordinates J55. MGUH 27778. Kysing-3 borehole, sample 1930, Upper Eocene. Paratype 2: Plate 5, fig. 11, Slide 1928 G1, England Finder coordinates S50/3. MGUH 27779. Kysing-3 borehole, sample 1928, Upper Eocene.

Dimensions of measured specimens. Total diameter 42 (54) 68 µm. Central body diameter 30 (41) 45 µm. Maximum height of septa 6 (9) 15 µm. (8 specimens measured)

Comparison. A palynomorph of uncertain affinity, *Horologinella?* sp. 1, described by De Coninck (1999) from approximately coeval strata is undoubtedly a related taxon. It differs by being quadrangular, rather than pentagonal, in outline and is much smaller. *Horologinella?* *pentagonalis* sp. nov. superficially resembles certain thin-walled species of the dinoflagellate cyst *Impagidinium*, in particular *Impagidinium pallidum* Bujak 1984 and *Impagidinium striolatum* (Wall 1967) Stover & Evitt 1978. However, none of the many specimens recovered exhibit diagnostic dinoflagellate cyst features, such as an archeopyle, paracingulum, parasulcus or other manifestations of paratabulation. The assignment to the dinoflagellate cyst genus *Horologinella* and the Division Dinoflagellata is therefore provisional.

Genus *Hystrichokolpoma* Klumpp 1953

Hystrichokolpoma spinosum Wilson 1988

Hystrichokolpoma sp. 1 Heilmann-Clausen and Costa, 1989, p. 467, pl. 15, figs. 10–12.

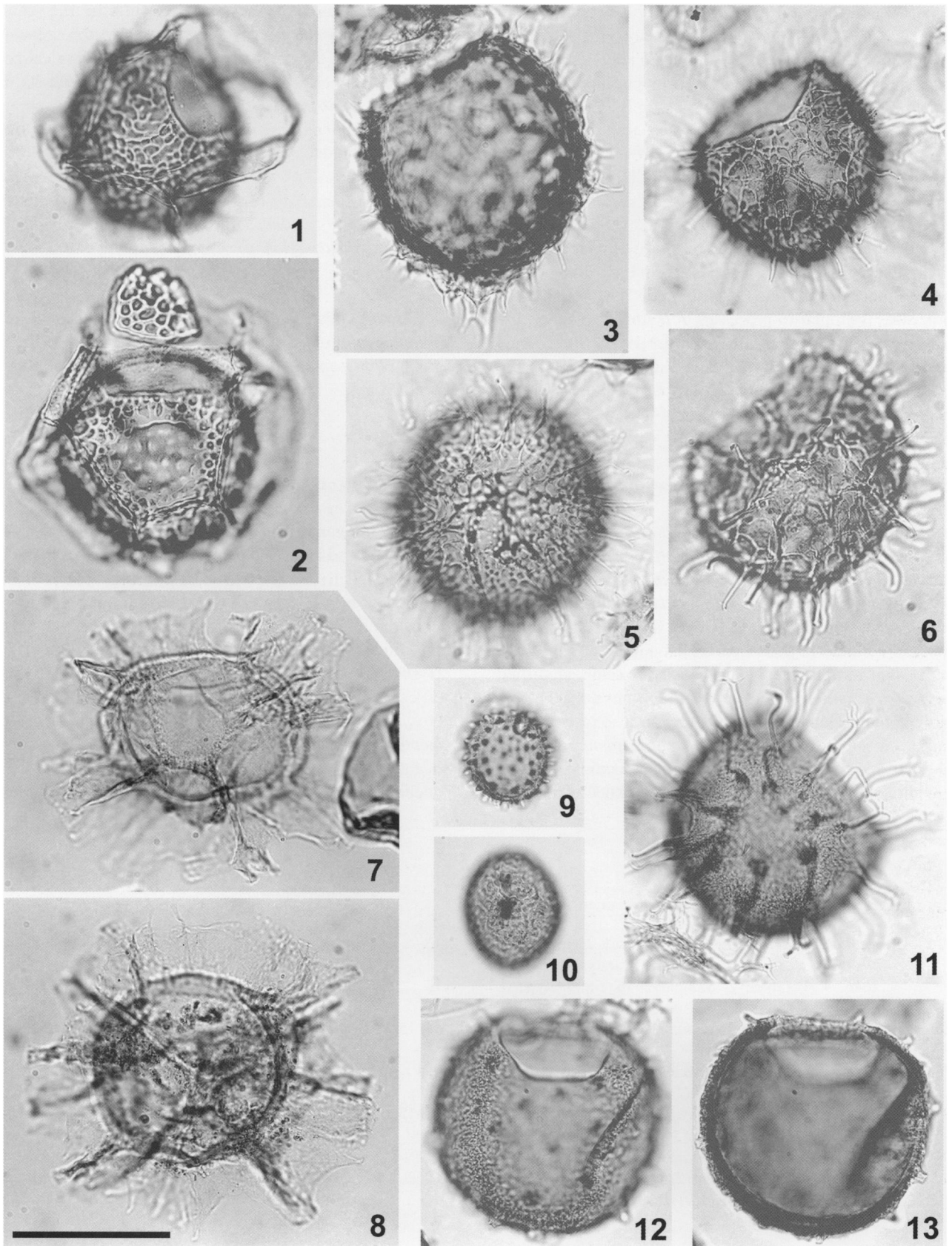
Remarks. *Hystrichokolpoma spinosum* was originally recorded from Mid Eocene strata in New Zealand (Wilson, 1988; Fensome, Gocht and Williams, 1996). In

PLATE 8

Bar scale in Fig. 8 = 50 µm applies to all specimens.

- 1, 2 *Pentadinium* cf. *lophophorum* (Benedek 1972) Benedek et al. 1982. 1: Sample 2664. 2: Sample 1906.
3–6 *Operculodinium eisenacki* sp. nov. 3: Paratype 1. Sample 2659. 4: Paratype 2. Sample 2661. 5: Holotype. Sample 2664. 6: Sample 2649.
7, 8 *Muratodinium fimbriatum* (Cookson & Eisenack 1967) Drugg 1970. Two specimens from sample 2667.

- 9, 10 *Operculodinium nanaconulum* Islam 1983–*O. placitum* Drugg & Loeblich 1967 Group. Two specimens illustrating the morphologic variation. 9: Sample 2633. 10: Sample 2643.
11–13 *Operculodinium divergens* (Eisenack 1954) Stover & Evitt 1978 Group. 11: Sample 2658. 12, 13: A specimen with rudimentary processes, shown in two different foci. Sample 2653.



northwest Europe this species occurs persistently in the Upper Ypresian in northern Germany and Denmark (Heilmann-Clausen and Costa, 1989 and unpublished observations). It is rare from the Upper Lutetian in the present material.

Hystrichokolpoma? sp. 1.

Plate 6, figs. 11–15

Description. A chorate dinoflagellate cyst with a smooth, finely punctate or granular central body, and large intratabular, hollow processes that are distally closed. The shape of the processes is similar to processes in *Hystrichosphaeridium tubiferum* (Ehrenberg 1838) Deflandre 1937, i.e., the processes are tubiform with irregular secate distal ends. A few processes may show incipient distal ramification. The number of processes in excysted specimens is 22 to 24, possibly 25. The archeopyle seems to be apical, Type tA. Paratabulation is probably reflected by the processes, with one process per paraplate. A few more slender processes appear to represent the parasulcus.

Comparison. The general appearance of these cysts is similar to *Hystrichosphaeridium tubiferum*, except for the processes being distally closed, which prevents allocation to *Hystrichosphaeridium*. Excysted *Hystrichosphaeridium tubiferum* usually have 25 processes (Evitt, 1985), and the number counted in these specimens is only slightly less. Individual paraplate series can usually be easily identified in *Hystrichosphaeridium tubiferum*; this has not been possible in the present cysts. The processes also resemble the large, closed processes of *Hystrichokolpoma rigaudae* Deflandre & Cookson 1955, but this species differs by having smaller paracingular processes and a differently

shaped antapical process. Allocation to the genus *Hystrichokolpoma* is provisional, because this genus is recognized by the paracingular and some parasulcal processes being clearly smaller than other processes. De Coninck (1986) described *Oligosphaeridium?* sp. cf. *Hystrichokolpoma rigaudae* with similar distally closed processes, but lacking paracingular processes.

Genus *Hystrichostrogylon* Agelopoulos 1964

Hystrichostrogylon aff. *holohymenium* Islam 1983

Plate 6, figs. 5, 6

Remarks. These forms differ from *Hystrichostrogylon holohymenium* by being more robust, and by not always having a full separation of the endophragm and periphragm.

Hystrichostrogylon sp. 1

Plate 6, fig. 1

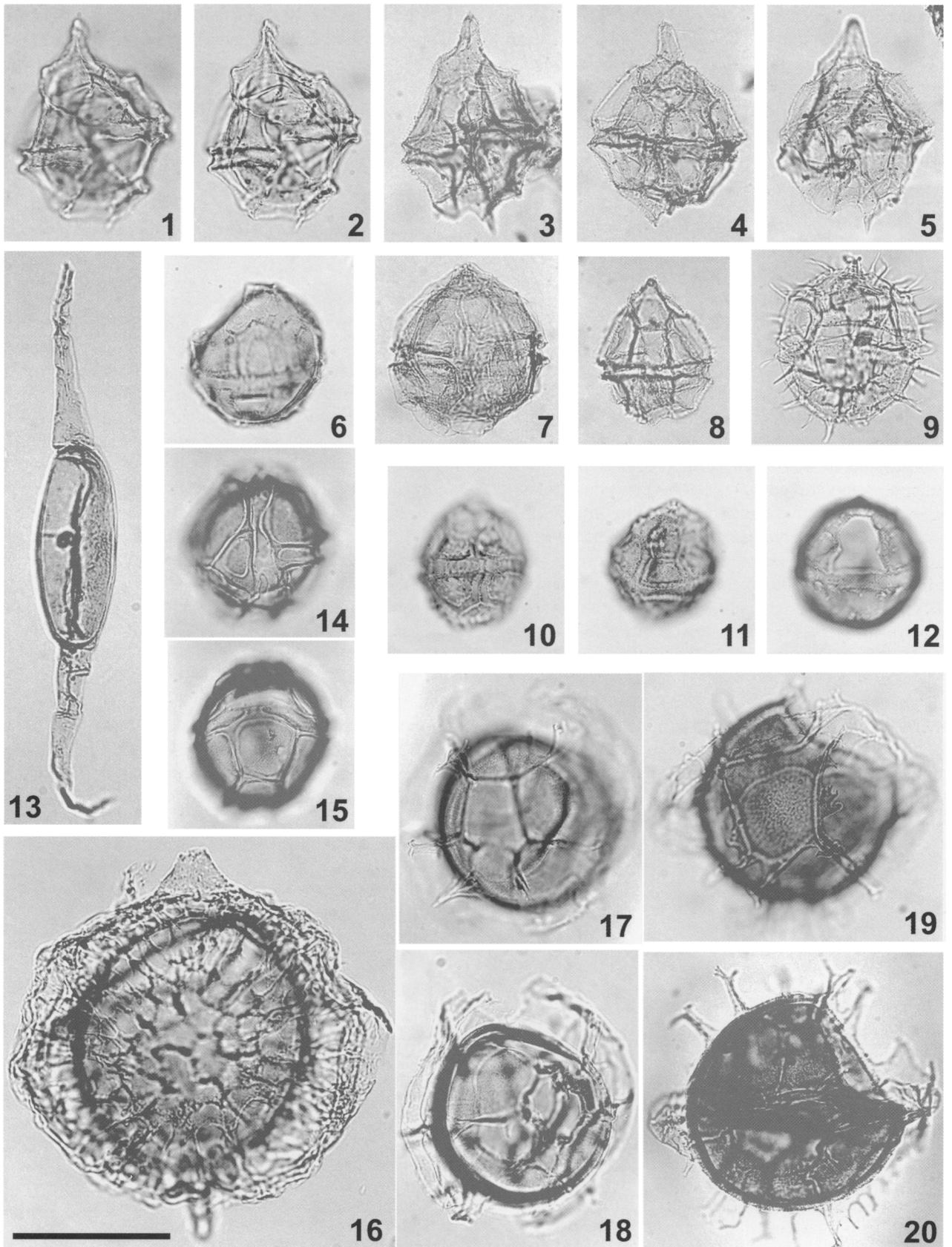
Description. A smooth-walled variety of *Hystrichostrogylon* in which the pericoel covers the central parts of the ventral surface, and includes the parasulcus. The apical and antapical parts of the cyst are not included in the pericoel. A large subcircular opening is present in the parasulcal part of the pericoel. The hole probably represents the flagellar scar.

Comparison. These cysts superficially resemble *Hystrichostrogylon membraniphorum* Agelopoulos 1964, especially because of the relative size of the pericoel. However the pericoel in *Hystrichostrogylon membraniphorum* is developed only in the hypocystal part of the ventral surface, and also includes the antapex. No opening is present in the pericoel. Relative to this position,

PLATE 9

Bar scale in Fig. 16 = 50 µm applies to all specimens.

- | | | | |
|--------|---|--------|--|
| 1–5 | <i>Phthanoperidinium cornutum</i> sp. nov. 1, 2: Holotype in two different foci. Sample 2644. 3: Paratype 1. Sample 2646. 4: Paratype 2. Sample 2646. 5: Paratype 3. Sample 2646. | 12 | <i>Phthanoperidinium clithridium</i> Bujak 1994. Sample 2638. |
| 6 | <i>Phthanoperidinium geminatum</i> Bujak in Bujak et al. 1980. Sample 2663. | 13 | <i>Palaeocystodinium</i> cf. <i>golzowense</i> Alberti 1961. Sample 2652. |
| 7 | <i>Phthanoperidinium levimurum</i> Bujak in Bujak et al. 1980. Sample 2666. | 14, 15 | <i>Pentadinium</i> cf. <i>taeniagerum</i> Gerlach 1961 in De Coninck (1985). 14: Ventral surface. 15: Dorsal surface (interior view). Sample 2638. |
| 8 | <i>Phthanoperidinium distinctum</i> Bujak 1994. Sample 2658. | 16 | " <i>Palmnickia lobifera</i> " Eisenack 1954. Sample 2652. |
| 9 | <i>Phthanoperidinium comatum</i> (Morgenroth 1966) Eisenack & Kjellström 1972. Sample 1906. | 17, 18 | <i>Pentadinium goniferum</i> Edwards 1982. Specimen in polar view. 17: Hypocyst. 18: Interior view of epicyst. Sample 2656. |
| 10, 11 | <i>Phthanoperidinium regalis</i> Bujak 1994. Two specimens from sample 2635. | 19, 20 | <i>Pentadinium goniferum</i> Edwards 1982. 19: Specimen in oblique view. Sample 2646. 20: Specimen in lateral view. Sample 2647. |



the pericoel is rotated towards the apex in *Hystrihostrogylon* sp. 1. In *Hystrihostrogylon coninckii* Heilmann-Clausen in Thomsen & Heilmann-Clausen 1985, the pericoel covers the entire ventral surface, and the homologue parasulcal hole (?flagellar scar) is larger.

Remarks. Because of the significant variability of pericoel development in this genus, we are reluctant to establish this form as a new species. Their recognition may, however, be of stratigraphic value.

Genus *Impagidinium* Stover & Evitt 1978
Impagidinium? sp. 1
 Plate 7, figs. 1–6

Impagidinium sp. cf. *I. multiplexum* De Coninck 1986, p. 14, pl. 4, figs. 14, 15, 23, 24.

Description. A relatively large, cavate dinoflagellate cyst with smooth, transparent periphragm and finely punctate, almost smooth, endophragm. Low parasutural folds or ridges are formed by the periphragm, indicating a paratabulation typical of this genus. A prominent pericoel is developed over a large part of the ventral surface, including the parasulcus, by separation of the phragma. In other parts of the cyst, the phragma are appressed, except for narrow pericoels beneath the parasutural folds.

Dimensions of measured specimens. Pericyst diameter 75 (80) 84 μm . (2 specimens measured)

Remarks. Few specimens of this distinctive cyst were observed, precluding a formal description. The attribution to *Impagidinium* is provisional due to the presence of a pericoel. The specimens are larger than those of De Coninck (1986), but are otherwise similar.

Genus *Kallosphaeridium* De Coninck 1969
 cf. *Kallosphaeridium capulatum* Stover 1977
 Plate 7, fig. 14

Remarks. The ornamentation of these dinoflagellate cysts consists of small, irregular, hollow conical, which may be fused at their bases, forming a vermicular pattern. The cysts are often folded and, due to the small number of specimens seen, the archeopyle type has not been identified with certainty. In contrast to *Elytrocysta brevis* Stover & Hardenbol 1994, these specimens do not have an ectophragm.

Genus *Lanternosphaeridium* Morgenroth 1966
Lanternosphaeridium sp. 1
 Plate 7, figs. 15–17

Description. This form comprises specimens of *Lanternosphaeridium* having a thick-walled, ellipsoidal endocyst which is enclosed in a periphragmal layer of fibrous material. The development of this fibrous covering is variable, from widely expanded in some specimens to more condensed in others. In some specimens, the fibrous covering is largely absent. The thickness of the fibrous covering may also be variably developed in different parts of a single cyst. The archeopyle is precingular, Type P (3" only). The morphologies form a continuum, and the entire morphologic range may be observed within a single assemblage, e.g. sample 2654.

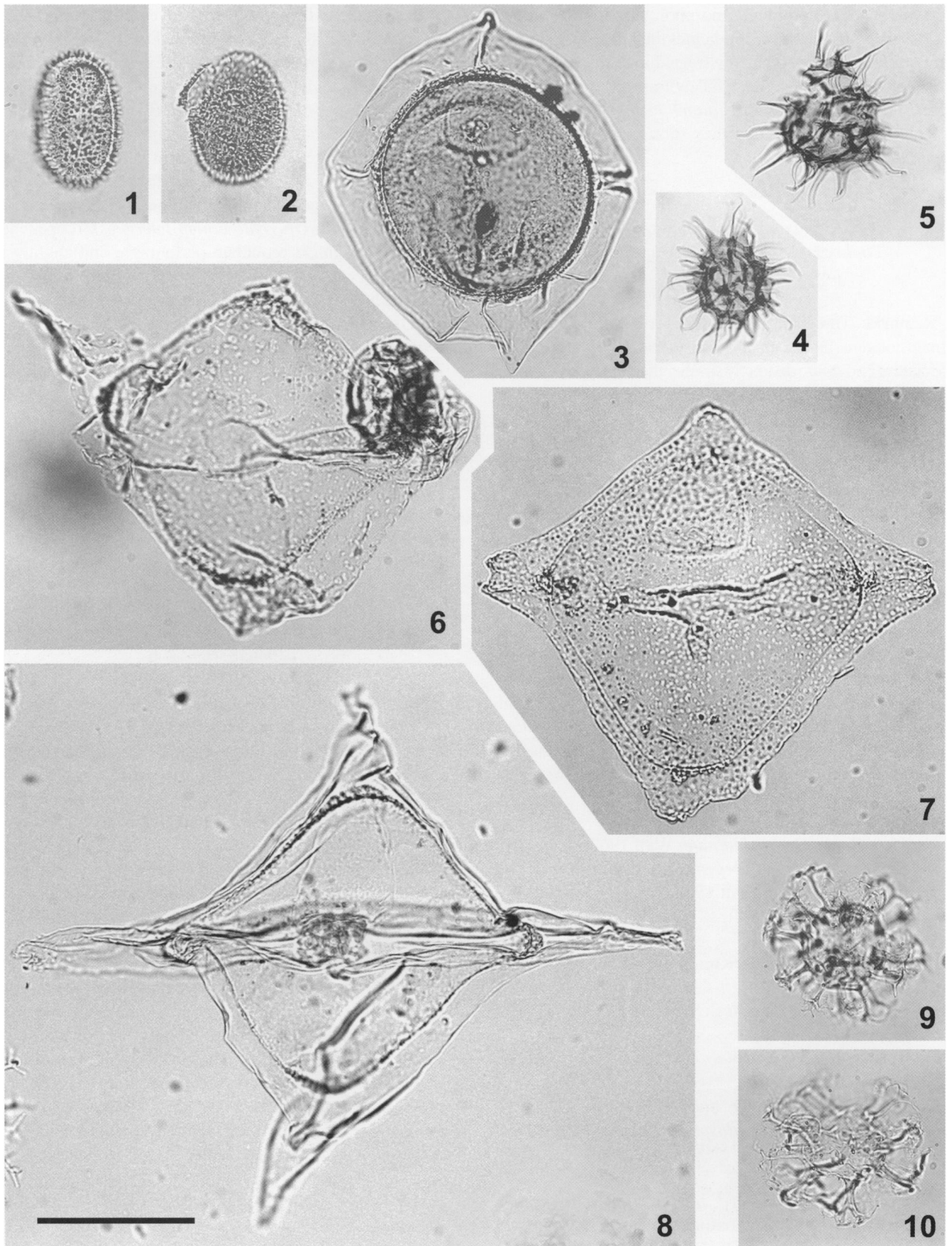
Dimensions of measured specimens. Thickness of fibrous periphragmal layer 1 (11) 21 μm . Endocyst length 69 (86) 108 μm . Endocyst breadth 63 (74) 87 μm . Endophragm, 2.5 (3) 4 μm . (12 specimens measured)

Comparison. These cysts differ from typical *Lanternosphaeridium lanosum* Morgenroth 1966 by the fibrous material being a little coarser and looser. Furthermore, the outer surface of the fibrous layer is smooth in *Lanternosphaeridium* sp. 1, whereas incipient spines are developed in *Lanternosphaeridium lanosum*. *Lanternosphaeridium* sp. 1 differs from *Palmnickia lobifera* Eisenack 1954 by lacking the distinct mesh-like pattern or maze on the outer surface of the endophragm, and by having a finer periphragm.

PLATE 10

Bar scale in Fig. 8 = 50 μm applies to all specimens.

- | | | | |
|------|---|-------|--|
| 1, 2 | <i>Pyxidiella? scrobiculata</i> (Deflandre & Cookson 1955) Cookson & Eisenack 1958. 1: Sample 2653. 2: Sample 2654. | 7 | <i>Rhombodinium perforatum</i> (Jan du Chêne & Châteauneuf 1975) Lentin & Williams 1977. Sample 1768. |
| 3 | <i>Rhombodinium draco</i> Gocht 1955. Sample 2662. | 8 | <i>Rhombodinium longimanum</i> Vozzhennikova 1967. Sample 1906. |
| 4, 5 | <i>Selenopemphix armata</i> Bujak in Bujak et al. 1980. Two specimens from sample 2666. | 9, 10 | <i>Reticulosphaera actinocoronata</i> (Benedek 1972) Bujak & Matsuoka 1986. 9: Sample 2667. 10: Sample 2668. |
| 6 | <i>Rhombodinium porosum</i> Bujak 1979. Sample 2665. | | |



Remarks. The continuous morphologic variation within *Lanternosphaeridium* sp. 1 indicates that these cysts represent a single species. They are treated informally because it is not clear whether they fall within the morphologic spectrum of *Lanternosphaeridium lanosum*, which is rare in this material, or whether they form a separate closely related species.

Genus *Lophocysta* Manum 1979
Lophocysta sulcolimbata Manum 1979
 Plate 7, figs. 11, 12

Remarks. Three specimens were recorded; their overall dimensions are slightly smaller than typical for this species and the central bodies are distinctly smaller than the type material.

Genus *Muratodinium* Drugg 1970
Muratodinium fimbriatum
 (Cookson & Eisenack 1967) Drugg 1970
 Plate 8, figs. 7, 8

Thalassiphora patula (Williams & Downie 1966) Stover & Evitt 1978; De Coninck, 2001, pl. 6, fig. 7.

Remarks. The specimens figured by De Coninck (2001) as *Thalassiphora patula* (Williams & Downie 1966) Stover & Evitt 1978, are closely comparable to specimens recovered in the upper Bartonian and Priabonian in the present study. They seem to be morphologically closer to *Muratodinium fimbriatum* than to *Thalassiphora patulum*.

Genus *Operculodinium* Wall 1967
Operculodinium divergens (Eisenack 1954)
 Stover & Evitt 1978 Group
 Plate 8, figs. 11–13

Hystrichosphaeridium tiara Klumpp, 1953, p. 390–391, pl. 17, figs. 9–10.

Hystrichosphaeridium divergens Eisenack, 1954, p. 67, pl. 9, figs. 13–15 only.

Cordosphaeridium uncinispinosum De Coninck, 1969, p. 32–33, pl. 9, figs. 6–8.

Operculodinium sp. aff. *O. divergens* (Eisenack 1954) Stover & Evitt 1978–*Cordosphaeridium multispinosum* Davey & Williams 1966; De Coninck, 1995, pl. 6, figs. 3, 4, 9, 10, 17.

Operculodinium sp. aff. *Cordosphaeridium funiculatum* Morgenroth 1966; De Coninck, 2001, pl. 2, figs. 1–3.

Description. This group comprises proximochorate to skolochorate cysts with subspherical to ellipsoidal bodies. The autophragm is thick (>4 µm). The cysts bear nontabular, slightly fibrous cones, spines or processes of subequal size in one specimen. The bases of the projections are circular and striated. The distal endings are bifurcate, trifurcate or irregular branched. The autophragm between the projections is fibrous and finely reticulate. The archeopyle is precingular (Type P, 3" only) and the operculum is free.

Remarks. The *Operculodinium divergens* Group is characterized by thick, reticulate periphragm and slightly fibrous projections. The size and shape of these projections are highly variable. The group encompasses three species, i.e. *Operculodinium divergens* (Eisenack 1954) Stover & Evitt 1978, *Operculodinium tiara* (Klumpp 1953) Stover & Evitt 1978 and *Operculodinium uncinispinosum* (De Coninck 1969) Islam 1983. They are placed into one group because of the frequent intergradations between these morphologies. In some specimens (for example Plate 8, figs. 12, 13) only truncate process bases are present; a similar variability has been observed among dinoflagellate cysts produced by a single living species; this is *Lingulodinium polyedrum* (Stein 1883) Dodge 1989 (see Kokinos and Anderson, 1995).

Operculodinium eisenackii sp. nov.
 Plate 8, figs. 3–6

Hystrichosphaeridium divergens forma *areolata* Eisenack, 1954, p. 67, pl. 9, fig. 16.

Operculodinium tiara (Klumpp 1953) Stover & Evitt 1978; Brinkhuis and Biffi, 1993, pl. 8, fig. 8.

Operculodinium sp. aff. *Cordosphaeridium funiculatum* Morgenroth 1966; De Coninck, 2001, pl. 11, figs. 1, 2.

Description. Proximate to proximochorate dinoflagellate cysts with a subspherical to ellipsoidal outline. No paratabulation is indicated, except for the archeopyle. The autophragm is ornamented, with a distinct coarse reticulum consisting of a dense meshwork of solid low ridges. Numerous slender fibrous processes arise at the junctions of the ridges. The processes usually have short bifurcate or pointed endings. A few processes may be proximally connected by trabeculae. The process bases are broad. The length of the processes and the degree of reticulation differ between specimens. A tendency to shorter processes on less coarse reticulate cysts has been noted. The archeopyle is precingular (type P, 3" only), the operculum is usually lost.

Derivation of name. For Alfred Eisenack, who first illustrated this species.

Designation of holotype. Plate 8, fig. 5, Slide 2664 H4, England Finder coordinates N52/1. MGUH 27780. Kysing-4 borehole, sample 2664, Middle Eocene. Specimen dimensions: Total length 111 μm ; total breadth 108 μm ; central body length 69 μm ; central body breadth 69 μm ; maximum length of processes 23 μm .

Designation of Paratype. Paratype 1: Plate 8, fig. 3, Slide 2649 H1, England Finder coordinates S45. MGUH 27781. Kysing-4 borehole, sample 2649, Middle Eocene. Paratype 2: Plate 8, fig. 4, Slide 2661 H1, England Finder coordinates K55/1. MGUH 27782. Kysing-4 borehole, sample 2661, Middle Eocene.

Dimensions of measured specimens. Total length 90 (105) 117 μm . Total breadth 81 (96) 111 μm . Central body length 69 (74) 84 μm . Central body breadth 66 (69) 72 μm . Maximum length of processes 12–31 μm . Thickness of autophragm 2 (3) 4 μm . (11 specimens measured)

Comparison. *Operculodinium eisenackii* sp. nov. is identical to ‘forma areolata’ of *Operculodinium divergens* (Eisenack 1954) Stover & Evitt 1978 figured in Eisenack (1954, pl. 9, fig. 16). It differs from the *Operculodinium divergens* Group by the coarsely reticulate autophragm. It differs from *Cordosphaeridium funiculatum* Morgenroth 1966 by the more numerous, simple and slender fibrous processes.

Operculodinium nanaconulum–
Operculodinium placitum Group
Plate 8, figs. 9, 10

Description. This group includes cysts with a finely granular central body. The cysts may bear short, conical to truncate spines (Plate 8, fig. 9) as in *Operculodinium nanaconulum* Islam 1983 and *Operculodinium placitum* Drugg & Loeblich 1967. In other specimens, groups of spines may be laterally fused and reduced in height, forming low and short rugulae (Plate 8, fig. 10). These cysts are often thick-walled and they dominate the group at some horizons. There seems to be gradual transitions between the different morphologies.

Genus “*Palmnickia*” Eisenack 1954

Remark. This genus is a junior synonym of *Samlandia* Eisenack 1954, according to Morgenroth (1966).

“*Palmnickia lobifera*” Eisenack 1954
Plate 9, fig. 16

Remarks. Morgenroth (1966) stated that “*Palmnickia lobifera*” falls within the morphologic range of *Samlandia chlamydophora* Eisenack 1954, and we agree that “*Palmnickia lobifera*” is a junior synonym of *Samlandia chlamydophora*. However, *Samlandia chlamydophora* displays significant morphologic variability. Specimens with high sculpture, i.e. a “*Palmnickia lobifera*” morphology, were only observed at certain levels in this material. The occurrence may, therefore, be stratigraphically useful and for this reason we have recognized such forms separately. Some of the specimens registered as “*Palmnickia lobifera*” differ from the typical morphology by having a less membranous and more fibrous periphragm. It is emphasized that the use of “*Palmnickia lobifera*” in the present study is not meant as a validation of this taxon.

Genus *Pentadinium* Gerlach 1961
Pentadinium goniferum Edwards 1982
Plate 9, figs. 17–20

Description. The specimens of *Pentadinium goniferum* in this study exhibit a typical morphology, and their size is in the middle of the size range for this species. The periphragm is thin and smooth, whereas the endophragm is thick with a granular structure and outer surface. The granulation is slightly finer than in the type material. The development of the equatorial pericoel is typical, and a few denticles may be present at the paracingular parasuture. Pericoel development at other parasutures is limited or entirely absent. Most processes are gonal in position, and are slightly expanded distally.

Dimensions of measured specimens. Pericyst length 86 (91) 95 μm . Pericyst breadth 70 (81) 92 μm . Pericyst dorsoventral 82 (86) 94 μm . Endocyst length 64 (66) 68 μm . Endocyst breadth 59 (62) 66 μm . Endocyst dorsoventral 58 (62) 67 μm . Processes, maximum length 16 μm . Endophragm, average thickness 2 μm . (6 specimens measured).

Remarks. *Pentadinium goniferum* was originally described from the Middle Eocene of the Atlantic and Gulf coastal plains of North America (Edwards, 1982). This is the first record from Europe.

Pentadinium cf. *lophophorum* (Benedek 1972)
Benedek et al. 1982
Plate 8, figs. 1, 2

Remarks. These forms bear the same distinctive kind of rugulate to reticulate sculpture on the endophragm as in

Pentadinium lophophorum. However, the size of the sculptural elements is smaller.

Genus *Phthanoperidinium* Drugg & Loeblich 1967

Phthanoperidinium cornutum sp. nov.

Plate 9, figs. 1–5

Phthanoperidinium sp. A, Châteauneuf, 1980, p. 145, pl. 27, figs. 6–7; De Coninck, 1986, p. 18, pl. 6, figs. 36–39.

Description. Dinoflagellate cysts belonging to the genus *Phthanoperidinium*; the specimens have smooth parasutural crests that are highest at the corners of the paraplates. The crests form a well-developed apical horn. Occasionally, fine denticules occur at the distal endings of the crests. The limits of the paracingulum and parasulcus are well marked. Between both ends of the strongly helicoidal paracingulum, the parasulcus is relatively narrow, but it widens considerably towards the antapex and apex. The archeopyle is formed by the loss of paraplate 2a.

Derivation of name. From the Latin *cornutus*, meaning with horn.

Designation of holotype. Plate 9, figs. 1, 2, Slide 2644 K3, England Finder coordinates Q36/2. MGUH 27783. Kysing-4 borehole, sample 2644, Middle Eocene. Specimen dimensions: Autocyst length 26 µm; autocyst breadth 20 µm.

Designation of paratype. Paratype 1: Plate 9, fig. 3, Slide 2646 J4, England Finder coordinates P39. MGUH 27784. Kysing-4 borehole, sample 2646, Middle Eocene. Paratype 2: Plate 9, fig. 4, Slide 2646 J4, England Finder coordinates P36. MGUH 27785. Kysing-4 borehole, sample 2646, Middle Eocene. Paratype 3: Plate 9, fig. 5, Slide 2646 J4, England Finder coordinates O39/4. MGUH 27786. Kysing-4 borehole, sample 2646, Middle Eocene.

Dimensions of measured specimens. Autocyst length 20 (25) 29 µm. Autocyst breadth 16 (18) 22 µm. (16 specimens measured).

Comparison. This species differs from *Phthanoperidinium levimurum* Bujak in Bujak et al. 1980 by having a non-granulate periphragm and by the occurrence of a long, sharp apical horn. *Phthanoperidinium cornutum* sp. nov. differs from *Phthanoperidinium distinctum* Bujak 1994 by having a much longer apical horn and by having thin, high parasutural crests. Both *Phthanoperidinium distinctum* and *Phthanoperidinium levimurum* differ from *Phthanoperidinium cornutum* sp. nov. in lacking the strongly helicoidal paracingulum.

Phthanoperidinium distinctum Bujak 1994

Plate 9, fig. 8

Remarks. Some of the specimens included here in *Phthanoperidinium distinctum* have finely denticulate parasutures. The denticles are also present in the specimen figured in Bujak (1994, pl. 4, fig. 10).

Genus *Rhombodinium* Gocht 1955

Rhombodinium porosum Bujak 1979

Plate 10, fig. 6

Remarks. A single specimen was recorded. The openings in the periphragm are slightly smaller than in the type material, but clearly larger and fewer than the holes in *Rhombodinium perforatum* (Jan Du Chêne & Châteauneuf 1975) Lentin & Williams 1977.

Genus *Selenopemphix* Benedek 1972

Selenopemphix septum sp. nov.

Plate 11, figs. 8–10

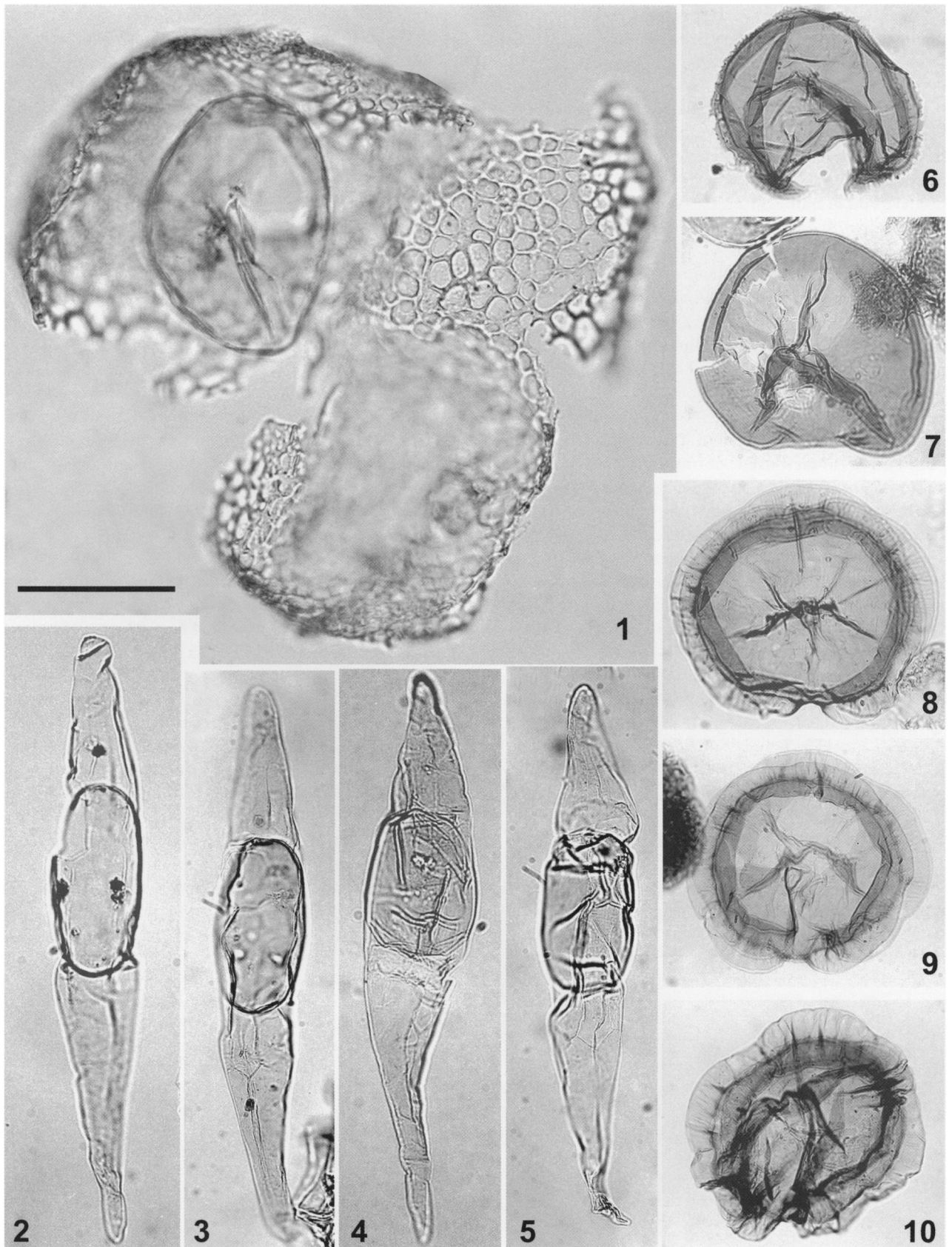
Description. Dinoflagellate cysts belonging to the genus *Selenopemphix*. The autocyst is subcircular in apical/antapical view. The epicyst and hypocyst are short; the epicyst is subconical. On the hypocyst, two small spines may be present on the antapical corners. The broad

PLATE 11

Bar scale in Fig. 1 = 50 µm applies to all specimens.

- 1 *Thalassiphora reticulata* Morgenroth 1966. Sample 1930.
2–5 *Svalbardella partimtabulata* sp. nov. 2: Paratype 3. Sample 2653. 3: Holotype. Sample 2653. 4: Paratype 1. Sample 2654. 5: Paratype 2. Sample 2653.
6 *Selenopemphix selenoides* Benedek 1972. Sample 2658.

- 7 *Selenopemphix nephroides* Benedek 1972. Sample 1773.
8–10 *Selenopemphix septum* sp. nov. 8: Holotype showing slightly offset archeopyle with operculum *in-situ*. Sample 1775. 9: Paratype. Sample 1773. 10: Sample 1773.



paracingulum is bordered by high septa with smooth distal margins. Radial fine folds or striae are usually present on the septa. The autophragm is smooth. The archeopyle is intercalary, Type I (2a), and occurs in a slightly leftward, asymmetric position. The paratabulation is expressed by the archeopyle and the paracingular septa. Folds or ridges are usually present on the epicyst and hypocyst and may possibly mark parasutures.

Derivation of name. From Latin *septum*, meaning partition, with reference to the high septa bordering the paracingulum.

Designation of holotype. Plate 11, fig. 8, Slide 1775 F2, England Finder coordinates K37/3-L37/1. MGUH 27787. Kysing coastal cliff, sample 1775, ?lowermost Oligocene. Specimen dimensions: Total cyst breadth 84 μm ; total cyst thickness 74 μm ; height of septa 8–12 μm .

Designation of paratype. Plate 11, fig. 9, Slide 1773 F3, England Finder coordinates U55/4-V55/2. MGUH 27788. Kysing-1 borehole, sample 1773, ?lowermost Oligocene.

Dimensions of measured specimens. Total cyst breadth 65 (75) 84 μm . Total cyst thickness 58 (68) 82 μm . Maximum height of septa 7 (14) 19 μm . (14 specimens measured).

Comparison. *Selenopemphix septum* sp. nov. is a typical species of the genus *Selenopemphix* except for its high paracingular septa. The only other species with high, smooth septa is *Selenopemphix warriensis* Biffi & Grignani 1983 from the Oligocene of Nigeria. *Selenopemphix warriensis* differs by having less high septa (4–7 μm), an elliptical autocyst and a wrinkled autophragm. *Selenopemphix weileri* Pross 1997, from the Oligocene of Germany, has similarly high septa, but the distal margin is denticulate.

Genus *Svalbardella* Manum 1960
Svalbardella partimtabulata sp. nov.
 Plate 11, figs. 2–5, Text-Figure 8

Description. Dinoflagellate cysts of the genus *Svalbardella* which are spindle-shaped, proximate and

cornucavate with a moderately long, blunt apical horn and a twice, or nearly twice, as long and less blunt antapical horn. Faint parasutural lines or low ridges are present on the periphragm. They are best developed on the dorsal side of the antapical horn and partly show the paratabulation of the cyst (Text-Figure 8). The paratabulation is peridinialean. The paracingulum is not clearly marked; in some specimens it may be vaguely indicated by a fine line. The periphragm is very finely reticulate, almost smooth; the endophragm is smooth. The archeopyle is intercalary, Type I/I (2a), the periarcheopyle is larger than the endoarcheopyle.

Derivation of name. From Latin *partim* meaning partly, and *tabula* meaning table, referring to the partly expressed paratabulation.

Designation of holotype. Plate 11, fig. 3 and Text-Figure 8, Slide 2653 H5, England Finder coordinates N50/1-2. MGUH 27789. Kysing-4 borehole, sample 2653, Middle Eocene. Specimen dimensions: Pericyst length 183 μm ; pericyst breadth 30 μm ; endocyst length 56 μm ; length of apical horn 46 μm ; length of antapical horn 81 μm .

Designation of paratype. Paratype 1: Plate 11, fig. 4, Slide 2654 K5, England Finder coordinates H32/2. MGUH 27790. Kysing-4 borehole, sample 2654, Middle Eocene. Specimen dimensions: Pericyst length 186 μm ; pericyst breadth 36 μm ; endocyst length 48 μm ; length of apical horn 45 μm ; length of antapical horn 93 μm . Paratype 2: Plate 11, fig. 5, Slide 2653 H6, England Finder coordinates H17/4-H18/3. MGUH 27791. Kysing-4 borehole, sample 2653, Middle Eocene. Paratype 3: Plate 11, fig. 2, Slide 2653 H6, England Finder coordinates Q21/1. MGUH 27792. Kysing-4 borehole, sample 2653, Middle Eocene.

Dimensions of measured specimens. Pericyst length 156 (178) 195 μm . Pericyst breadth 24 (32) 36 μm . Endocyst length 42 (53) 62 μm . Length of apical horn 38 (47) 51 μm . Length of antapical horn 74 (81) 93 μm . (12 specimens measured).

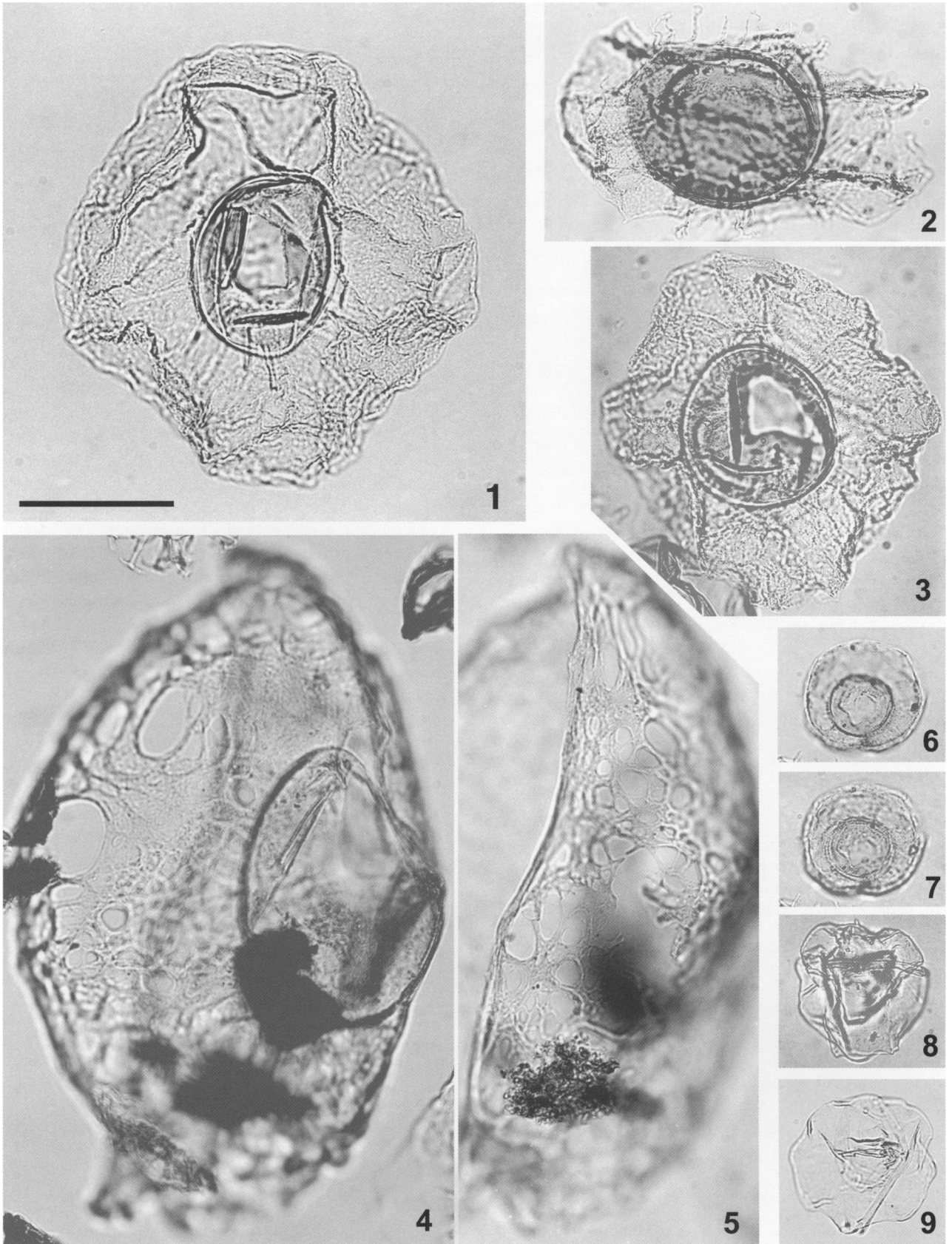
Comparison. *Svalbardella partimtabulata* sp. nov. is closely related to *Svalbardella cooksoniae* Manum 1960,

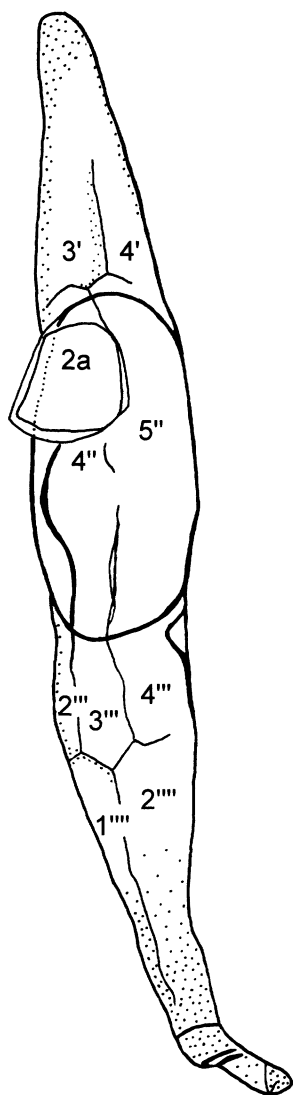
PLATE 12

Bar scale in Fig. 1 = 50 μm applies to all specimens.

1–3 *Thalassiphora gracilis* sp. nov. 1: Holotype. Sample 2638. 2: Paratype 2 in lateral view, showing processes on ventral and dorsal surfaces. Sample 2650. 3: Paratype 1. Sample 2665.
 4, 5 *Thalassiphora fenestrata* Liengjarern et al. 1980. 4: Interior view of right lateral surface. 5: Same specimen, left lateral margin of periphragm. Sample 1930.

6, 7 *Stephodinium? parvum* De Coninck 1986. Specimen in different foci. Sample 2666.
 8 *Thalassiphora? cf. pansa* Stover 1977 in De Coninck (1986). Uncertain identification. Sample 1930.
 9 *Thalassiphora? cf. pansa* Stover 1977 in De Coninck (1986). Sample 1930.





Text-Figure 8. *Svalbardella partimtabulata* sp. nov. Dorsal surface of the holotype with partially expressed paratabulation. The perioeculum is *in-situ*, but the anterior part appears to be missing, as it is shorter than the periarcheopyle. A fold of the periphragm follows the parasuture between 2''' and 3''' and continues to the archeopyle margin, giving a false impression of a parasuture.

but differs by its long antapical horn which is less blunt than the much shorter apical horn. The new species also differs by its clearly visible paratabulation on the antapical horn, and by its less distinct reticulation of the periphragm.

Genus *Thalassiphora* Eisenack & Gocht 1960

Thalassiphora gracilis sp. nov.

Plate 12, figs. 1–3; Plate 14, fig. 3

?*Thalassiphora* cf. *velata* (Deflandre & Cookson 1955)

Eisenack & Gocht 1960; Manum, 1976, pl. 2, fig. 14.

?*Thalassiphora* sp. aff. *T.* cf. *velata* (Deflandre & Cookson) in Manum 1976; De Coninck, 1986, p. 20, pl. 10, fig. 12.

Description. Dinoflagellate cysts of the genus *Thalassiphora*; cavate, with the pericyst completely enclosing the endocyst. The phragma are separated everywhere except middorsally and midventrally, where the periphragm is appressed to the endophragm. The pericyst outline in dorsoventral view is lobate to angular due to folds in the periphragm. The pericyst is dorsoventrally flattened. The endocyst is subspherical. The periphragm is somewhat crumpled, thin and translucent with scattered fine granules and may vary from almost smooth to finely fibrous. On the middorsal surface of the periphragm, a few weakly developed radiating striae are usually formed by alignment of the surface ornament. The endophragm is distinctly thicker and darker colored than the periphragm. It is finely punctate, apparently due to a finely spongy structure. On the middorsal and midventral surfaces, where the phragma are appressed, a number of simple, conical or hairlike spines are usually developed; these are up to 10 μm long. The archeopyle is precingular, Type P (3'' only). Apart from the archeopyle, the paratabulation is only vaguely indicated by the folds in the periphragm.

Derivation of name. From Latin *gracilis* meaning thin or fine, with reference to the thin, translucent periphragm.

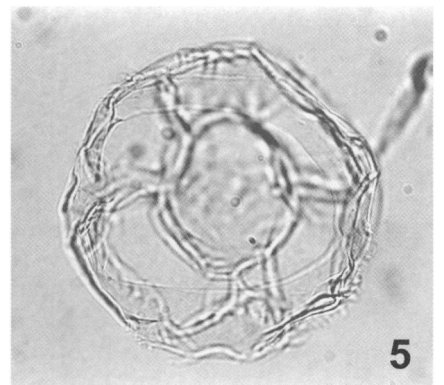
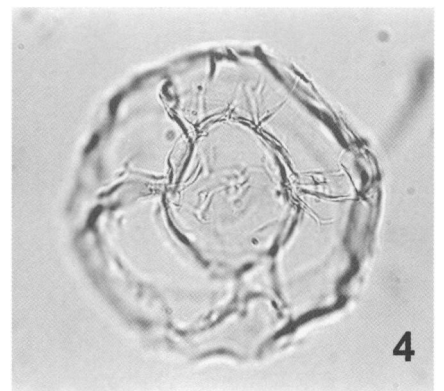
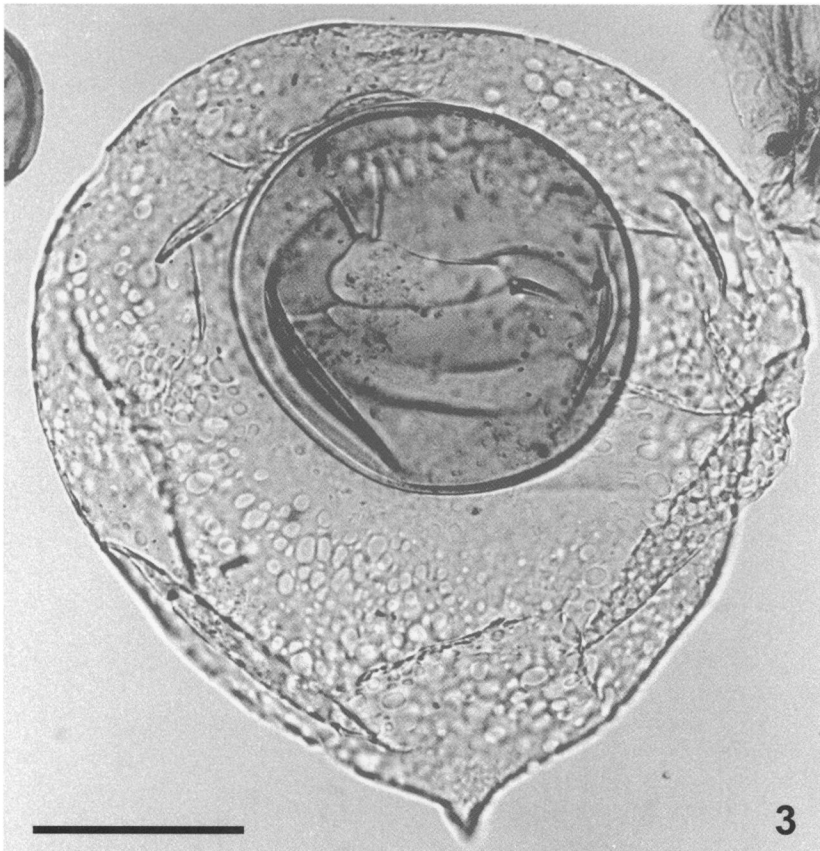
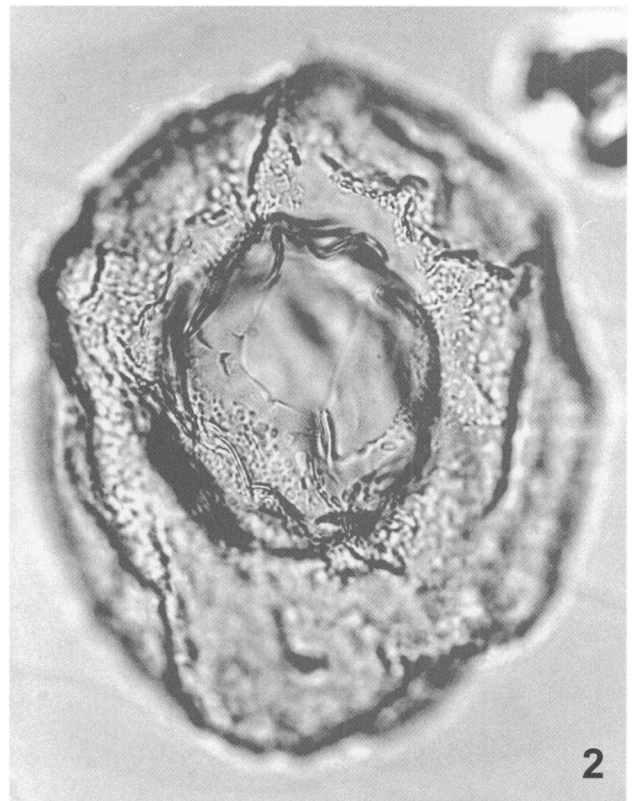
Designation of the holotype. Plate 12, fig. 1, Slide 2638 K5, England Finder coordinates L43/1. MGUH 27793. Kysing-4 borehole, sample 2638, Middle Eocene. Specimen dimensions: Pericyst length 143 μm ; pericyst breadth

PLATE 13

Bar scale in Fig. 3 = 50 μm applies to all specimens.

- 1–2 *Thalassiphora microperforata* sp. nov. Holotype. 1: Ventral surface. 2: Interior view of dorsal surface. Sample 2644.
- 3 *Thalassiphora microperforata* sp. nov. Paratype 2. Sample 1906.

- 4, 5 *Thalassiphora?* cf. *spinifera* (Cookson & Eisenack 1965) Stover & Evitt 1978 in De Coninck (1986). 1: Interior view of dorsal surface with furcate processes. 2: Same specimen, ventral surface. Denticulate parasutures are visible. Sample 2666.



131 μm ; endocyst length 62 μm ; endocyst breadth 48 μm .

Designation of the paratype. Paratype 1: Plate 12, fig. 3, Slide 2665 G1, England Finder coordinates S25/4. MGUH 27794. Kysing-4 borehole, sample 2665, Upper Eocene. Paratype 2: Plate 12, fig. 2, Slide 2650 J4, England Finder coordinates M39/2. MGUH 27795. Kysing-4 borehole, sample 2650, Middle Eocene. Paratype 3: Plate 14, fig. 3, Slide 2659 H2, England Finder coordinates Q32/2. MGUH 27796. Kysing-4 borehole, sample 2659, Middle Eocene.

Dimensions of measured specimens. Pericyst length 88 (109) 143 μm . Pericyst breadth 94 (115) 131 μm . Endocyst length 47 (56) 66 μm . Endocyst breadth 48 (56) 66 μm . Thickness of endophragm 0.5 (1.5) 2 μm . (9 specimens measured).

Comparison. *Thalassiphora gracilis* sp. nov. closely resembles *Thalassiphora pelagica* (Eisenack 1954) Eisenack & Gocht 1960, from which it differs by the more irregular outline of the pericyst, the thinner, translucent and crumpled periphragm, and the presence of spines and of radiating striae. The two species occur together in the samples studied herein, where they form two morphologically discrete populations. A form with a coarsely granular central body described in De Coninck (1986) as "*Thalassiphora* sp. aff. *T. cf. velata* (Deflandre & Cookson) in Manum 1976" is provisionally included in the species. Similar specimens with granular endocysts are recorded in samples 2634 and 2651.

Thalassiphora microperforata sp. nov.
Plate 13, figs. 1–3; Plate 14, fig. 2

Thalassiphora sp. 1, Firth, 1996, pl. 10, fig. 4.

Description. Dinoflagellate cysts of the genus *Thalassiphora*; cavate, with a dorsoventrally flattened pericyst. The endocyst is subspherical or ellipsoidal, formed by a thin, smooth endophragm. The periphragm is attached to the endocyst midventrally and at the posterior margin of the precingular archeopyle. Elsewhere the phragma are separate. The periphragm encloses the central body except

for a relatively small circular opening immediately above the endoarcheopyle. The periphragm is smooth and perforated. The perforations are unevenly distributed. On the ventral surface, the perforations are relatively large and few. The number of perforations increases, and their size decreases, towards the lateral and dorsal surfaces of the periphragm. The paratabulation is only indicated by the archeopyle, which is interpreted as being precingular, Type P (3" only).

Derivation of name. From the small holes in the periphragm.

Designation of the holotype. Plate 13, figs. 1, 2, Slide 2644 K3, England Finder coordinates R27. MGUH 27797. Kysing-4 borehole, sample 2644, Middle Eocene. Specimen dimensions: Pericyst diameter 168 μm ; endocyst diameter 82 μm .

Designation of the paratype. Paratype 1: Plate 14, fig. 2, Slide 2644 K3, England Finder coordinates G25/4. MGUH 27798. Kysing-4 borehole, sample 2644, Middle Eocene. Paratype 2: Plate 13, fig. 3, Slide 1906 G1, England Finder coordinates S37/2. MGUH 27799. Kysing-3 borehole, sample 1906, Upper Eocene.

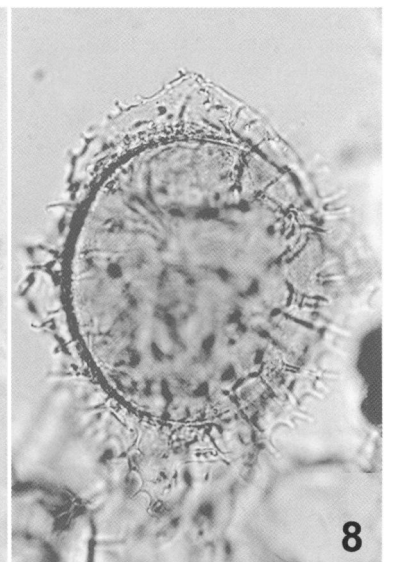
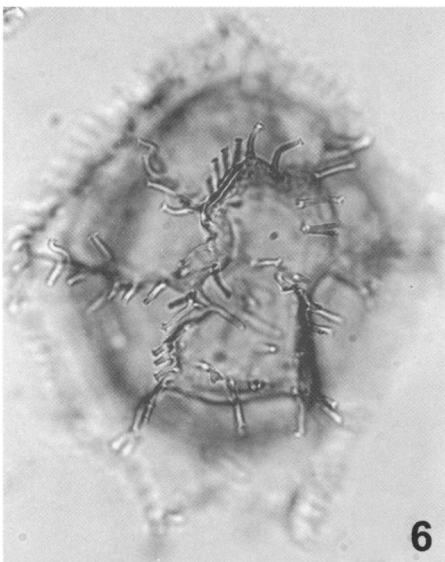
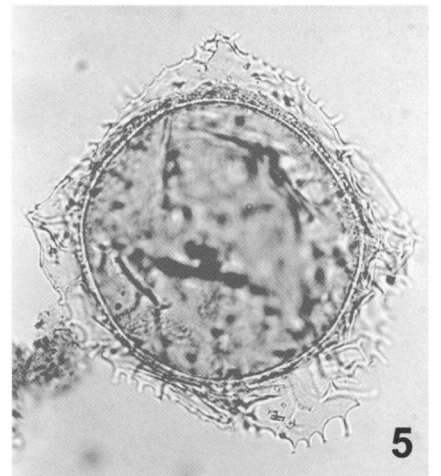
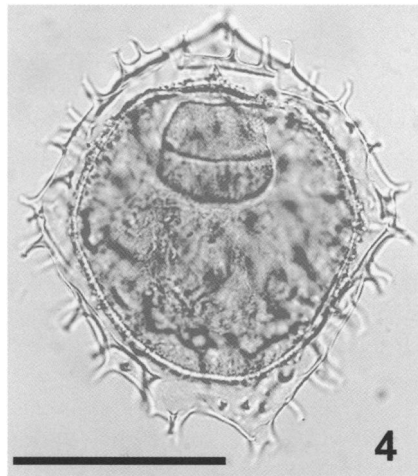
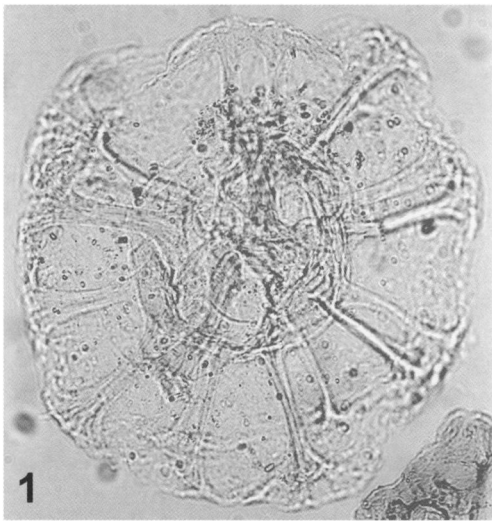
Dimensions of measured specimens. Pericyst diameter 141 (146) 174 μm . Endocyst diameter 68 (78) 99 μm . (6 specimens measured).

Comparison. *Thalassiphora microperforata* sp. nov. differs from *Thalassiphora pelagica* (Eisenack 1954) Eisenack & Gocht 1960 as emended by von Benedek & Gocht, (1981), and from *Thalassiphora fenestrata* Liengjarearn et al. 1980. In both these species the periphragm is only attached to the dorsal side of the central body and forms a large opening on the ventral surface. *Thalassiphora microperforata* sp. nov. is closely related to *Thalassiphora reticulata* Morgenroth 1966, which also has a ventrally attached periphragm with a small opening above the archeopyle. *Thalassiphora microperforata* sp. nov. differs from *Thalassiphora reticulata* by the membranous periphragm with uneven distribution of small perforations. Only within the range of typical *Thalassiphora reticulata* were some intermediate specimens between *Thalassiphora*

PLATE 14

Bar scale in Fig. 4 = 50 μm applies to all specimens.

- | | | | |
|---|---|---------|---|
| 1 | <i>Cordosphaeridium cantharellus</i> (Brosius 1963) Gocht 1969. A specimen with continuous ectophragm. Sample 2652. | 4, 5, 8 | <i>Wetzeliella ovalis</i> Eisenack 1954. 4: Sample 2656. 5 and 8: Sample 2647. |
| 2 | <i>Thalassiphora microperforata</i> sp. nov. Paratype 1. Sample 2644. | 6, 7 | <i>Wilsonidium echinosuturatum</i> (Wilson 1967) Lentin & Williams 1976. 6: Ventral surface. 7: Same specimen, median focus. Sample 2643. |
| 3 | <i>Thalassiphora gracilis</i> sp. nov. Paratype 3. Sample 2659. | | |



microperforata and *Thalassiphora reticulata* encountered. In this study, these intermediate specimens were recorded as *Thalassiphora cf. microperforata*.

Genus *Wilsonidium* Lentin & Williams 1976
Wilsonidium echinosuturatum (Wilson 1967)
 Lentin & Williams 1976
 Plate 14, figs. 6, 7; Plate 15, figs. 1, 2

Wilsonidium echinosuturatum (Wilson 1967) Lentin & Williams 1976; Heilmann-Clausen and Costa, 1989, pl. 7, figs. 5–7.

Remarks. In sample 2643, several specimens with striking similarity to the type material from New Zealand were recorded. These specimens display a pronounced parasutural distribution of the processes. In specimens from other levels, most processes are distributed in a similar way, but the paratabulation is blurred by the presence of nontabular processes.

Division CHLOROPHYTA Pascher 1914
 Class CHLOROPHYCEAE Kützing 1843
 Genus *Palambages* O. Wetzel 1961
Palambages? sp. 1
 Plate 15, figs. 13–16

Description. A small palynomorph, shaped like a hollow sphere. The wall is composed of a layer of many small vesicles, appearing as a layer of small bubbles. The inner surface of the wall seems to be smooth. The outer surface is buckled, resembling the surface of closely packed small bubbles.

Remark. The allocation to *Palambages* is uncertain due to the small size of the vesicles ?or cells.

Group ACRTARCHA Evitt 1963
 Subgroup SPHAEROMORPHITAE
 Downie, Evitt & Sarjeant 1963
 Sphaeromorph acritarch sp. 1
 Plate 15, figs. 5–10

Description. Small spherical, thick walled palynomorphs with a small subcircular pylome. The wall is two-layered. The thick and dense inner part is punctate with a finely granular, indistinctly prismatic, structure. The thinner, outer part is looser in structure and appears to consist of a thin filmy membrane, which is more or less in contact with the inner part of the wall. There is no thickening or other structural differentiation at the margin of the pylome. An operculum has been observed in some specimens. One specimen (Plate 15, fig. 9) shows the presence of two pylomes.

Dimensions of measured specimens. Diameter of cyst body 26 (28) 29 μm . Diameter of pylome 5 (7) 8 μm . Total wall thickness 1.5–2 μm . (5 specimens measured).

GENERAL PALYNOFACIES CHARACTERISTICS

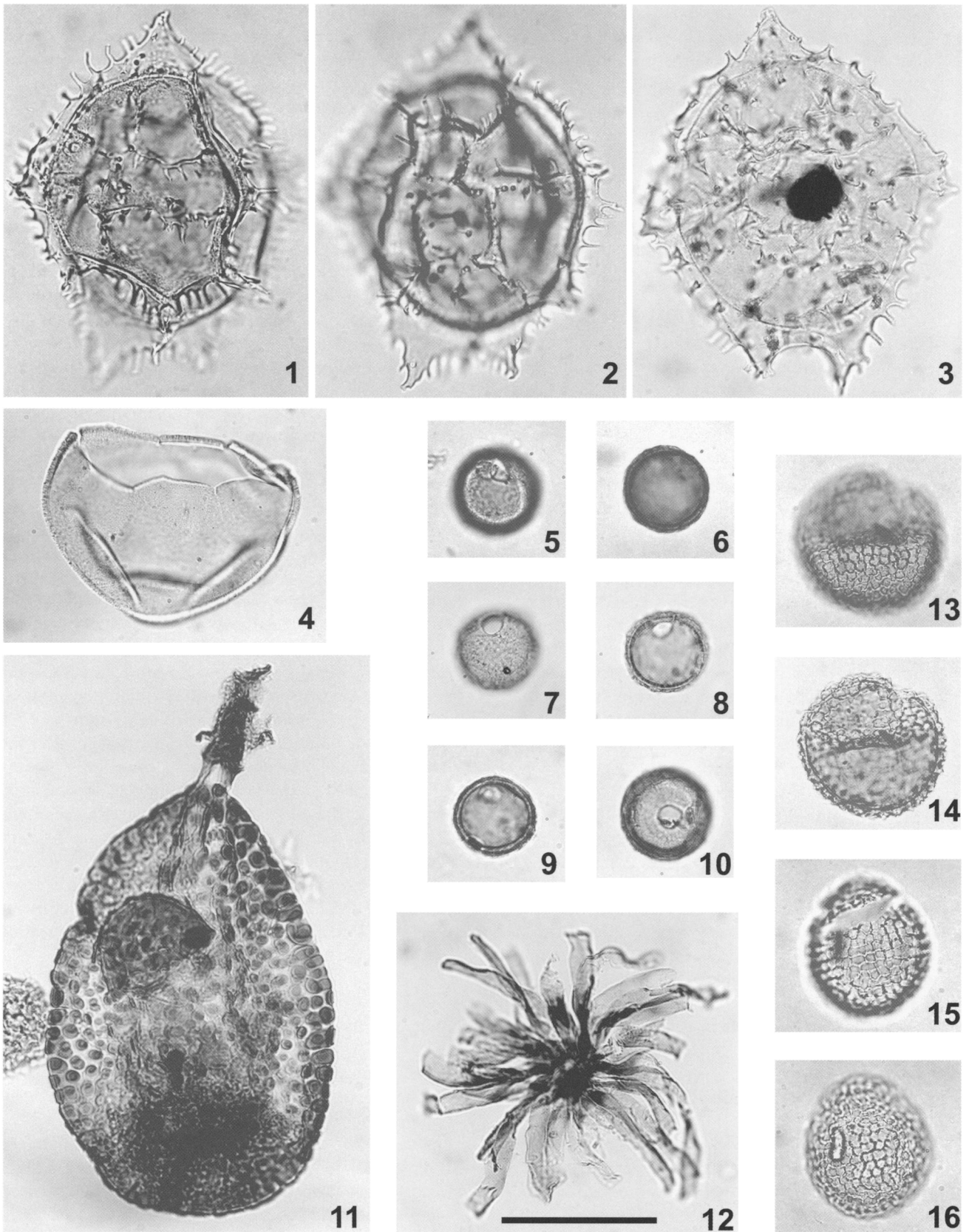
The analysis of the relative proportions of main types of organic particles (> 20 μm) allows for a subdivision of the section into the following facies intervals:

- 1) The Søvind Marl Formation is characterized by an almost pure pelagic facies. Dinoflagellate cysts constitute more than 90% of the organic particles in the

PLATE 15

Bar scale in Fig. 12 = 50 μm applies to all specimens.

- | | | | |
|------|--|--------|--|
| 1, 2 | <i>Wilsonidium echinosuturatum</i> (Wilson 1967) Lentin & Williams 1976. 1: Dorsal surface. 2: Same specimen, interior view of ventral surface. Sample 2643. | 9 | Sphaeromorph acritarch sp. 1. Specimen with two pylomes. Sample 1930. |
| 3 | <i>Wetzeliiella articulata</i> Eisenack 1938 - <i>Wetzeliiella ovalis</i> Eisenack 1954 in De Coninck (1977). Sample 2636. | 10 | Sphaeromorph acritarch sp. 1. Sample 1928. |
| 4 | <i>Batiacasphaera explanata</i> Bujak in Bujak et al. 1980. Sample 2637. | 11 | <i>Stylodiniopsis maculatum</i> Eisenack 1954. Sample 2660. |
| 5, 6 | Sphaeromorph acritarch sp. 1. A specimen with slightly displaced operculum. Two different foci. Sample 1928. | 12 | Plant-hair in Eisenack (1954). Sample 2664. |
| 7, 8 | Sphaeromorph acritarch sp. 1. A specimen in two different foci. Prismatic wall-structure is seen in 8. Sample 1928. | 13, 14 | <i>Palambages?</i> sp. 1. Specimen in two different foci. Sample 2667. |
| | | 15, 16 | <i>Palambages?</i> sp. 1. Specimen in two different foci. Sample 1768. |



interval from 154 m to ca. 36 m. In the highest part, above 36 m, they account for ca. 80% of the particles. The remaining organic matter is mainly amorphous aggregates and the inner linings of foraminifera.

- 2) The Moesgaard Clay marks a considerable shift in facies, and includes a mixed assemblage of marine and terrestrial particles. Dinoflagellate cysts only account for ca. 20–40%, and the remaining particles are mainly amorphous aggregates and brown woody debris. This facies suggests a middle shelf environment with some oxygen deficiency at the sea floor, and some river transport from land areas.
- 3) The Kysing Marl shows a reduced terrestrial influence. Here dinoflagellate cysts increase to 40–50%, the remaining particles are mainly amorphous aggregates, bisaccate pollen, inertinite grains, and inner linings of foraminifera.
- 4) The upper part of the Kysing Marl (sample 1768) and the Viborg Formation show an important increase in the proportion of bisaccate pollen grains. In the lower part of this interval, bisaccate pollen accounts for 20–40%, and increase to ca. 50% in the highest 3 samples of the Viborg Formation. Dinoflagellate cysts account for 30–50% in the lower part and ca. 30% in the upper part. The dominance of bisaccate pollen may result from a shorter distance to land areas. However, the dominance could also reflect a shift in the terrestrial vegetation, perhaps related to the global climatic cooling that is indicated in the earliest Oligocene (Zachos et al., 2001).

BIOSTRATIGRAPHY

The assemblages of rich and well-preserved dinoflagellate cysts in the Kysing borehole contain many taxa with well-defined first and/or last occurrences throughout the section; these events define a detailed biostratigraphic subdivision. The total assemblage of organic-walled microplankton is shown in Table 1, while the stratigraphically most useful species are shown in Table 2.

Indigenous versus reworked dinoflagellate cysts

The distribution of reworked dinoflagellate cysts is shown separately in Table 1, part 4. As may be seen from the table, the Søvind Marl Formation is virtually free of reworked dinoflagellate cysts. The calcareous nannofossils in this

unit are likewise devoid of reworking (E. Thomsen, personal communication). This is in good agreement with the hemipelagic and non-turbiditic depositional environment deduced from sedimentology (Heilmann-Clausen et al., 1985). In contrast, the Moesgaard Clay is relatively rich in reworked dinoflagellate cysts. These cysts are mainly derived from differing Paleocene and Lower Eocene stratigraphic intervals. The reworked cysts and the landward shift of the palynofacies suggest a glacioeustatic sea level fall during deposition of the Moesgaard Clay. The Kysing Marl is almost devoid of reworked dinoflagellate cysts, while moderate reworking, again of early Paleogene dinoflagellate cysts, was observed in the Viborg Formation.

The dinoflagellate cyst zonation of the Danish Basin

The existing dinoflagellate cyst zonation of the Danish Basin (Heilmann-Clausen, 1988) can be applied to the Kysing section (Table 2):

Samples 2633 to 2640, characterized by common to abundant *Phthanoperidinium regalis*, belong to the *Phthanoperidinium regalis* Zone (new name for the *Phthanoperidinium geminatum* Zone). The top of the zone is defined by the lowermost occurrence of *Enneadocysta arcuata*. When the zone was introduced in 1988, the species *Phthanoperidinium regalis* had not been established, and specimens in the zone were at that time referred to *Phthanoperidinium geminatum*. However, they show the diagnostic 'keyhole' archeopyle and must therefore be referred to *Phthanoperidinium regalis*, not *Phthanoperidinium geminatum*, and the name of the zone must be changed accordingly.

Samples 2641 to 2668 are referred to the *Enneadocysta arcuata* Zone, based on the lowermost occurrence of this species in sample 2641, and the absence of *Phthanoperidinium regalis* and *Thalassiphora reticulata*. Samples 1906 to 1776 are referred to the *Thalassiphora reticulata* Zone, based on the lowermost occurrence of this species in sample 1906 and the absence of *Wetzeliella gochtii*.

Major dinoflagellate cyst events in the Kysing section

The many dinoflagellate cyst events recorded in the Kysing section allow a much higher stratigraphic resolution than the zonation by Heilmann-Clausen (1988). The gradual change of the assemblages indicates stratigraphic completeness for most of the section. Hiatuses are lithologically indicated by a glauconite-rich level between samples 2665 and 2666 and at the base of the Moesgaard

Clay. More pronounced shifts of the assemblages, mainly new appearances, were observed at these levels.

Key biostratigraphic dinoflagellate cyst events are shown in Table 2; the three most prominent ones are described below:

1. *Phthanoperidinium regalis* is common to abundant in the lowermost samples, and the abrupt apparent extinction of *Phthanoperidinium regalis* (and its close relative *Phthanoperidinium clithridium*) above sample 2638 is a prominent feature. Nothing in the remaining assemblage of dinoflagellate cysts, the nannofossil zonation, or lithology suggests an unconformity at this level. *Phthanoperidinium regalis* is previously known to be frequent in the upper part of the Lillebælt Clay Formation (Beds L5 and L6) and in the lowermost part of the Søvind Marl Formation in other Danish sections (Heilmann-Clausen, 1988).
2. *Costacysta bucina* is persistent in the lower part of the section, with an uppermost occurrence in sample 2654. *Costacysta bucina* has been recognized by industrial palynologists in the offshore North Sea area and was previously also recorded in a Middle Eocene sample from the Faeroes shelf (Waagstein and Heilmann-Clausen, 1995). Until recently, *Costacysta bucina* had never been reported from onshore sections. However, studies of the West Siberian Basin and the Dniepr–Donetz Depression have revealed the presence of *Costacysta bucina* in the Middle Eocene of both regions (A. I. Iakovleva, personal communication, 2005). The full range of *Costacysta bucina* in Denmark can now be established by the data from the Kysing borehole, combined with unpublished studies of other outcrops and boreholes in Denmark: The lowermost record is in the *Dracodinium pachydermum* Zone of Heilmann-Clausen (1988), in the topmost part of Bed L2 of the Lillebælt Clay Formation. This horizon is of earliest Lutetian age according to Heilmann-Clausen and Costa (1989) and De Coninck (1991). The highest record is in the *Enneadocysta arcuata* Zone of Heilmann-Clausen (1988), coinciding with the first occurrence of *Svalbardella partimtabulata*. The highest record is shortly below the lowermost occurrence of *Chiropteridium eoceanicum* at Grundfjør. The Grundfjør section is referred to biozone NP16 (Thiede et al., 1971). In agreement with this, *Costacysta bucina* is absent in a section of (upper) biozone NP16 and biozone NP17 from the former marl pit at Søvind, where *Chiropteridium eoceanicum* occurs at the base. *Costacysta bucina* is likewise absent in samples of upper biozone NP16 and biozone NP17 in the Viborg 1 borehole. In summary, the

range of *Costacysta bucina* approximately coincides with the Lutetian Stage. Paleoecologically, the exclusively offshore and Danish Basin records of the species suggest it preferred an outer neritic–oceanic environment. The maximum abundance of *Costacysta bucina* (2%) is found at Kysing. In other sections studied, it usually constitutes close to 1% of the total dinoflagellate cyst assemblage. The taxon is even more rare in the lower part of its range (Beds L2 to L4).

3. The prominent appearance of *Enneadocysta arcuata* in sample 2641 is the most striking shift in the dinoflagellate cyst assemblage throughout the Kysing section. *Enneadocysta arcuata* is common to abundant in all samples, from its inception. The cause for this sudden event is unclear, as no evidence from the bio- or lithostratigraphy indicates a hiatus. The simultaneous appearances of *Heteraulacacysta porosa* and *Wilsonidium echinosuturatum*, however, may suggest a change in the watermass characteristics at this time. *Enneadocysta arcuata* is known from all parts of the northwest European Tertiary Basin, up to the Norwegian–Greenland Sea, and from several other regions of the Northern Hemisphere, as discussed below.

Correlation with other regions

Many stratigraphic and taxonomic studies of Middle and Upper Eocene dinoflagellate cysts have been carried out in northwest Europe since the late 1960s. These include, in particular; in the Hampshire–London Basin: Eaton (1971; 1976), Costa and Downie (1976), Bujak (1976; 1979), Bujak et al. (1980), Liengjarern et al. (1980), Islam (1983); in the Belgian Basin: De Coninck (1977; 1981; 1985; 1986; 1995a, b; 1999); in the Paris Basin: Châteauneuf and Gruas-Cavagnetto (1968; 1978), Châteauneuf (1979; 1980); and in Northern Germany: Agelopoulos (1967), Gocht (1969), Heilmann-Clausen and Costa (1989), Köthe (1990; 2003). Other studies have been carried out in the offshore North Sea, in particular Ioakim (1979), Costa and Manum (1988), Gradstein et al. (1992; 1994), Bujak (1994) and Bujak and Mudge (1994). From the Norwegian–Greenland Sea studies mainly include: Manum (1976), Manum et al. (1989), Damassa et al. (1990), Firth (1996) and Eldrett et al. (2004).

The dinoflagellate cyst events in the Kysing Borehole are correlated with recent studies from the central North Sea and Norwegian–Greenland Sea. A full stratigraphic discussion of the many northwest European dinoflagellate cyst records is outside the scope of the study; but selected events

Table 2 (continued).

SAMPLES	<i>Thalassiphora</i> ? spinifera in DeC 86	<i>Muratodinium fimbriatum</i>	<i>Rhombodinium draco</i>	<i>Thalassiphora fenestrata</i>	<i>Enneadocysta fenestrata</i>	<i>Phthanoperidinium comatum</i>	<i>Rhombodinium perforatum</i>	<i>Rhombodinium porosum</i>	<i>Thalass. ? cf. spinifera</i> in DeC 86	<i>Gochtodinium spinula</i>	<i>Hapsocysta kysingensis</i>	<i>Hystriochokolpoma</i> ? sp. 1	<i>Membranophoridium aspinatum</i>	<i>Palambages</i> ? sp. 1	<i>Selenoperphix armata</i>	<i>Stephodinium</i> ? parvum	<i>Reticulosphaera actinocoronata</i>	<i>Selenoperphix coronata</i>	<i>Distatodinium bifidi</i>	<i>Hystriochostrogylon coninckii</i>	<i>Lophocysta sulcolimbata</i>	<i>Melitasphaeridium asterium</i>	<i>C. coleothrypta rotundata</i> s. DeC 86	<i>Homotryblium floripes</i>	<i>Homotryblium tenuispinosum</i>	<i>Horologinella</i> ? pentagonalis	<i>Polysphaeridium zoharyi</i>	<i>Rhombodinium longimanum</i>	<i>Thalassiphora reticulata</i>	<i>Lentinia serrata</i>	<i>Oligosp.</i> ? cf. <i>H. rigaudae</i> in DeC 86	<i>Thalassiphora</i> ? cf. <i>pansa</i> in DeC 86	<i>Glaphrocysta aff. inculta</i> in DeC 86	<i>Distatodinium paradoxum</i>	<i>Impagidinium</i> ? sp. 1	<i>Selenoperphix septum</i>	<i>Thalassiphora succincta</i>								
1776	-	-	-	-	1	-	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	0	0	-	-	0	-	-	0	-	1	-	-	0	0	-	-								
1775	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	?	0	-	-	0	-	-	0	0	0	0	0	0	-							
1774	-	-	-	-	1	-	-	-	-	-	-	1	-	1	-	-	1	-	-	-	-	0	0	-	-	0	-	-	0	-	-	-	-	0	0	0	0	-							
1773	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	2	-	-	0	-	-	-	-	-	-	0	0	0	-						
1771	-	-	-	1	0	-	-	-	-	-	0	-	-	-	-	-	1	-	-	-	-	1	1	-	-	0	-	-	0	-	-	-	-	-	-	0	0	0	-						
1768	-	-	1	0	1	0	-	-	-	-	-	-	1	-	-	0	-	-	-	-	-	1	1	1	-	0	-	-	0	-	-	-	-	-	-	-	-	-							
1932	-	0	-	1	0	-	0	-	0	-	-	0	-	0	1	-	1	-	1	-	3	1	0	-	0	-	-	0	-	0	-	-	0	-	-	-	-	-							
1930	0	-	0	0	0	0	-	-	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	2	-	1	-	0	0	1	-	0	0	-	-	-	-	-	-						
1928	0	-	0	-	6	cf	-	-	-	-	-	0	-	0	-	1	-	0	-	0	-	1	0	-	0	?	-	cf	-	0	1	-	-	-	-	-	-	-	-						
1926	-	-	-	6	-	-	0	1	1	0	-	1	-	-	1	-	-	-	-	-	1	1	1	-	0	0	cf	-	0	0	-	-	-	-	-	-	-	-	-						
1922	?	-	0	?	11	0	-	0	-	0	-	cf	-	-	-	-	-	-	-	-	2	0	-	0	1	0	0	0	-	-	-	-	-	-	-	-	-	-							
1919	-	-	-	1	6	0	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	0	1	0	-	1	0	-	-	-	-	-	-	-	-	-	-	-						
1916	-	-	cf	-	0	5	-	-	-	-	0	-	-	2	-	-	-	-	-	-	0	?	0	0	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-						
1906	-	0	1	-	10	0	-	-	-	0	-	0	-	1	-	-	-	-	-	-	1	0	1	1	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-					
2668	-	1	0	1	-	2	1	-	?	-	0	-	0	-	1	0	0	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
2667	0	0	0	0	?	7	-	0	-	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
2666	-	0	0	1	0	1	-	1	0	1	0	0	0	1	0	-	-	-	-	-	-	-	-	-	-	-	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2665	-	0	0	0	2	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
2664	-	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
2663	-	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
2662	-	0	0	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2661	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2660	-	-	-	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2659	0	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
2658	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2657	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2656	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2655	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2654	-	-	-	-	-	-	-	-	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2653	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2652	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2651	-	-	-	cf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
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2642	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
2641	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
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2639	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2638	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2637	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2636	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
2635	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2634	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2633	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

▲▲ *Selen. septum*, *Impag.*? sp. 1
▼ *Areosphaeridium michoudii*
▼ *Melitasphaer. pseudorecurvatum*
▲▲ *Homotr. floripes*, *Thal. reticulata*
▲ *Melitasphaeridium asterium*
▲ *Reticulosphaera actinocoronata*
▲ *Membranophoridium aspinatum*
▼ *Phthanoperidinium distinctum*

in northwest Europe will be discussed in connection with the offshore studies. The first occurrence of *Enneadocysta arcuata* is treated separately.

The first occurrence of *Enneadocysta arcuata* in northwest Europe

Enneadocysta arcuata is included in most reviews of stratigraphically important dinoflagellate cyst taxa (e.g. Williams and Bujak, 1985; Haq et al., 1988; Stover et al., 1996; Hardenbol et al., 1998; Eldrett et al., 2004; Powell and Brinkhuis, 2004). However, there is some disagreement as to the age of its first occurrence, and this event therefore needs to be clarified. The northwest European first occurrences seem to be in upper biozone NP14–lower biozone NP15, where *Enneadocysta arcuata* is rare and sporadic and has only been recorded in the north German Wursterheide and Gartow boreholes (Heilmann-Clausen and Costa, 1989; Köthe, 1990) and in the Belgian Hijfte borehole, where its inception is in an undifferentiated biozone NP13/NP14 interval (SVS, personal observation). In the mid-upper biozone NP15, *Enneadocysta arcuata* is present in the Belgian Basin in almost all samples (from base of the Lede Formation and upwards), but it is generally rare in this interval (De Coninck, 1981; 1985; 1995a). In contrast, *Enneadocysta arcuata* is common in almost all Belgian samples of Bartonian to early Rupelian age (De Coninck, 1995a). In Northern Germany it likewise becomes common to abundant (as part of the *Enneadocysta pectiniformis*–*Enneadocysta arcuata* complex) in dinoflagellate cyst zone D10 from near the base of biozone NP16, according to Köthe (1990). There seems little doubt that the first and abundant occurrence of *Enneadocysta arcuata* at Kysing is synchronous with the base of Zone D10 in Northern Germany and with the marked increase in abundance observed in the Belgian Basin.

In southern England, *Enneadocysta arcuata* first occurs in Fisher Bed VIII of the Bracklesham Beds in the Whitecliff section, Isle of Wight according to Eaton (1971; 1976). In the otherwise excellent compilation of previous studies of the English Eocene, Bujak et al. (1980, p. 23), apparently in error, quoted Eaton (1976) for the first occurrence of the species two samples deeper, in Fisher Bed VII. The presumed error was repeated by Williams and Bujak (1985) and Powell (1992) who both quoted the Bujak et al. (1980) zonation. The calcareous nannoplankton in the same section was studied by Aubry (1983; 1986), who referred Fisher Bed VII to the upper part of biozone NP14. The overlying Beds VIII–XVII yielded no calcareous nannofossils, while biozone NP16

was identified in Bed XVIII. According to C. King (personal communication 2004) the contact between Beds VII and VIII is erosional and indicates a significant hiatus. Fisher Beds VIII–XVII (with Eaton's 1971 and 1976 first records of the taxon) can probably be correlated with the Belgian Lede Formation based on the presence of the stratigraphically important benthic foraminifer *Nummulites variolarius* in both intervals (Eaton, 1976; De Coninck, 1985). The first occurrence of *Enneadocysta arcuata* in the Norwegian–Greenland Sea is discussed in the following section.

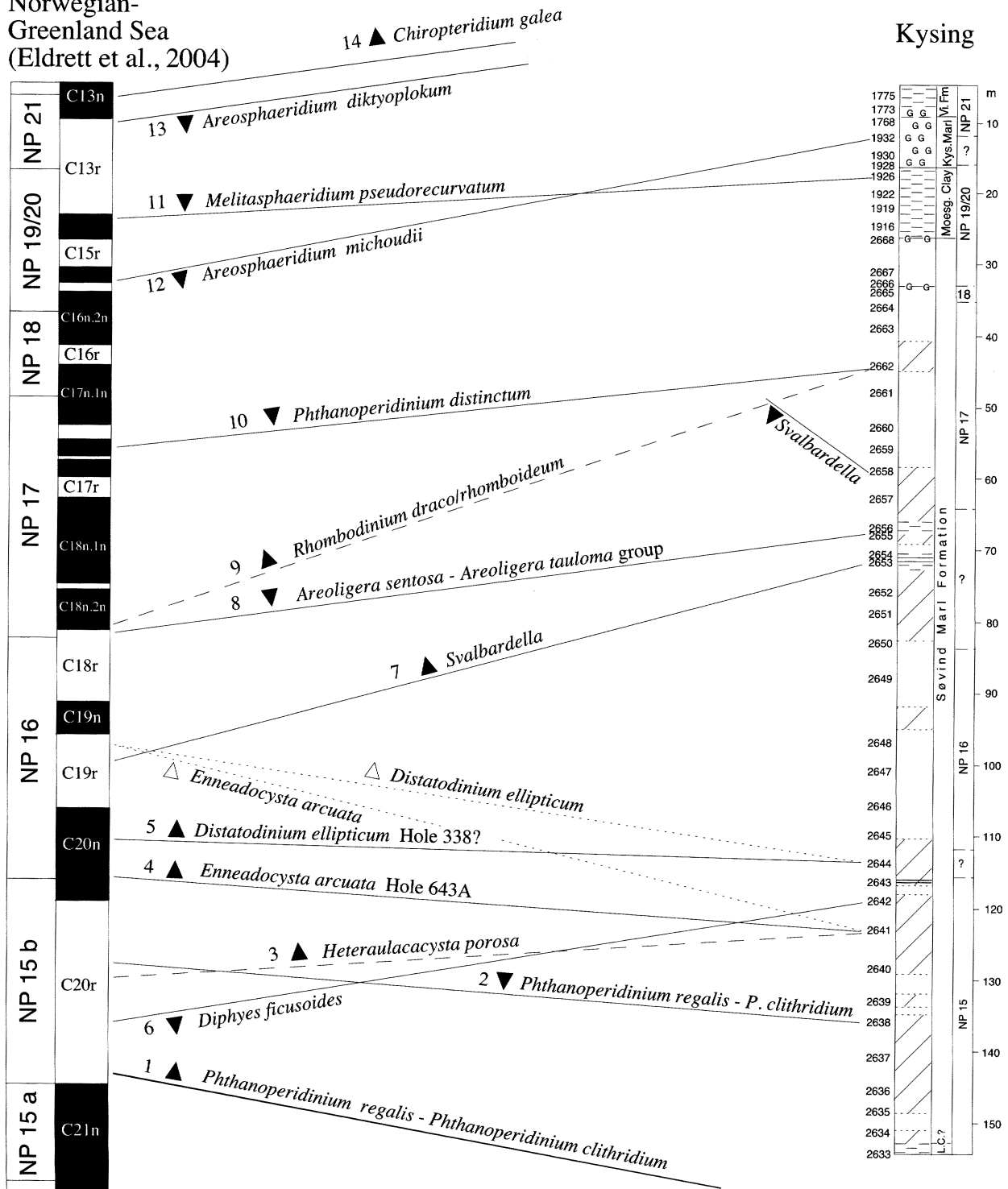
Norwegian–Greenland Sea (Eldrett et al., 2004)

In a recent study on Eocene and Oligocene dinoflagellate cysts from the Norwegian–Greenland Sea, Eldrett et al. (2004) described several events shared with the Kysing section. Eldrett et al. (2004) analyzed 3 different sections and on this basis created a synthetic composite section using graphic correlation. This method averages the primary data. However, for a precise correlation, it is necessary to consult the original data. In Text-Figure 9, a correlation between Kysing and the composite section of Eldrett et al. (2004) is illustrated, but with some data from their individual analyzed sections included. The comparison with the Eldrett et al. (2004) sections is particularly important because these authors identified magnetic polarity zones in their sections. The magnetozones were interpreted as magnetochrons by Eldrett et al. (2004) on basis of initial biostratigraphically derived ages in Firth (1996). This allowed Eldrett et al. (2004) to relate the dinoflagellate cyst events to the global geomagnetic polarity timescale and to indicate NP chronozones, even in the absence of calcareous nannofossils in the sections. Calcareous nannofossil (NP) biozones are identified in most of the Kysing section (E. Thomsen, unpublished information, Text-Figure 2), and hence also part of the corresponding chronozones. This allows comparison of the relative age of dinoflagellate cyst events recorded in the Danish Basin and the Norwegian–Greenland Sea on basis of independent chronostratigraphic indicators (NP chronozones). The events are discussed below, in the order they are recorded at Kysing; the numbers of events refer to Text-Figure 9. For simplicity we refer to NP zones, rather than NP chronozones in the Norwegian–Greenland Sea.

- 1) The first occurrence of the *Phthanoperidinium regalis*–*Phthanoperidinium clithridium* complex is in mid NP15 in the Norwegian–Greenland Sea. The first occurrence in the Danish Basin was recorded

Norwegian-Greenland Sea
(Eldrett et al., 2004)

Kysing



Text-Figure 9. Correlation between the Kysing section and the study by Eldrett et al. (2004) from the Norwegian–Greenland Sea. Events numbers 4 and 5 are shown with full lines in specified holes studied by Eldrett et al. (2004). The same events in their composite section are shown with dotted lines. Other Norwegian–Greenland Sea events are from the composite section of Eldrett et al. (2004). The dashed lines indicate less distinct/diachronous events at Kysing. The symbols in the Kysing section are as in Text-Figure 2.

- by Heilmann-Clausen (1988) in the Viborg-1 borehole, in an interval assigned by Thiede et al. (1980) to the biozone NP14. However, the index fossil of NP14, *Discoaster subloadoensis*, was only questionably identified by the latter authors. According to E. Thomsen (personal communication), who subsequently examined this interval in Viborg-1, it may well represent biozone NP15. It is therefore reasonable to assume that the first occurrence of the *Phthanoperidinium regalis*–*Phthanoperidinium clithridium* complex is synchronous and may take place in NP15 over the entire North Sea Basin–Norwegian–Greenland Sea region.
- 2) The last occurrence of *Phthanoperidinium regalis*–*Phthanoperidinium clithridium* is in upper NP15 both in the Norwegian–Greenland Sea and at Kysing. This event is therefore synchronous in the two regions.
 - 3) The first occurrence of *Heteraulacacysta porosa* virtually coincides with the last occurrence of the *Phthanoperidinium regalis*–*Phthanoperidinium clithridium* complex in the Norwegian–Greenland Sea. *Heteraulacacysta porosa* is rare in the lower part of its range at Kysing and appears to be slightly younger, although its inception is still in biozone NP15. In northern Germany, *Heteraulacacysta porosa* also seems to be sporadic in the lower part of its range: Its oldest occurrence is in biozone NP15 in the Wursterheide Borehole and in biozone NP16 in the Gartow Borehole (Köthe 1986; 1990).
 - 4, 5) In the Norwegian–Greenland Sea, the first occurrences of *Enneadocysta arcuata* and *Distatodinium ellipticum* seem to occur in mid NP16, in the upper part of Chron C19r (Eldrett et al., 2004, text-fig. 11). This is markedly later than at Kysing, where *Enneadocysta arcuata* is abundant already in the upper part of unequivocal biozone NP15, while *Distatodinium ellipticum* appears at the biozone NP15/NP16 transition. The apparent strong diachronism may be an artefact caused by graphic correlation used by Eldrett et al. (2004). The oldest first occurrence of *Enneadocysta arcuata* recorded by Eldrett et al. (2004) is in Hole 643A where it takes place in the lower part of Chron 20n (Eldrett et al., 2004: table 1, text-fig. 7), which is close to the NP15/NP16 boundary. In nearby Hole 338, the first occurrences of *Enneadocysta arcuata* and *Distatodinium ellipticum* were recorded in Chron 19n (Eldrett et al., 2004, Table 1). However, according to their text-figs. 4, 6 and 8, the polarity is unknown in this part of the section. Judging from other events in adjacent samples from Hole 338, in particular the first occurrence of *Heteraulacacysta porosa*, it seems more likely that this level is still within Chron 20n. The two events therefore seem to be synchronous with the first occurrences at Kysing.
 - 6) The last occurrence of *Diphyes ficusoides* appears to be somewhat diachronous. This species is clearly *in-situ* in the uppermost biozone NP15 at Kysing, but apparently became extinct near the middle of NP15 in the Norwegian–Greenland Sea (below the extinction of the *Phthanoperidinium regalis*–*Phthanoperidinium clithridium* complex) in each of the boreholes studied by Eldrett et al. (2004). It cannot be excluded, however, that the apparent diachronism is due to the difficulties in separating the morphologically close *Diphyes pseudoficusoides* from *Diphyes ficusoides* in our analysis.
 - 7) *Svalbardella* is only present in a narrow, nannofossil-free interval in the Kysing borehole, between samples referred to biozone NP16 and biozone NP17. In the Norwegian–Greenland Sea, *Svalbardella* has a much longer range. This difference supports earlier interpretations of *Svalbardella* as a Boreal genus (Head and Norris, 1989; Van Simaey et al., 2005), and also suggests that the laminated clay layer (Text-Figure 2) in which *Svalbardella* occurs in the Kysing borehole was associated with a cooling event.
 - 8) The last occurrence of the *Areoligera tauloma*–*Areoligera sentosa* Group in the Kysing borehole is synchronous with the last occurrence of *Areoligera tauloma* in the Norwegian–Greenland Sea near the NP16/NP17 boundary. Both taxa last occur close to the biozone NP16/NP17 boundary in the Barton Beds, southern England (Costa et al., 1976, p. 275; Bujak and Mudge, 1994 p. 452). This biostratigraphic event thus seems to be an excellent chronostratigraphic marker in the entire North Sea Basin–Norwegian–Greenland Sea region.
 - 9) The first occurrence of *Rhombodinium draco* (which we consider synonymous with *Rhombodinium rhomboideum*) is clearly younger in the Kysing borehole. In the Viborg-1 borehole, dated with calcareous nannofossils by Thiede et al. (1980), we have recorded the first occurrence of *Rhombodinium draco* close to the base of biozone NP17, and the species is persistent in the overlying part of the zone. In contrast to Kysing, the Viborg-1 datum seems to be synchronous with the Norwegian–Greenland Sea. *Rhombodinium draco* is

uncommon at Kysing, and the delayed appearance may be due to its rarity. In England the first occurrence of *Rhombodinium draco* is in Zone BAR-1 (Bujak et al., 1980), in strata referred to biozone NP16 by Aubry (1983). In northern Germany, *Rhombodinium draco* first occurs in an interval without calcareous nannofossils, above strata with NP16 nannofossils (Köthe 1986; 1990).

- 10) The last occurrence of *Phthanoperidinium distinctum* is synchronous in the upper part of NP17 and therefore seems to be an excellent biostratigraphic marker in the North Sea Basin–Norwegian–Greenland Sea region. In contrast, the first occurrence of this species is highly diachronous, delayed at Kysing. Possibly we define *Phthanoperidinium distinctum* more narrowly than Eldrett et al. (2004), due to the introduction of *Phthanoperidinium cornutum*. The first occurrence of *Phthanoperidinium distinctum* of Eldrett et al. (2004) is almost synchronous with the first occurrence of *Phthanoperidinium cornutum* in the uppermost NP15.
- 11) The highest persistent occurrence of *Melita-sphaeridium pseudorecurvatum* in biozone NP19/NP20 at Kysing and in the Norwegian–Greenland Sea may be synchronous.
- 12) *Areosphaeridium michoudii* seems to be *in-situ* at Kysing up to its last occurrence near the base of biozone NP21. In the Norwegian–Greenland Sea information is only available from Hole 913B, where *Areosphaeridium michoudii* becomes extinct in the lower part of NP19/NP20. Its last occurrence therefore appears to be somewhat earlier at high latitudes.
- 13) The last occurrence of *Areosphaeridium diktyoplokus* takes place well above the top of the Kysing profile (see Section 3), and the event seems to be synchronous over the whole region.
- 14) The first occurrence of *Chiropteridium galea* has been recorded in the Danish Basin above the top of *Areosphaeridium diktyoplokus*; in strata of biozone NP22 of the Linde Clay, Linde-1 borehole (Heilmann-Clausen, 1995a, b; Thomsen, 1995).

In summary, there seems to be a high degree of synchronicity of dinoflagellate cyst events between the Norwegian–Greenland Sea and Kysing, when compared to the independent age control available in both regions. This suggests an overall similarity of the watermasses. Except

for *Svalbardella*, diachronism that might be caused by paleoclimatic differentiation is below the time-resolution of this study.

Central and northern North Sea (Bujak and Mudge, 1994)

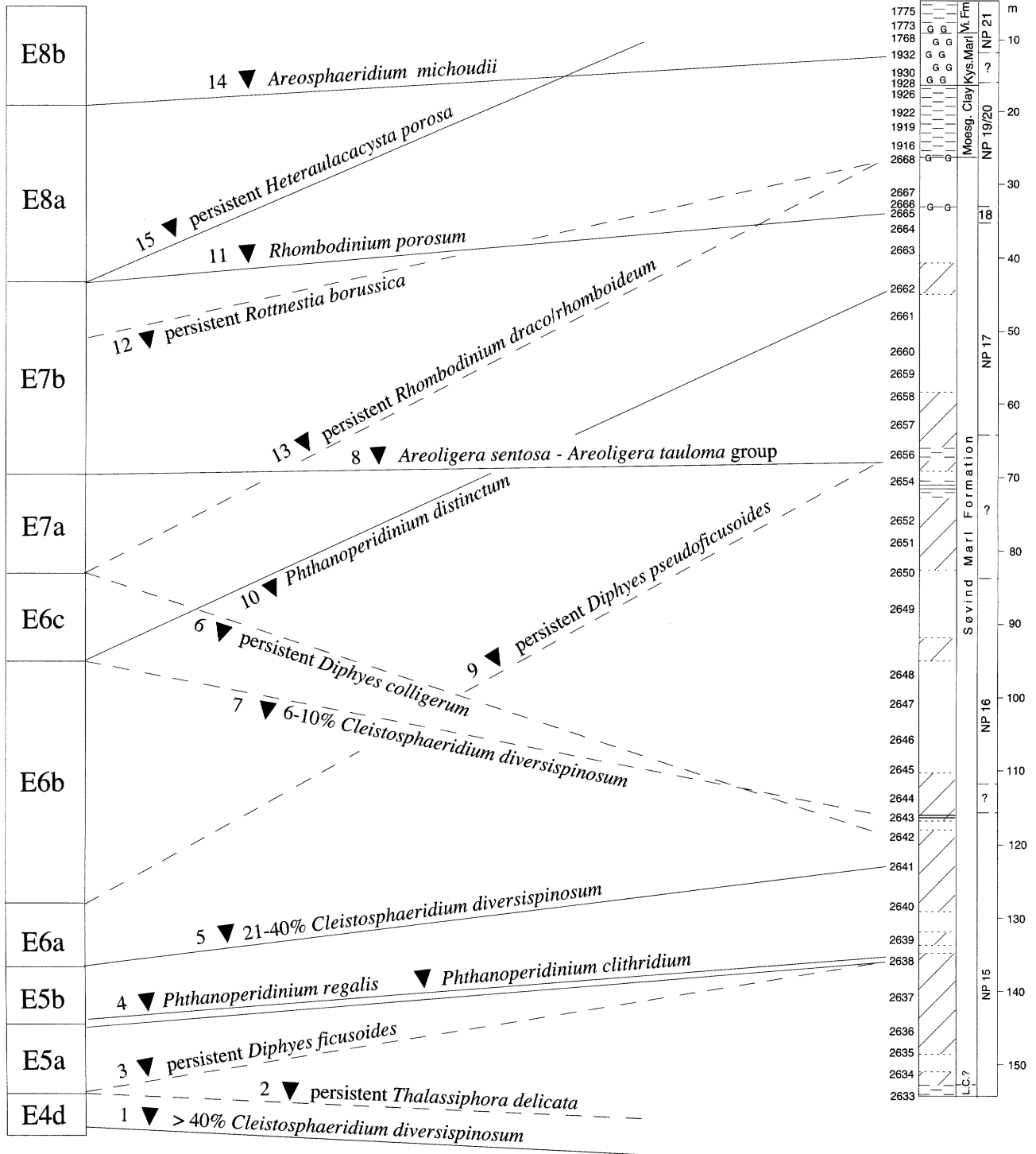
A detailed dinoflagellate cyst zonation was established for the Eocene from the offshore North Sea area by Bujak and Mudge (1994), and slightly revised by Mudge and Bujak (1996). This zonation is based on a high number of studied wells, mainly using ditch cuttings samples. As a consequence, only highest occurrence events are used in this zonation. Bujak and Mudge (1994) indirectly calibrated their events with the NP zonation, based on information from onshore sections.

The Kysing borehole is the first onshore section recording several taxa used in the Bujak and Mudge (1994) zonation. The correlation is shown in Text-Figure 10. Unfortunately the correlation of several events results in lines of diachroneity, and it is therefore necessary to clarify which of these lines may represent synchronism. Each event is commented below in the order they are recorded in the Kysing section.

- 1) The last occurrence of superabundant (>40%) *Systematophora placacantha* in Bujak and Mudge (1994), here referred to *Cleistosphaeridium diversispinosum*, is below the base of the Kysing section. This species is known to dominate the dinoflagellate cyst assemblages of the older *Wetzeliella 'articulata-ovalis'* Zone (Heilmann-Clausen, 1988); and *Cleistosphaeridium diversispinosum* exceeds 40% in only one of the Kysing samples.
- 2) *Thalassiphora delicata* is present in the majority of our samples up to sample 2662, but it usually accounts for less than 1% of the total dinoflagellate cyst assemblage. Unpublished observations show that *Thalassiphora delicata* is more persistently present at older levels in the Danish Basin.
- 3) The last persistent occurrence of *Diphyes ficusoides* is not a distinct event in the Kysing borehole and presumably takes place in sample 2638 or 2642. The event seems to be somewhat diachronous, but it is difficult to differentiate between this species and *Diphyes pseudoficusoides* (see comments on the Norwegian–Greenland Sea).
- 4) The last occurrence of *Phthanoperidinium regalis* (and the simultaneous last occurrence of *Phthano-*

North Sea
(Bujak and Mudge, 1994)

Kysing



Text-Figure 10. Correlation between Kysing and the study by Bujak and Mudge (1994) from the North Sea. Dashed lines indicate less distinct events at Kysing. The symbols in the Kysing section are as in Text-Figure 2.

- peridinium clithridium*) is a prominent and synchronous event in the Danish Basin, the central North Sea and the Norwegian–Greenland Sea as discussed above.
- 5) The last abundant occurrence (21–40%) of *Cleistosphaeridium diversispinosum* recorded (as *Systematophora placacantha*) by Bujak and Mudge (1994) correlates with sample 2641; the event seems to be synchronous between the central North Sea and Denmark.
 - 6) The last persistent occurrence of *Diphyes colligerum* was recorded in sample 2642, but this species is *in-situ* in several samples also at much higher levels, and Köthe (1990) recorded it in several samples from the Lower Oligocene. The event is therefore indistinct and not useful for correlation.
 - 7) The last occurrence of common (6–10%) *Cleistosphaeridium diversispinosum* is the third gradual decline ‘event’ of *Cleistosphaeridium diversispinosum* used (as *Systematophora placacantha*) by Bujak and Mudge (1994). At Kysing the event is not distinct, but may occur in sample 2643, apparently somewhat earlier than in the central North Sea. *Cleistosphaeridium diversispinosum* continues to the top of the Kysing section and usually accounts for 1–5% at these higher levels.
 - 8) As discussed above, the top of the *Areoligera sentosa*–*Areoligera tauloma* group is synchronous in southern England, Denmark and the Norwegian–Greenland Sea. Therefore, this event can also be considered as synchronous in the central North Sea.
 - 9) The last persistent occurrence of *Diphyes pseudoficusoides* is in sample 2656. This is younger than in the central North Sea, but the event is not distinct.
 - 10) The last occurrence of *Phthanoperidinium distinctum* is a clear event in the Kysing borehole and is synchronous in the Norwegian–Greenland Sea. It is therefore surprising that the event is apparently much earlier in the central North Sea. In the Kysing section, *Phthanoperidinium distinctum* is relatively common (2%) at the top of its range, and is clearly *in-situ*. According to A.J. Powell (personal communication, 2005), *Phthanoperidinium distinctum* does occur in younger strata in the North Sea and the last occurrence indicated by Bujak and Mudge (1994) may be its last persistent occurrence.
 - 11) The record here of *Rhombodinium porosum* in the single sample of biozone NP18 may be synchronous with the last persistent occurrence in the North Sea.
 - 12) The last persistent occurrence of *Rottnestia borussica* at Kysing in sample 2668 seems to be much younger compared to the records from the North Sea. According to A.J. Powell (personal communication, 2005), *Rottnestia borussica* is rare in the North Sea at this level.
 - 13) The last persistent occurrence of *Rhombodinium draco* is highly diachronous and occurred much earlier in the North Sea than at Kysing. In the Hampshire Basin, southern England, *Rhombodinium draco* was last recorded in the Middle Headon Beds (Liengjarern et al., 1980). The base of these beds are within biozone NP19/NP20 (Aubry, 1983). The last persistent occurrence at Kysing seems broadly synchronous with that of the Hampshire Basin. It should be noted however, that *Rhombodinium draco* reappeared in the late Rupelian to early Chattian (Köthe, 1990; Van Simaey et al., 2004; 2005).
 - 14) The last occurrence of *Areosphaeridium michoudii* at Kysing (sample 1932, near the NP19/NP20–NP 21 biozonal boundary) is a distinct feature. The event is likely to be synchronous in the North Sea. Mudge and Bujak (1996) presumed a correlation with the base of biozone NP19/NP20, but the authors stated that the correlation was uncertain.
 - 15) The last occurrence of *Heteraulacacysta porosa* is clearly diachronous, and takes place much earlier in the North Sea compared to the onshore Danish sections. *Heteraulacacysta porosa* occurs persistently to the top of the Kysing section, although it is less common in biozone NP21. We have observed a similar distribution in the Viborg-1 borehole. The Danish record agrees with the range in northern Germany, where *Heteraulacacysta porosa* last occurs in the Early Oligocene (Köthe, 1990).
- In summary, several events above Subzone E5b of Bujak and Mudge (1994) seem to occur earlier in the North Sea than at Kysing. In contrast, as discussed above, there is a general synchronicity of events (including last occurrence events) between Kysing and the Norwegian–Greenland Sea. This similarity with the Norwegian–Greenland Sea excludes the possibility that the diachronism relative to the central North Sea may be due to reworking at Kysing. The proximity of the central North Sea, and the similar basinal

settings, suggest strongly that the apparent diachronism may not be genuine. Since most of the diachronism is due to indistinct events (dashed lines in Text-figure 10), the explanation may be that these events are difficult to identify consistently by different workers, or may be diluted by the effects of downhole contamination in ditch cuttings samples.

The Eocene/Oligocene boundary

The distribution of dinoflagellate cysts in the Eocene/Oligocene boundary stratotype in Italy and other Italian sections have been described by Brinkhuis and Biffi (1993), Brinkhuis (1994) and Brinkhuis and Visscher (1995). According to these studies, no major dinoflagellate cyst event characterizes the boundary itself. Furthermore, it has been argued that the position of the GSSP should be reevaluated, as it has been shown to correlate to the middle of the Priabonian stratotype (Brinkhuis and Visscher, 1995).

Nevertheless, a tentative correlation to the existing boundary in Italy is possible by using the last persistent occurrence of *Cordosphaeridium funiculatum*. This event is indicated to occur close to the Eocene/Oligocene boundary (Brinkhuis and Biffi, 1993). At Kysing, *Cordosphaeridium funiculatum* is persistently present up to sample 1932. Relying on the synchronism of this event, which has also been used to locate the boundary in Belgium (Vandenbergh et al., 2003), the boundary would be located in the upper part of the Kysing Marl, close to the base of the Viborg Formation.

CONCLUSIONS

The Kysing borehole section includes rich and well-preserved Middle Eocene to probably earliest Oligocene assemblages of dinoflagellate cysts. Several new taxa are present, and among these, one new genus and twelve new species are formally described. Morphologic transitions occur between some previously described taxa; these are treated as informal groups.

According to palynofacies, most of the succession, the Søvind Marl Formation, was deposited in an almost purely pelagic environment. In contrast, the palynofacies of the overlying Moesgaard Clay indicates a terrestrially influenced middle shelf environment. Furthermore, a significant episode of reworking is observed in the Moesgaard Clay. An important regression therefore marks the lower boundary of this unit. The temporary shift in the depositional environment of the Moesgaard Clay may be caused by a glacioeustatic sea level fall. In the uppermost part of the section, in the Viborg Formation near the Eocene/

Oligocene boundary, a moderate increase in reworked dinoflagellate cysts may again suggest a shorter distance to land areas. The strong increase and dominance of bisaccate pollen near the base of the Viborg Formation may be caused by more proximal conditions, but may also result from a shift in the terrestrial vegetation during a climatic cooling.

The gradual change of the dinoflagellate cyst assemblages observed through most of the Kysing section demonstrates that sedimentation was almost continuous during the time span of ca. 12 Ma. Hiatuses are indicated by more pronounced shifts at a glauconite-rich level at ca. 33 m in the Søvind Marl Formation, and at the base of the Moesgaard Clay. In particular two of the many dinoflagellate cyst events are distinctive, namely the last occurrence of *Phthanoperidinium regalis* and the first occurrence of *Enneadocysta arcuata*. Both species are common to abundant within their ranges; the sudden disappearance of *Phthanoperidinium regalis* and the marked appearance and flourishing of *Enneadocysta arcuata* suggest major changes in watermass properties throughout the entire North Sea Basin.

Many of the events identified at Kysing have been recognized in published studies from northwest Europe, the North Sea and the Norwegian–Greenland Sea. Similarity is especially great with the North Sea and the Norwegian–Greenland Sea, and Kysing is the first onshore section recording several events only known from offshore regions. Where independent age control is available, mainly from the Norwegian–Greenland Sea, most events appear to be synchronous. The published data on the age of the first occurrence of *Enneadocysta arcuata* in southern England and in the Norwegian–Greenland Sea are reinterpreted, and we conclude that the first common occurrences of this species are synchronous. An isolated occurrence of the genus *Svalbardella* suggests a short cooling event in the early Bartonian. The study shows that a biostratigraphic resolution finer than the calcareous nannofossil NP zonation can be achieved with dinoflagellate cysts; with a chronostratigraphic significance throughout a large region of mid to high northern latitudes. The Eocene/Oligocene boundary may be tentatively located close to the base of the Viborg Formation on basis of the last persistent occurrence of *Cordosphaeridium funiculatum*.

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