



## Dinoflagellate cyst and spore-pollen spectra from the Lower Oligocene Krabbedalen Formation at Kap Brewster, East Greenland

Krzysztof BIRKENMAJER<sup>1</sup>, Przemysław GEDL<sup>1</sup> and Elżbieta WOROBIEC<sup>2</sup>

<sup>1</sup>*Instytut Nauk Geologicznych PAN, Senacka 1, 31-002 Kraków, Poland  
<ndbirken@cyf-kr.edu.pl> <ndgedl@cyf-kr.edu.pl>*

<sup>2</sup>*Instytut Botaniki PAN, Lubicz 46, 31-512 Kraków, Poland  
<e.worobiec@botany.pl>*

**Abstract:** Shallow-marine deposits of the Krabbedalen Formation (Kap Dalton Group) from Kap Brewster, central East Greenland, yielded rich dinoflagellate cyst and pollen-spore assemblages. Previously, this formation yielded also rich mollusc and foraminifer age-diagnostic assemblages. A Lower Oligocene age of the Krabbedalen Formation seems to be supported by the dinoflagellate cyst assemblage analysis, while the pollen-spore assemblages point to a wider stratigraphic age range within Oligocene–Middle Miocene.

**Key words:** Greenland, Kap Brewster, Early Oligocene, biostratigraphy, palynology, dinoflagellate cyst assemblages.

### Geological setting

Shallow-marine to brackish Palaeogene deposits of the Kap Dalton Group (Eocene–Oligocene) crop out in central East Greenland from Kap Brewster (Savoia Halvø, Scoresby Sund) in the north-east, along Blossville Kyst, to Kap Dalton in the south-west (Fig. 1). They post-date a huge complex of Upper Paleocene–Lower Eocene tholeiitic flood basalts formed during opening of the northern Atlantic Ocean.

From Kap Brewster, Hassan (1953) described field sections and determined ages of the sediments, based on mollusc content. The first author mapped and sampled the area (Figs 2, 3) during the 1971 Geological East Greenland Expedition organized by the Geological Survey of Greenland (Birkenmajer 1972).

Four main lithostratigraphic units have been distinguished in the area of Kap Brewster (Hassan 1953; Birkenmajer 1972; Birkenmajer and Jednorowska 1977, 1997; Nøhr-Hansen and Piasecki 2002): (1) Paleocene marine deposits which un-

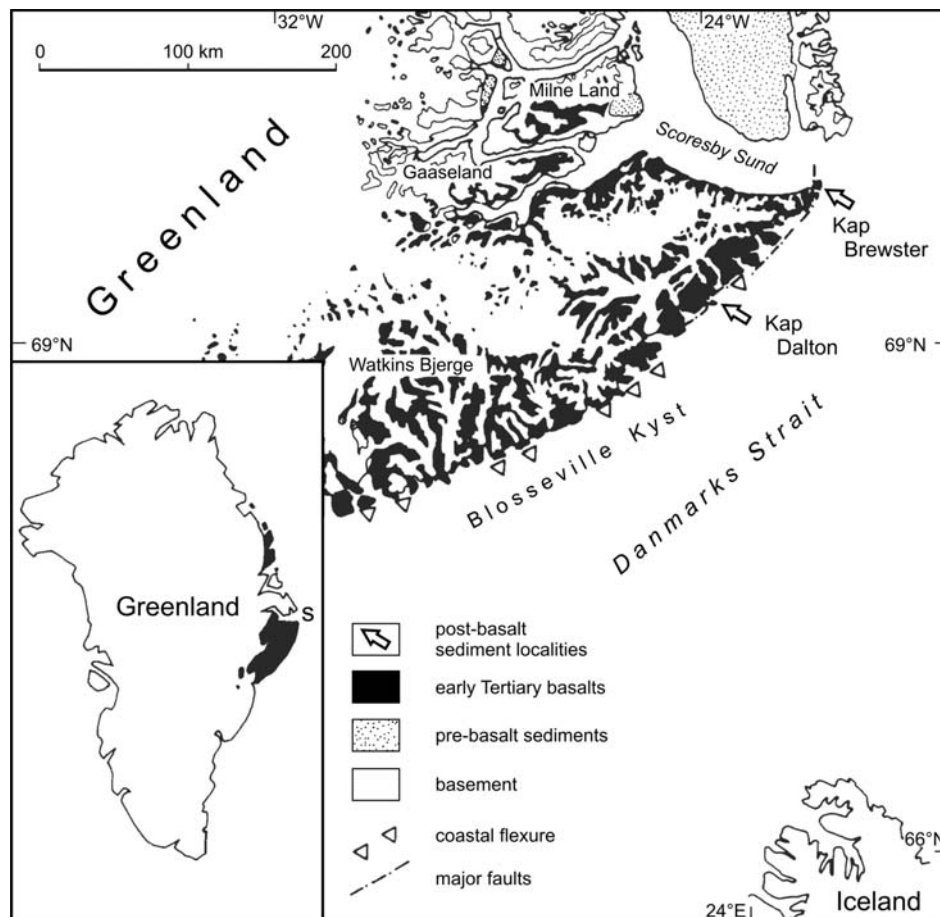


Fig. 1. Location map of Kap Brewster and Kap Dalton in central East Greenland. Geological features based on Soper *et al.* (1976a), Tertiary basalts in black; S – Scoresby Sund.

derlie plateau basalts; (2) plateau-basalts with sediment intercalations (Blosseville Group, Paleocene–Eocene); (3) older post-basalt deposits (Kap Dalton Group, Eocene–Oligocene); (4) younger post-basalt deposits (Kap Brewster Formation, Miocene).

Savoia Halvø is dissected by a major NE-trending dip-slip normal fault called the Muslingehjørnet fault (Fig. 2). It downthrows to the east by more than 1000 m (Birkenmajer 2000). The pre-basalt (Paleocene) sediments crop out in the western upthrown Søstrene block below a thick complex of the plateau basalt lavas of the Blosseville Group. Basement of the Kap Dalton Group formed by the plateau-basalt lavas (with some sediment intercalations) is exposed in the eastern, downthrown Kastellet block. The Kap Dalton Group sediments occupy a small, fault-bounded depression in the central part of Savoia Halvø, while deposits of the Kap Brewster Formation fill cliff-ravines developed during Miocene along the Muslingehjørnet fault.

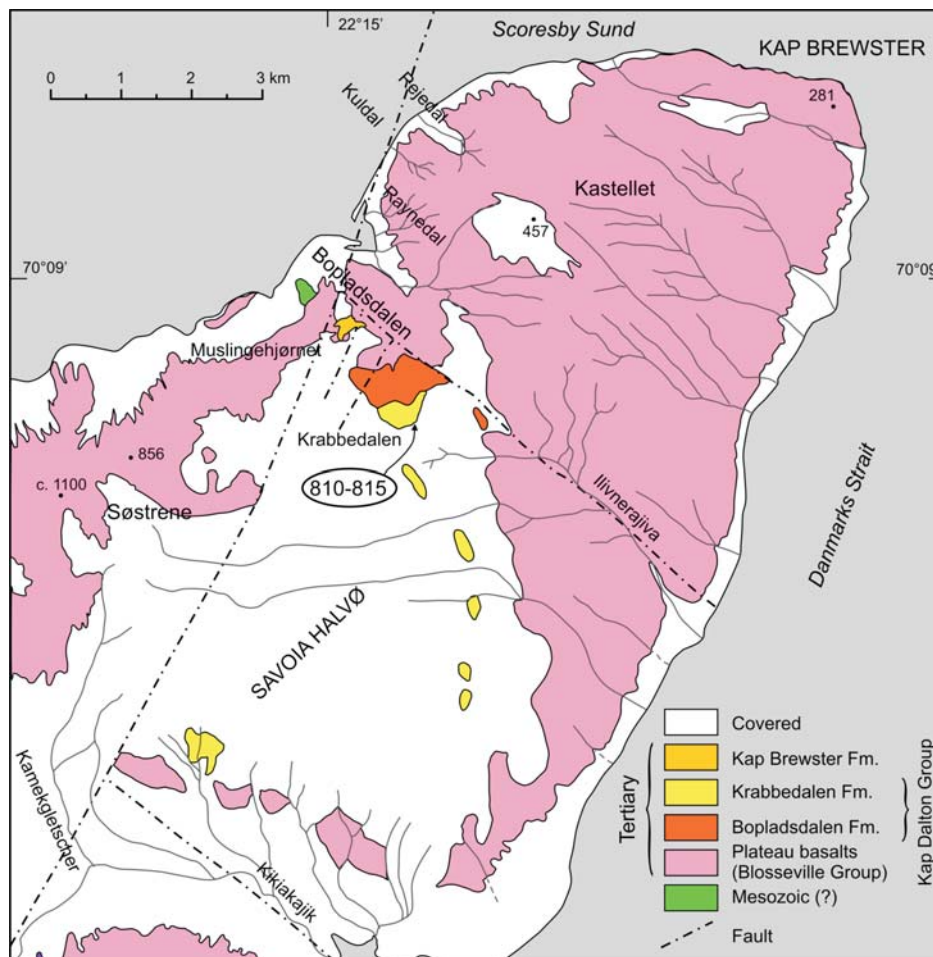


Fig. 2. Geological map of Savoia Halvø, central East Greenland (Birkenmajer 1972, Birkenmajer and Jednorowska 1997). Circled numbers – sample localities in the Krabbedalen Formation; altitudes in metres above sea level.

### Kap Dalton Group

This unit was named the Kap Dalton series by Hassan (1953), renamed formation by Birkenmajer (1972), subsequently raised to group rank by Birkenmajer and Jednorowska (1977). It consists of two formations: the Bopladsdalen Formation (lower) and the Krabbedalen Formation (upper). They are separated from one another by a sedimentary hiatus (Table 1).

**Bopladsdalen Formation.** — This unit (Bopladsdalen Member – Birkenmajer 1972; Bopladsdalen Formation – Birkenmajer and Jednorowska 1977) is maximum about 80 m thick. From underlying tholeiitic basalts of the Blosseville Group it is divided by a stratigraphic gap (Table 1).

Table 1  
Palaeogene succession at Blosseville Kyst, central East Greenland (Birkenmajer and Jednorowska 1977). At Kap Dalton modified from Soper *et al.* (1976b) and Soper and Costa (1976); at Savoia Halvø (Kap Brewster), modified after Hassan (1953) and Birkenmajer (1972). Vertical hatching denotes sedimentary gaps.

Chronostratigraphy			Lithostratigraphy	
Series	Stage	KAP DALTON	SAVOIA HALVØ	
Oligocene	L. Chattian			
	E. Rupelian			
Eocene	L. Bartonian/Priabonian	Kap Dalton Group	Kap Dalton Group	
	M. Bruxellian/Lutetian			
	E. Ypresian/Cuisian	Bopladsdalen Fm.	Bopladsdalen Fm.	
Paleocene	L. Landenian/Spornacian	Blosseville Group	Blosseville Group	
	L. Heersian/Thanetian			
	E. Montian/Danian			
Late Cretaceous	Maastrichtian	Kangerdlugssuaq Group	'infra-basalt sediments'	

The formation begins with a basal conglomerate up to 2 m thick (layer No 4 of Hassan 1953) which consists of very well rounded, mainly basaltic pebbles, weakly cemented by basaltic detritus which, sometimes, is enriched with mollusc-shell detritus and carbonized wood fragments. This is a fossil marine beach deposit.

The basal conglomerate is succeeded by yellow-weathered flaggy sandstones with marine and brackish mollusc shells, pieces of driftwood with *Teredo* borings, and scattered basalt pebbles ("Cyrena beds", layers 5a–e of Hassan 1953). The mollusc fauna is indicative of the Eocene (Hassan 1953).

The Bopladsdalen Formation represents a sediment wedge thickest in the north and tapering out towards the south at a distance of barely 3 km. Lithologic character of the deposits and their fauna indicate a brackish-water to shallow-marine environment, probably a delta apron laid down in an estuary by an ancient river which flowed from the north or west.

**Krabbedalen Formation.** — This unit (Krabbedalen Member – Birkenmajer 1972; Krabbedalen Formation – Birkenmajer and Jednorowska 1977) corresponds to the "Coeloma beds" of Hassan (1953, layer No 6). The formation rests peneconformably (with a break) upon the Bopladsdalen Formation in the north, but comes in direct contact with basalts of the Blosseville Group in the south. It fills a small graben located east of the Muslingehjørnet fault. The best section of the

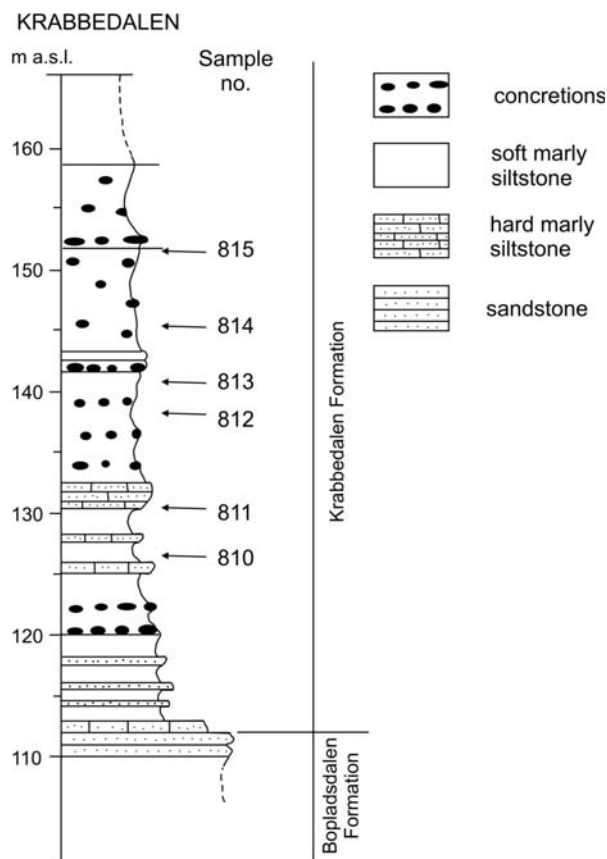


Fig. 3. Simplified lithostratigraphic column of the Krabbedalen Formation at Krabbedalen, Savoia Halvø, with sample numbers (Birkenmajer and Jednorowska 1997).

Krabbedalen Formation is at Krabbedalen (Figs 2, 3) where this unit is about 50 m thick. South of Krabbedalen, where the exposures are poor, the thickness of the formation may increase to 100 m or more.

The Krabbedalen Formation consists of alternating grey to yellowish marly siltstones and hard calcareous siltstones, often containing single pebbles of basalt and other rocks. According to Hassan (1953), its rich shallow-marine macrofauna probably indicates an Early Oligocene age of the deposits.

A preliminary foraminiferal study suggested a latest Eocene to Early Oligocene ages for a higher part of the formation based on the presence of *Globigerina ampliapertura* Bolli in the middle part of the section, and of an Oligocene species *Reophax tappuensis* Asano close to the top of the section (Birkenmajer and Jednorowska 1977). A more complete foraminiferal study that followed, included 33 foraminiferal species belonging to 23 genera and 17 families (Birkenmajer and Jednorowska 1997). Agglutinated foraminifera dominate the assemblage while calcareous benthos (one species only) is second in frequency. Unusually large tests

sizes of some agglutinated foraminifers, particularly those of *Cyclammina cancellata* Brady and *Reophax pilulifer* Brady, were interpreted as a response to cooling of the Early Oligocene coastal waters by the East Greenland Current.

The study by Birkenmajer and Jednorowska (1997) confirmed the previous age estimates of the Krabbedalen Formation. It was pointed out, however, that age-range of *Cyclammina placenta* (Reuss), stratigraphically the most valuable species in our foraminiferal assemblage, is slightly wider: Late Eocene–Oligocene. Thus stratigraphic value of the only planktonic form in the foraminiferal assemblage, revised as *Globigerina cf. ampliapertura* Bolli has been weakened.

The present studies of dinoflagellate cysts (by P. Gedl) and pollen and spores (by E. Worobiec) widen the spectrum of microfossils from the Krabbedalen Formation. The dinoflagellate cyst assemblages confirm a Lower Oligocene age of the deposits, the pollen-spore spectra are less conclusive in this respect (Oligocene–Middle Miocene).

## Methods

The samples were processed in the Micropalaeontological Laboratory of the Institute of Geological Sciences (Polish Academy of Sciences, Kraków Research Centre) according to the following procedure: 30 g of cleaned and crushed rock was treated with 38% chloric acid (HCl) to remove carbonates, sieved on 15 µm sieve (with ultrasonic treatment), treated with 40% hydrofluoric acid (HF) to remove silicates, neutralized and sieved again on 15 µm sieve (with ultrasonic treatment). Organic matter was separated from undissolved or insoluble particles with heavy liquid ( $\text{ZnCl}_2 + \text{HCl}$ ; s.g. = 2.0 g/cm<sup>3</sup>), sieved on 15 µm nylon sieve and transferred into glycerine water for storing. Glycerine-gelatine jelly was used as a mounting medium. No nitric acid (HNO<sub>3</sub>) treatment was applied. The rock samples, palynological residuum and slides are stored in the collection of the Institute of Geological Sciences (Kraków Research Centre), Polish Academy of Sciences in Kraków.

## Results

**Organic-walled dinoflagellate cysts.** — Organic-walled dinoflagellate cysts occur in all studied samples, but composition of their assemblages differs from sample to sample (Table 2). A species list is given in Appendix 1.

The lowermost sample 810 yielded a well preserved dinoflagellate cyst assemblage highly dispersed within land plant remains (mainly sporomorphs, also cuticle fragments). Relatively diversified assemblage consists almost entirely of gonyaulacoids – most frequent are *Lingulodinium machaerophorum* (Fig. 4P–S), *Pentadi-*



Table 2  
 Distribution of dinoflagellate cysts in the Krabbedalen Formation at Savoia Halvø (central East Greenland).

Number	Species	Sample							Number	Species	Sample						
			810	811	812	813	814A	814B				815	810	811	812	813	814A
1	<i>Batiacasphaera minuta</i>		x	x			x		46	<i>Litosphaeridium</i> sp.							
2	<i>Achomosphaera alvicornu</i>		x	x			x		47	<i>Pseudoceratium</i> sp.			x				
3	<i>Pyxidinospis</i> sp. 1 Manum et al. 1989		x				x		48	<i>Charlesdowniea</i> sp.			x				
4	<i>Cordosphaeridium minimum</i>		x	x	x		x		49	<i>Wetzeliella</i> sp.			x				
5	<i>Pentadinium laticinctum</i>		x	x	x		x		50	<i>Subtilisphaera</i> sp.			x				
6	<i>Impagidinium japonicum</i>		x						51	<i>Trithyrodinium</i> sp.				x			
7	<i>Lingulodinium machaerophorum</i>		x	x	x	x	x		52	<i>Cribroperidinium tenuitabulatum</i>				x			
8	<i>Spiniferites pseudofurcatus</i>		x	x			x		53	<i>Palaeoperidinium?</i> sp.				x			
9	<i>Glaphyrocysta</i> sp.		x				x		54	<i>Dapsilidinium</i> sp.				x			
10	<i>Impagidinium velorum</i>		x						55	<i>Cordosphaeridium cantharellum</i>				x			
11	<i>Chlamydophorella?</i> sp. A		x	x	x	x	x	x									
12	<i>Phthanoperidinium comatum</i>		x	x			x										
13	<i>Corrudinium incompositum</i>		x	x													
14	<i>Deflandrea</i> sp.		x		x		x										
15	<i>Membranophoridium</i> sp.		x														
16	<i>Spiniferella cornuta</i>		x														
17	<i>Palaeocystodinium golzowense</i>		x	x	x	x	x										
18	<i>Operculodinium centrocarpum</i>		x	x	x		x										
19	Dinoflagellate cyst sp. A		x	x			x										
20	<i>Spiniferites</i> sp.		x	x	x	x	x	x									
21	<i>Habibacysta?</i> sp. A		x														
22	<i>Stoveracysta</i> sp.		x				x										
23	<i>Deflandrea heterophlycta</i>		x														
24	<i>Pentadinium taeniagerum</i>		x														
25	<i>Alterbidinium</i> sp.		x	x													
26	<i>Glaphyrocysta semitecta</i>		x	x			x										
27	<i>Mendicodinium</i> sp. A WrennKokinos1986		x	x													
28	<i>Achomosphaera ramulifera</i>		x		x												
29	<i>Achomosphaera</i> sp.		x	x			x										
30	<i>Impagidinium</i> sp.		x				x										
31	<i>Impagidinium sphaericum</i>		x	x			x										
32	<i>Nematosphaeropsis</i> sp.		x														
33	<i>Phthanoperidinium ameonum</i>		x														
34	<i>Apectodinium</i> sp.		x	x	x												
35	<i>Alterbidinium</i> sp. A		x	x	x												
36	<i>Impagidinium aculeatum</i>		x														
37	<i>Habibacysta?</i> sp. B		x														
38	<i>Operculodinium hirsutum</i>		x														
39	<i>Lentinia serrata</i>				x		x										
40	<i>Kallosphaeridium</i> sp.				x												
41	<i>Reticulatosphaera?</i> sp.				x		x										
42	<i>Achomosphaera</i> sp. A				x												
43	Peridinioid sp. A				x												
44	<i>Vozzhennikovia</i> sp.				x												
45	<i>Oligosphaeridium</i> sp.					x											

*nium laticinctum* (Fig. 5R, S), *Spiniferites* spp. (Fig. 6G, H, T), *Achomosphaera* sp. (Fig. 6A, B) and small subspherical proximate taxa like *Batiacasphaera minuta* (Fig. 7A–C), *Chlamydophorella?* sp. A (Fig. 7K–M), *Corrudinium incompositum* (Fig. 7U–Y) and *Stoveracysta* sp. (Fig. 7Z<sub>4</sub>, Z<sub>5</sub>). Rare specimens of *Impagidinium* occur in this sample (Fig. 5A–C, K, M, N). There are almost no peridinioids except of single specimens of *Deflandrea* sp. (Fig. 8F), *Palaeocystodinium golzowense* and thin-walled *Alterbidinium* sp. (Fig. 9F).

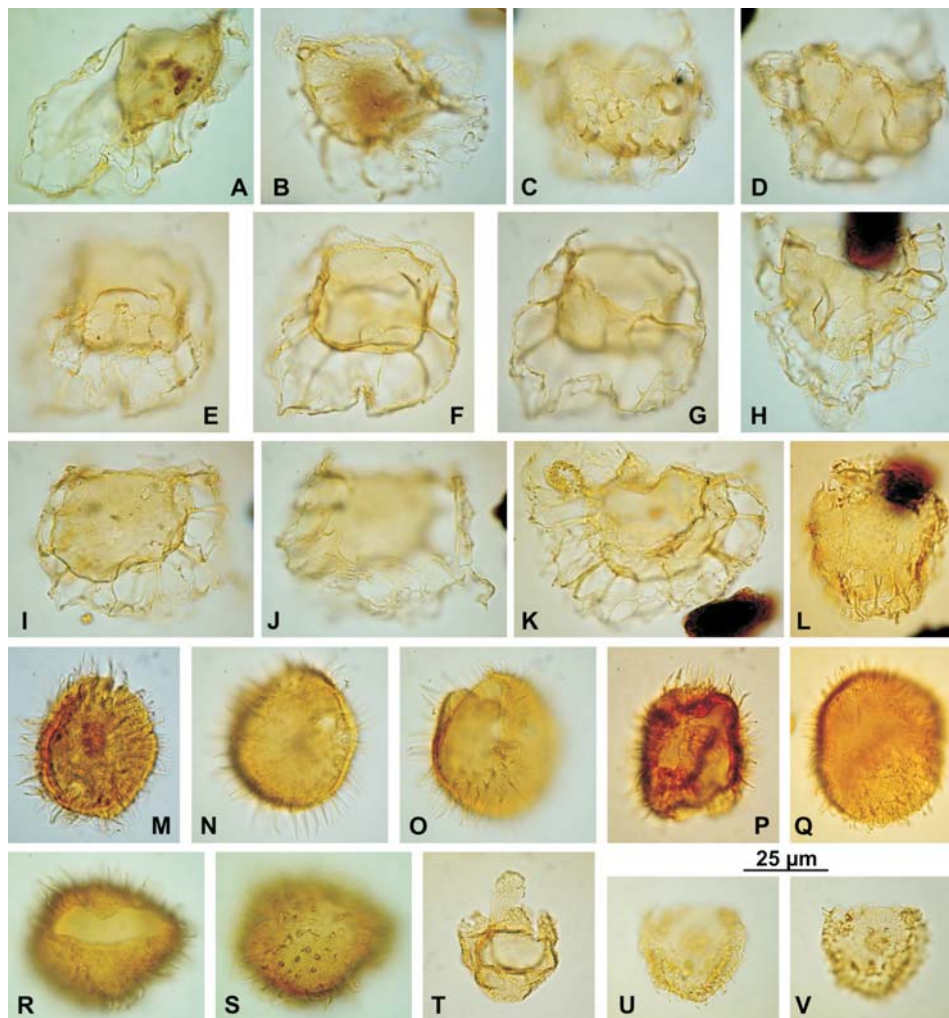


Fig. 4. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A.** *Glaphyrocysta semitecta* (sample 810). **B.** *Glaphyrocysta semitecta* (sample 814A). **C, D.** *Glaphyrocysta semitecta* (same specimen, various foci; sample 814A). **E–G.** *Glaphyrocysta semitecta* (same specimen, various foci; sample 814A). **H.** *Glaphyrocysta semitecta* (sample 814A). **I, J.** *Glaphyrocysta semitecta* (same specimen, various foci; sample 814A). **K.** *Glaphyrocysta semitecta* (sample 814A). **L.** *Glaphyrocysta* sp. (sample 814A). **M.** *Lingulodinium machaerophorum* (sample 814A). **N, O.** *Lingulodinium machaerophorum* (same specimen, various foci; sample 812). **P.** *Lingulodinium machaerophorum* (sample 810). **Q.** *Lingulodinium machaerophorum* (sample 810). **R, S.** *Lingulodinium machaerophorum* (same specimen, various foci; sample 810). **T.** *Kallosphaeridium* sp. (sample 814A). **U, V.** *Pseudoceratium* sp. (same specimen, various foci; sample 813).

A noticeable change of dinoflagellate cyst assemblage takes place in sample 811. Most frequent are peridinioids represented by *Alterbidinium* sp. A specimens (36%; Fig. 9A–E, G, H) and *Svalbardella* sp. (up to 10%; Fig. 100–Q). Among



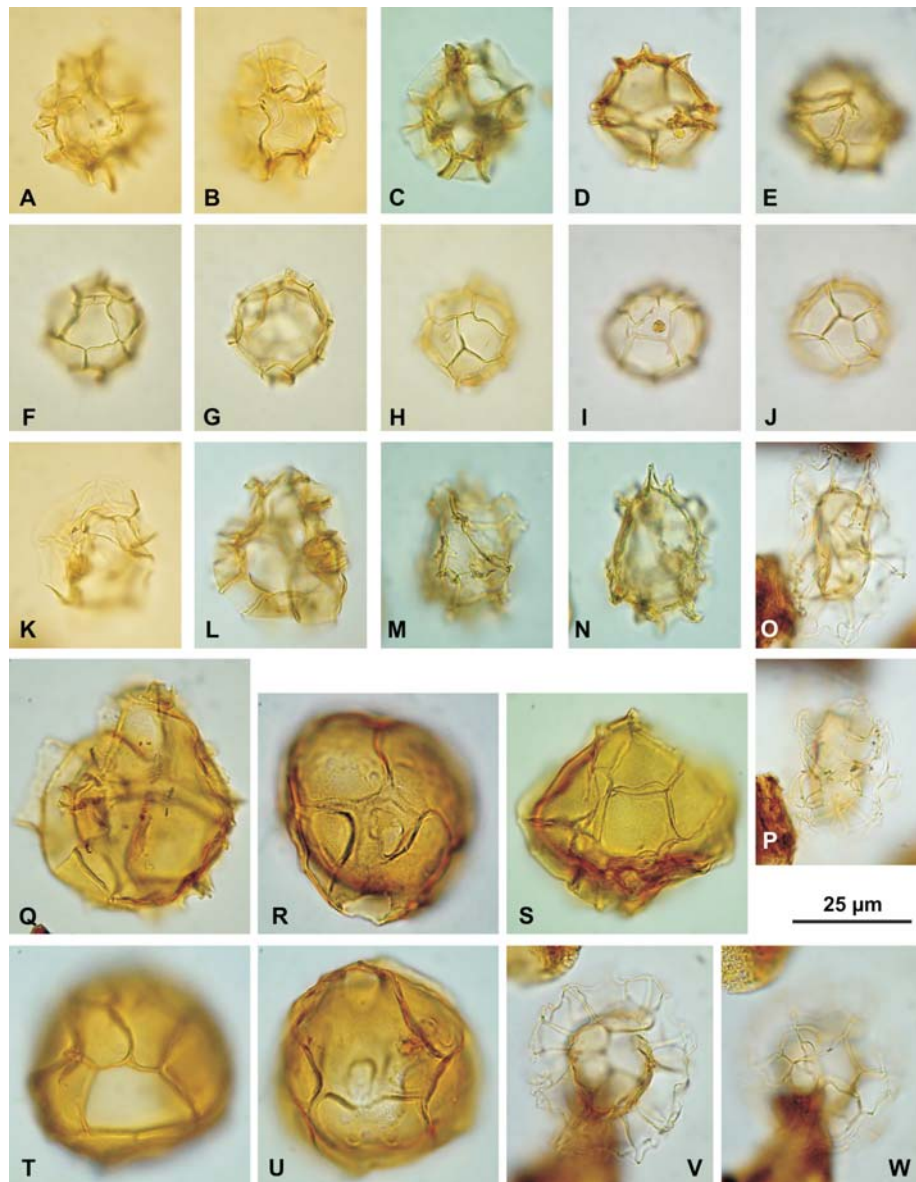


Fig. 5. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A, B.** *Impagidinium japonicum* (same specimen, various foci; sample 810). **C.** *Impagidinium japonicum* (sample 810). **D, E.** *Impagidinium aculeatum* (same specimen, various foci; sample 811). **F–H.** *Impagidinium sphaericum* (same specimen, various foci; sample 811). **I, J.** *Impagidinium sphaericum* (same specimen, various foci; sample 811). **K.** *Impagidinium velorum* (sample 810). **L.** *Impagidinium* sp. (sample 814A). **M, N.** *Impagidinium* sp. (same specimen, various foci; sample 810). **O, P.** *Nematospaeropsis* sp. (same specimen, various foci; sample 811). **Q.** *Impagidinium* sp. (sample 814A). **R.** *Pentadinium laticinctum* (sample 810). **S.** *Pentadinium laticinctum* (sample 810). **T, U.** *Pentadinium laticinctum* (same specimen, various foci; sample 812). **V, W.** *Nematospaeropsis* sp. (same specimen, various foci; sample 811).

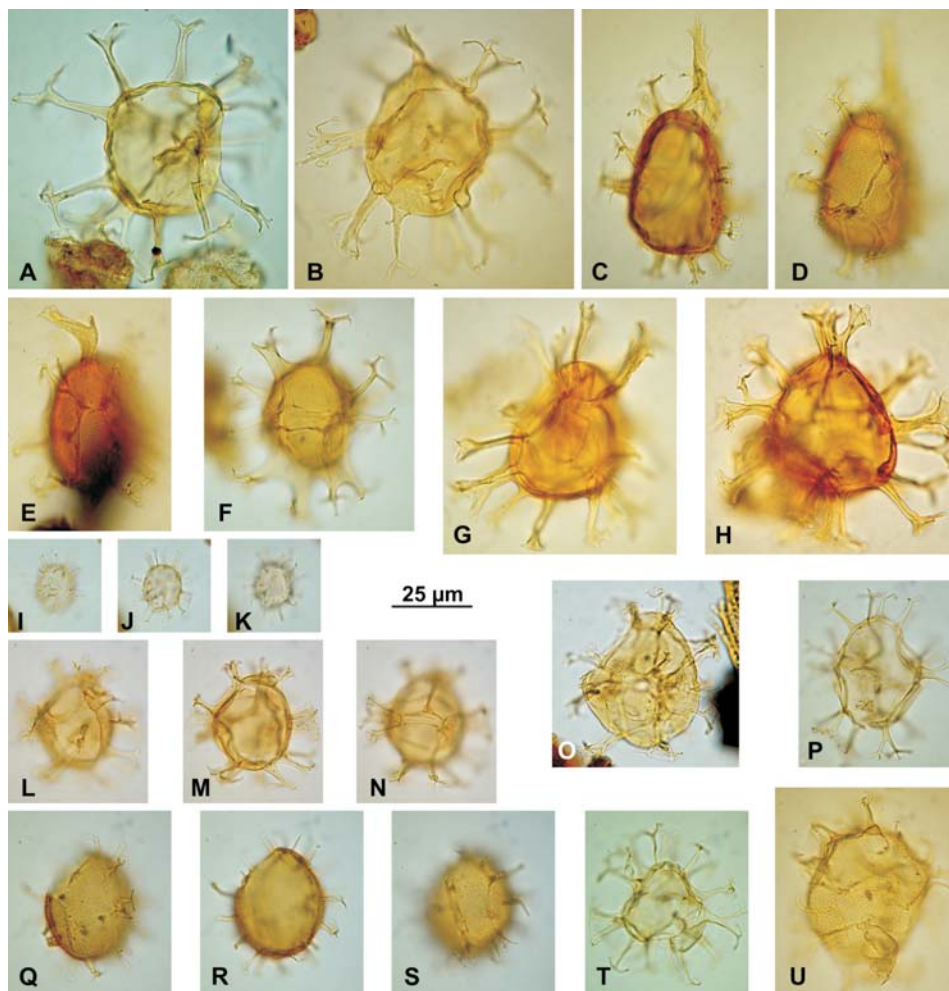


Fig. 6. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A.** *Achomosphaera alcicornu* (sample 810). **B.** *Achomosphaera ramulifera* (sample 810). **C, D.** *Spiniferella cornuta* (same specimen, various foci; sample 810). **E.** *Spiniferella cornuta* (sample 810). **F.** *Spiniferites* sp. (sample 811). **G.** *Spiniferites pseudofurcatus* (sample 810). **H.** *Spiniferites pseudofurcatus* (sample 810). **I–K.** *Achomosphaera* sp. A (sample 812). **L–N.** *Spiniferites* sp. (sample 811). **O.** *Spiniferites* sp. (sample 814A). **P.** *Spiniferites* sp. (sample 811). **Q–S.** *Spiniferites* sp. (sample 812). **T.** *Spiniferites* sp. (sample 810). **U.** *Spiniferites* sp. (sample 814A).

gonyaulacoids, *Spiniferites* sp. is most frequent (app. 15%; Fig. 6P). All others, so common in previous sample (*e.g.* *Lingulodinium machaerophorum*, *Pentadinium laticinctum* and small subspherical proximate taxa), are rare, whereas *Impagidinium* sp. (Fig. 5D–J) and *Nematosphaeropsis* sp. (Fig. 5O, P, V, W) are more common – 3% each. Palynofacies of sample 811 is dominated by sporomorphs, but here dark brown phytoclasts play a significant role (up to 20%); they were almost absent in 810 sample.

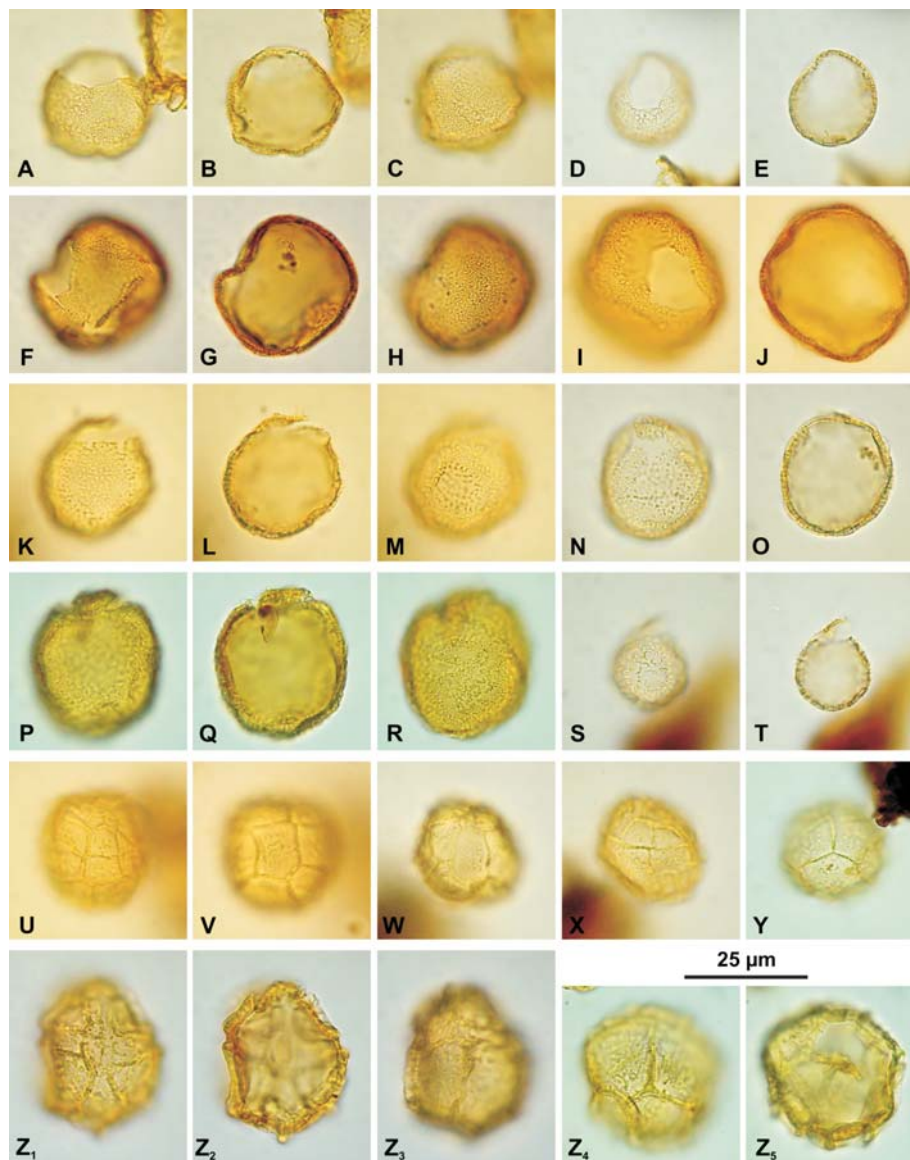


Fig. 7. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A–C.** *Batiacasphaera minuta* (same specimen, various foci; sample 810). **D, E.** *Batiacasphaera minuta* (same specimen, various foci; sample 811). **F–H.** *Pyxidinoopsis* sp. 1 *sensu* Manum *et al.* (1989; same specimen, various foci; sample 814A). **I, J.** *Pyxidinoopsis* sp. 1 *sensu* Manum *et al.* (1989; same specimen, various foci; sample 810). **K–M.** *Chlamydophorella?* sp. A (same specimen, various foci; sample 810). **N, O.** *Chlamydophorella?* sp. A (same specimen, various foci; sample 811). **P–R.** *Habibacysta?* sp. A (same specimen, various foci; sample 811). **S, T.** *Habibacysta?* sp. B (same specimen, various foci; sample 811). **U, V.** *Corrudinium incompositum* (same specimen, various foci; sample 810). **W, X.** *Corrudinium incompositum* (same specimen, various foci; sample 810). **Y.** *Corrudinium incompositum* (sample 810). **Z<sub>1</sub>–Z<sub>3</sub>.** *Stoveracysta* sp. (same specimen, various foci; sample 814A). **Z<sub>4, 5</sub>.** *Stoveracysta* sp. (same specimen, various foci; sample 810).



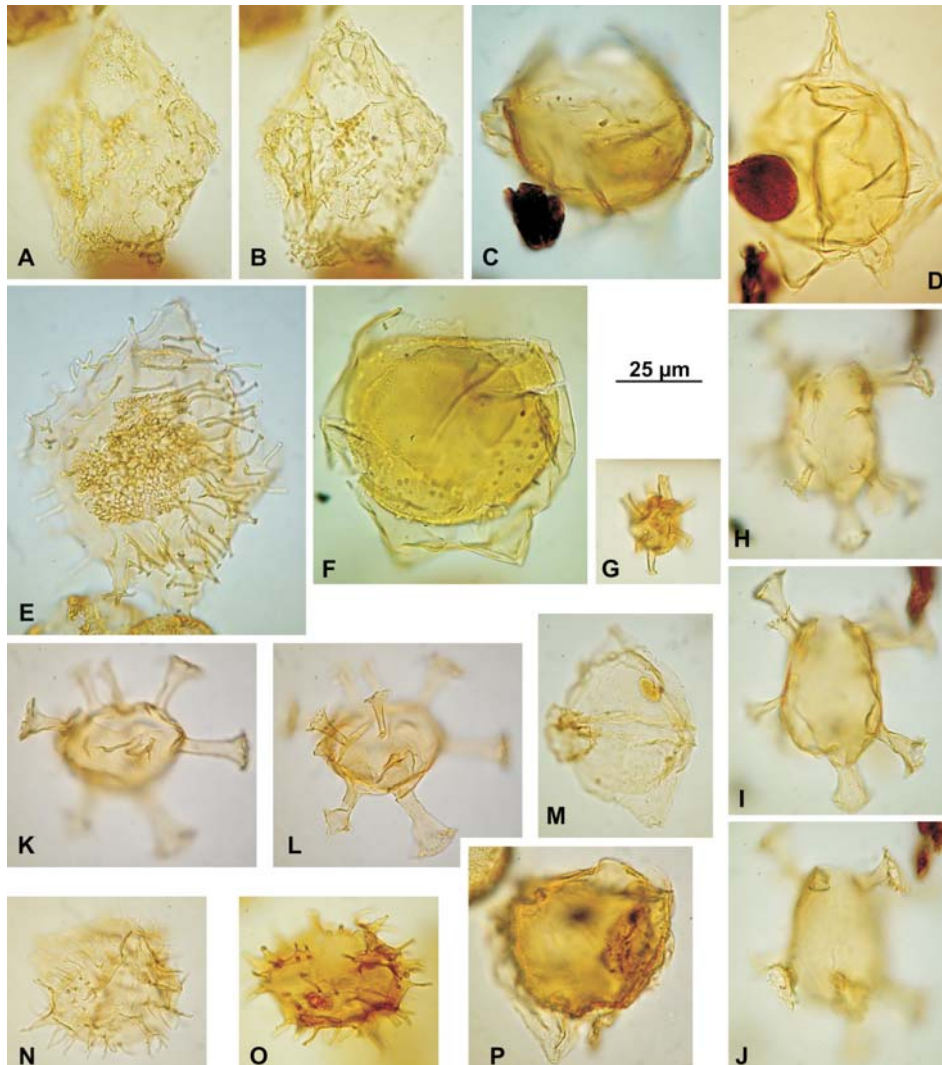


Fig. 8. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A, B.** *Charlesdownia* sp. (same specimen, various foci; sample 813). **C.** *Deflandrea* sp. (sample 812). **D.** *Deflandrea* sp. (sample 812). **E.** *Wetzeliella* sp. (sample 813). **F.** *Deflandrea heterophlycta* (sample 810). **G.** *Litosphaeridium* sp. (sample 813). **H–J.** *Oligosphaeridium* sp. (same specimen, various foci; sample 813). **K, L.** *Oligosphaeridium* sp. (same specimen, various foci; sample 813). **M.** *Subtilisphaera* sp. (sample 813); **N.** *Apectodinium* sp. (sample 812). **O.** *Apectodinium* sp. (sample 811). **P.** *Membranophoridium* sp. (sample 810).

A further increase in frequency of peridinioids takes place in sample 812, where they constitute over 65%. They are represented there mainly by *Svalbardella* sp. (40%) and *Lentinia serrata* (Fig. 9I–P) – over 20%. Palynofacies of this sample is similar to the one from sample 811, but differs by occurrence of infrequent, but large-sized (over 1 mm) cuticle fragments.

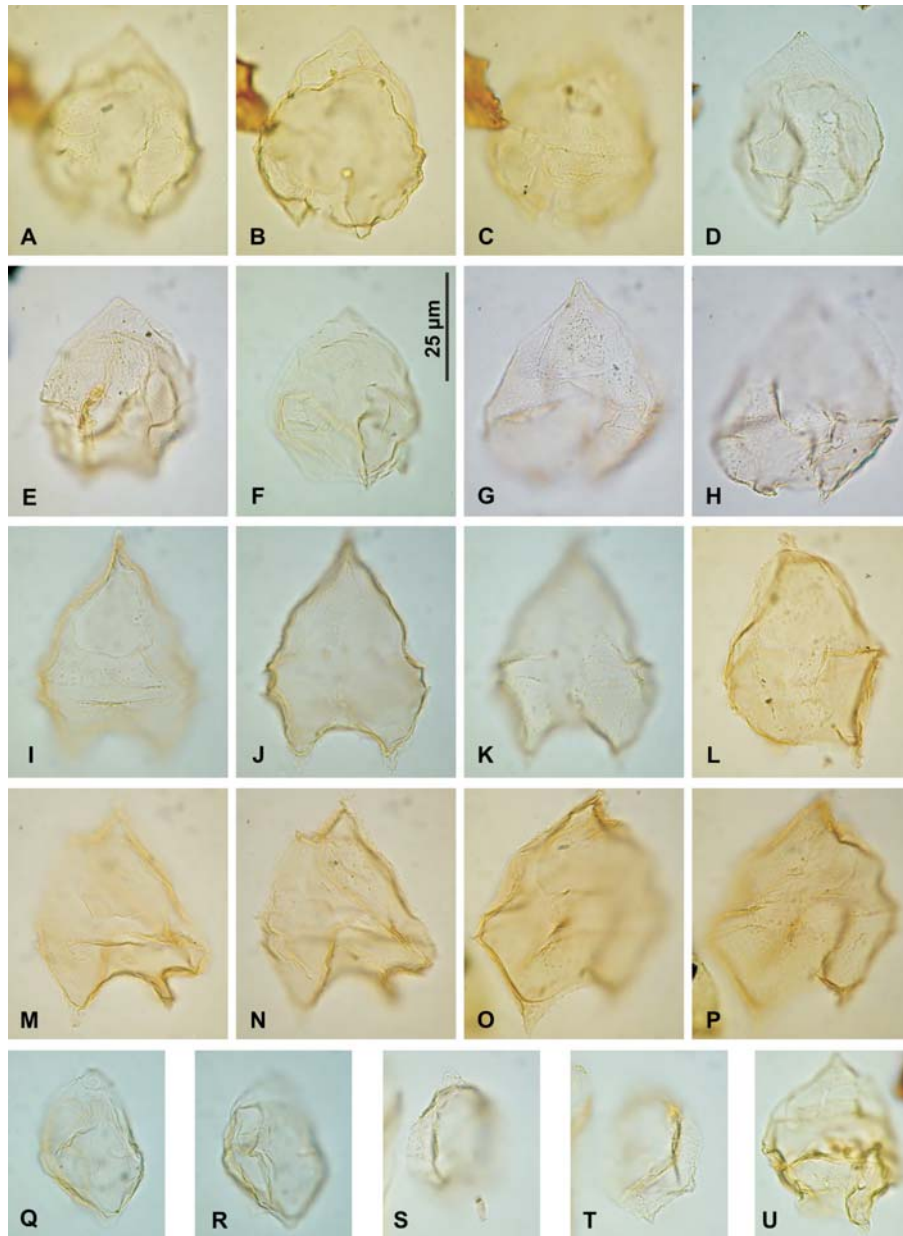


Fig. 9. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A–C.** *Alterbidinium* sp. A (same specimen, various foci; sample 811). **D.** *Alterbidinium* sp. A (sample 811). **E.** *Alterbidinium* sp. A (sample 811). **F.** *Alterbidinium* sp. (sample 810). **G, H.** *Alterbidinium* sp. A (same specimen, various foci; sample 811). **I–K.** *Lentinia serrata* (same specimen, various foci; sample 812). **L.** *Lentinia serrata* (sample 812). **M, N.** *Lentinia serrata* (same specimen, various foci; sample 812). **O, P.** *Lentinia serrata* (same specimen, various foci; sample 812). **Q, R.** Peridinioid sp. A (same specimen, various foci; sample 812). **S, T.** *Vozzhennikovia* sp. (same specimen, various foci; sample 812). **U.** *Trithyrodinium* sp. (sample 814A).



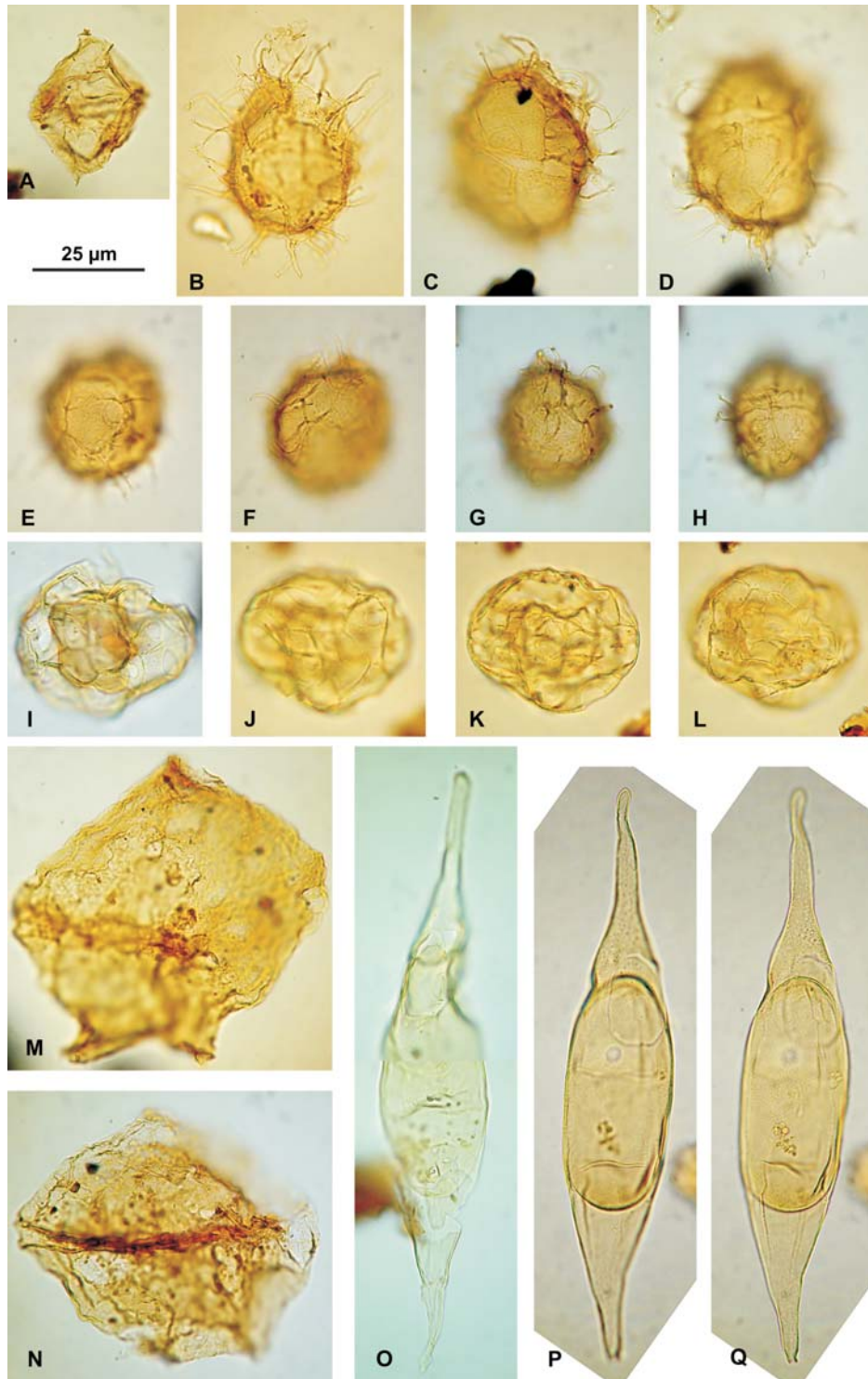
Palynofacies of sample 813 is similar to the one from sample 812. However, especially pollen grains are poorly preserved bearing corrosion features. Dinoflagellate cysts are very rare in this sample. Some of them are recycled from Cretaceous strata: *Litosphaeridium* sp. (one specimen; Fig. 8G), *Subtilisphaera* sp. (one specimen; Fig. 8M), *Pseudoceratium* sp. (one specimen; Fig. 10U, V) and *Oligosphaeridium* sp. (three specimens; Fig. 8H–L). Beside this, a few specimens of poorly preserved peridinioids, single specimens of *Chlamydomphorella?* sp. A, *Lingulodinium machaerophorum*, *Spiniferites* sp. and *Svalbardella* sp. have been found. In this sample, three specimens of Wetzelielloideae, almost absent in the remaining samples, have been found: *Apectodinium* sp., *Charlesdowniea* sp. (Fig. 8A, B) and *Wetzeliella* sp. (Fig. 8E).

Sample 814A yielded a relatively rich and diversified dinoflagellate cyst assemblage. Similarly as in other studied samples, they are strongly dispersed within dominating terrestrial elements, which in case of this sample consist mainly of dark-brown to blackish phytoclasts (up to 70%), sporomorphs (25%) and cuticle remains. Dinoflagellate cysts from this sample resemble the ones from basal sample 810. Their assemblage also consists chiefly of gonyaulacoid taxa. *Spiniferites ramosus*, *Pentadinium laticinctum*, *Lingulodinium machaerophorum*, *Glaphyrocysta semitecta* (Fig. 4B–K), and small proximate subspherical taxa including *Batiacasphaera minuta*, *Chlamydomphorella?* sp. A, and *Stoveracysta* sp. (Fig. 7Z<sub>1</sub>–Z<sub>3</sub>) are the most frequent. Among peridinioids, *Phthanoperidinium comatum* (Fig. 10B–D, G, H) is the most frequent species. The other peridinioids occur as rare specimens, including *Palaeocystodinium golzowense*, *Lentinia serrata*, *Deflandrea* sp., and *Trithyrodinium* sp. (Fig. 9U). The most pronounced difference between dinoflagellate cyst assemblages from samples 810 and 814A is the frequent occurrence of *Glaphyrocysta semitecta* and *Phthanoperidinium comatum* in the latter sample.

Palynofacies of the topmost sample 815 is similar to the one from the basal interval of the studied section. It consists of rather well preserved sporomorphs (over 70%), cuticle remains and dark-brown phytoclasts. Dinoflagellate cysts are extremely rare in this sample. Only few specimens of *Spiniferites ramosus* and *Chlamydomphorella?* sp. A have been found.

**Spore-pollen analysis.** — Pollen grains and spores are very frequent in the sediment in question. Their preservation varies from excellently preserved speci-

Fig. 10. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland) →  
 A. *Phthanoperidinium ameonum* (sample 811). B. *Phthanoperidinium comatum* (sample 814A).  
 C, D. *Phthanoperidinium comatum* (same specimen, various foci; sample 814A). E, F. *Phthanoperidinium comatum* (same specimen, various foci; sample 810). G, H. *Phthanoperidinium comatum* (same specimen, various foci; sample 814A). I. Dinoflagellate cyst sp. A (sample 814A). J–L. Dinoflagellate cyst sp. A (same specimen, various foci; sample 814A). M. *Palaeoperidinium?* sp. (sample 814A). N. *Palaeoperidinium?* sp. (sample 814A). O. *Svalbardella* sp. (sample 812). P, Q. *Svalbardella* sp. (same specimen, various foci; sample 812).



mens to completely corroded ones (especially bisaccate pollen grains) with highly damaged structure.

Bisaccate pollen related to conifers (Pinaceae), as well as other gymnosperms (*e.g.* Cupressaceae = Taxodiaceae/Cupressaceae), strongly prevail among pollen grains, while angiosperms are represented by a few pollen grains only. In addition, relatively frequent, variable in form well preserved spores of Lycopodiaceae, Selaginellaceae and ferns have been found.

All identified taxa have been classified to an appropriate palaeofloristical element (see Table 3) following the checklist of selected sporomorphs from the Neogene deposits by Ziemińska-Tworzydło *et al.* (1994). The following elements have been distinguished in the studied material: palaeotropical (P), including tropical (P1) and subtropical (P2), as well as arcotertiary (A), which includes warm-temperate (A1) and cool-temperate (A2).

Data from pollen spectra of six samples are shown in the pollen diagram (Fig. 12). Selected microphotographs of pollen and spores are shown on Figs 13 to 15.

**Spores.** — The spores found in the sediment in question represent mainly the families Lycopodiaceae, Selaginellaceae, and Osmundaceae; the others occur subordinately.

Spores from the genus *Retitriletes* related to the family Lycopodiaceae are present in all studied samples, being the most variable in form. Six morphological taxa have been distinguished: *Retitriletes annotinioides* Krutzsch, *R. frankfurtensis* Krutzsch, *R. lusaticus* Krutzsch, *R. pseudoclavatus* Krutzsch, *R. punctoides* Krutzsch, and *Retitriletes* sp. Lycopodiaceae spores are also reported from other Tertiary Arctic sites (*e.g.* Koreneva *et al.* 1976; Head *et al.* 1989a; Boulter and Manum 1996; Richter and LePage 2005).

Spores of Selaginellaceae (*Echinatisporis*) are relatively less frequent, but they are present in all studied samples. A noticeable feature of their occurrence is that these spores occur sporadically in tetrads.

Spores related to ferns of the family Osmundaceae (*Baculatisporites* and *Rugulatisporites*) also occur in all studied samples. They are well known from Tertiary Arctic palynofloras (Manum 1962; Koreneva *et al.* 1976; Boulter and Kvaček 1989; Head *et al.* 1989a), being occasionally reported as “baculate triletes” (Boulter and Manum 1989; Manum *et al.* 1989). Interestingly, from the Arctic Tertiary, macroremains of *Osmunda* (Manum 1962; Boulter and Kvaček 1989) are also known, what shows that these ferns were important components of the fossil plant communities during Tertiary in high latitudes.

Other spores, which are related to Schizaeaceae/Cyatheaceae (*Leiotriletes wolffii* Krutzsch, *L. maxoides/maximus*, *Leiotriletes* sp.), Polypodiaceae/Davalliaceae [*Laevigatosporites haardti* (Potonié *et* Venitz) Thomson *et* Pflug, *L. major* Cookson *ex* Krutzsch, *L. nitidus* (Mamczar *ex* Krutzsch) Krutzsch, and *Perinomonoletes* sp.], Pteridaceae (*Cryptogrammasporis* sp.) and others [*e.g.* *Corrugatisporites* cf. *graphicus* Nagy, *Foveotriletes* sp., *Monoleiotriletes gracilis* Krutzsch,

Table 3  
Results of sporomorph analysis of the Krabbedalen Formation at Savoia Halvø (central East Greenland). S – spores, G – Gymnospermae, An – Angiospermae, V – varia (indeterminate pollen and spores), P – phytoplankton (fresh-water), F – fungi.

Taxon (botanical affinity)	Palaeo- floristic element	Sample						
		815	814A	814B	813	812	811	810
S <i>Baculatisporites</i> spp. (Osmundaceae)	P/A	78	28	2	28	8	15	60
S <i>Cicatricosisporites</i> sp. (Schizaeaceae)	P1			1				
S cf. <i>Concavisporites</i> sp. (?Gleicheniaceae)	P					1		
S <i>Corrugatisporites</i> cf. <i>graphicus</i> Nagy ( <i>Lygodium</i> )	P2	1			1			
S <i>Cryptogrammasporis</i> sp. (Pteridaceae)	A1	1	1		2			1?
S <i>Echinatisporis</i> spp. ( <i>Selaginella</i> )	P/A	174	1		162	18	32	10
S cf. <i>Favoisporis</i> sp. (?Pteridaceae/?Ophioglossaceae/?Hymenophyllaceae)	P/A	1						
S <i>Foveotriletes</i> spp. (unknown botanical affinity)	unknown		1				1	
S <i>Intrapunctisporis</i> sp. (?Lygodiaceae)	P?				1			
S <i>Laevigatisporites</i> spp. (Polypodiaceae/Davalliaceae)	P/A	2	6		8	10	8	1
S <i>Leiotriletes</i> spp. (Schizaeaceae/Cyatheaceae)	P	56	22		17	46	20	8
S <i>Monoleiotriletes gracilis</i> Krutzsch (unknown botanical affinity)	unknown					1		
S <i>Neogenisporis</i> spp. (pro parte Gleicheniaceae)	P1				2	1		1
S <i>Perinomonoletes</i> sp. (Polypodiaceae/Davalliaceae)	P/A					2		
S <i>Retitriletes</i> spp. ( <i>Lygodium</i> )	P/A	102	24		86	46	56	18
S <i>Radialisporis radiatus</i> (Krutzsch) Jansonius et Hills (Lygodiaceae/Parkeriaceae)	P	1			1	3		2
S <i>Rugulatisporites quintus</i> Pflug et Thomson ( <i>Osmunda</i> )	P/A	7	1		8	6	29	
S <i>Toroisporis</i> sp. (?Cyatheaceae/?Lygodiaceae)	P	1			1			
S <i>Verrucatisporites favus</i> (Potonié) Thomson et Pflug (Dennstaedtiaceae)	P/A						1	
G <i>Abiespollenites</i> spp. ( <i>Abies</i> )	A	22			1	18	5	8
G <i>Cedripites</i> spp. ( <i>Cedrus</i> )	A1	146	14		64	46	54	10
G <i>Inaperturopollenites</i> spp. (Cupressaceae)	A1					22		
G cf. <i>Keteleeripollenites</i> sp. (? <i>Keteleeria</i> )	A1					1		
G <i>Laricispollenites</i> sp. ( <i>Larix/Pseudotsuga</i> )	A	1						
G <i>Piceapollis</i> spp. ( <i>Picea</i> )	A	164	12		74	396	75	24
G <i>Pinus haploxyton</i> type/ <i>Cathayapollis</i> spp. (Pinaceae, <i>Pinus</i> , <i>Cathaya</i> )	A1	660	234		306	738	330	132
G <i>Pinuspollenites</i> spp. - <i>Pinus sylvestris</i> type (Pinaceae, <i>Pinus</i> )	A	2316	372		1064	1524	654	162
G <i>Sciadopityspollenites</i> spp. ( <i>Sciadopitys</i> )	A1	10	1		6	124	25	3
G <i>Sequoiapollenites</i> spp. ( <i>Sequoia</i> ? <i>Cryptomeria</i> )	A1		1			10		
G small bisaccates indet. (corroded)	A?	708	1380	5	2790	34	159	2940
G <i>Zonalapollenites</i> sp. ( <i>Tsuga</i> )	A1	24	1		1		15	3
An <i>Diervillapollenites</i> sp. ( <i>Diervilla</i> / <i>Weigela</i> )	A2					1		
An <i>Ericipites ericius</i> (Potonié) Potonié + <i>E. callidus</i> (Potonié) Krutzsch (Ericaceae)	A	3	1			1	3	1
An <i>Ericipites roboreus</i> (Potonié) Krutzsch (Ericaceae, <i>Rhododendron</i> )	A		2			1		
An <i>Intratrirporipollenites microreticulatus</i> Mai (Malvaceae, <i>Tilioideae</i> )	A		1					
An <i>Lonicerapollis gallwiti</i> Krutzsch (Caprifoliaceae, <i>Lonicera</i> )	A1	1						
An ? <i>Pistillipollenites mcgregori</i> Rouse (?Flacourtiaceae/?Gentianaceae)	P				1			
An <i>Quercoidites</i> sp. ( <i>Quercus</i> )	P/A						1	
An ? <i>Saxonipollis</i> sp. (?Droseraceae/? <i>Aldrovanda</i> )	P				1			
An <i>Tricolporipollenites</i> sp.	?				2		1	
V Varia (pollen and spores indet.)	?		1				2	
V Mesozoic palynomorphs	X							1
V Paleozoic palynomorphs	X		1					
P <i>Botryococcus</i> cf. <i>neglectus</i> (West et West) Komarek et Marven	X	1						
P <i>Sigmopollis</i> sp. (fresh-water plankton, ?Cyanophyta)	X	3						
F Microthyriaceae indiff.	X					2	1	
<b>SUM</b>		<b>4483</b>	<b>2105</b>		<b>8 4627</b>	<b>3060</b>	<b>1487</b>	<b>3384</b>



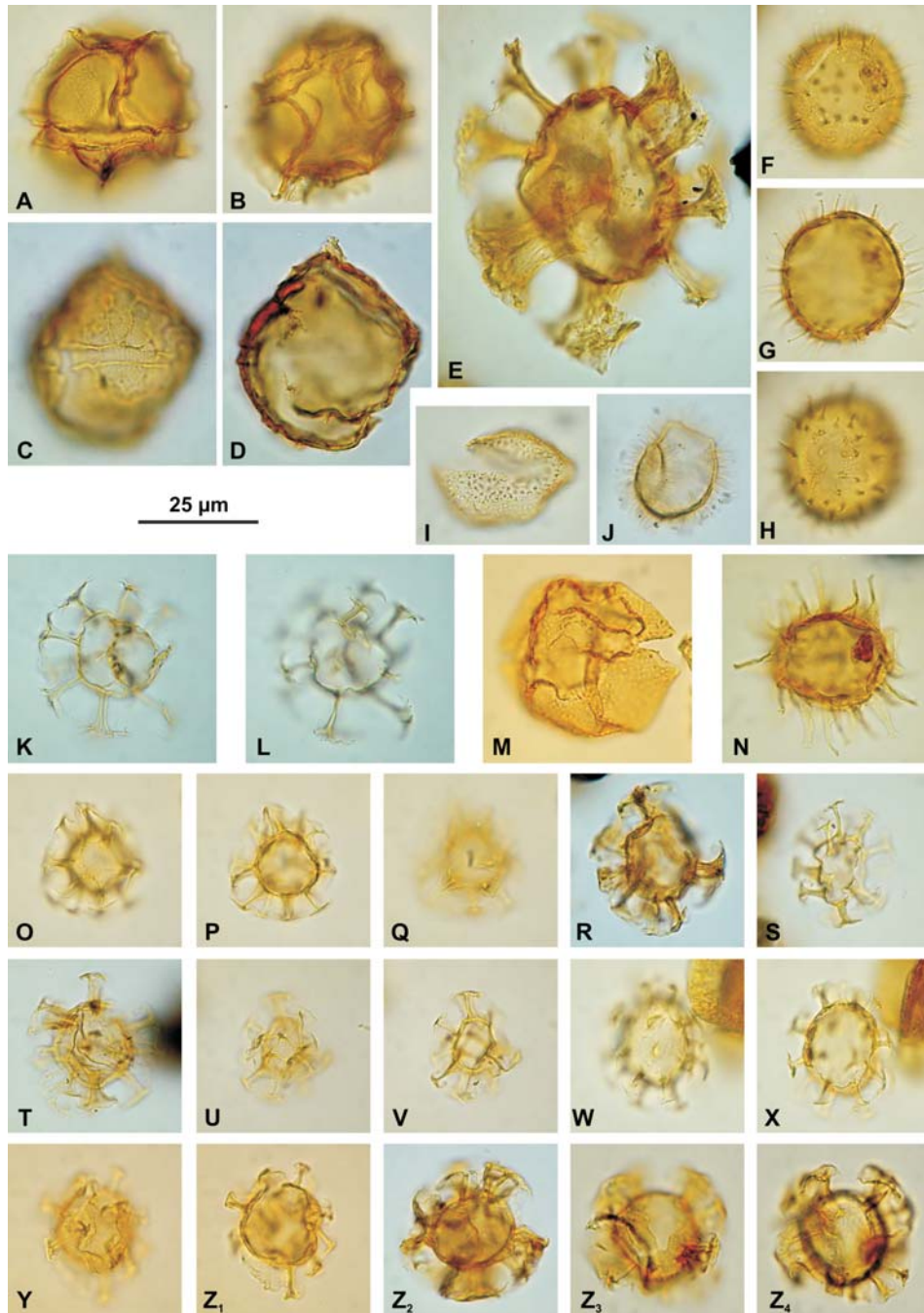


Fig. 11. Dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A, B.** *Pentadinium taeniagerum* (same specimen, various foci; sample 810). **C, D.** *Cribroperidinium tenuitabulatum* (same specimen, various foci; sample 814A). **E.** *Cordosphaeridium cantharellum* (sample 814A). **F–H.** *Operculodinium centrocarpum* (same specimen, various foci; →



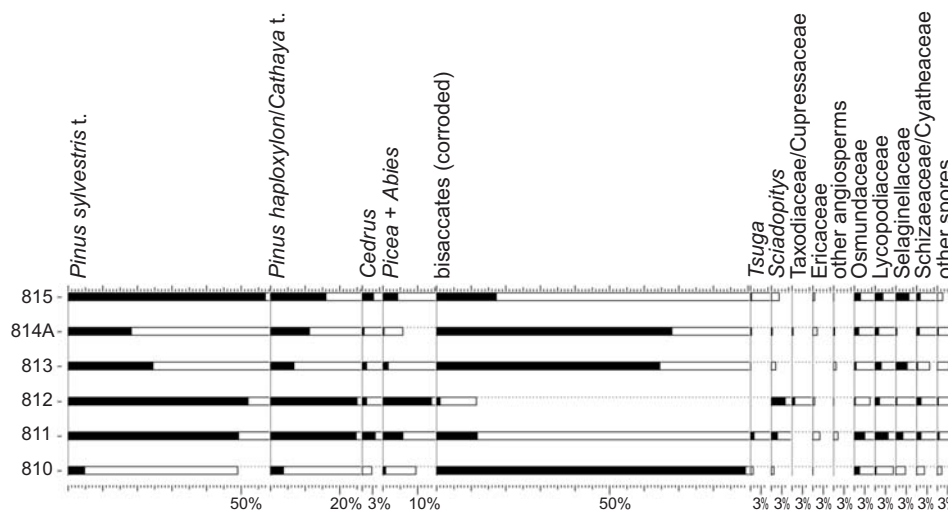


Fig. 12. Percentage diagram of selected pollen and spore taxa from the Krabbedalen Formation at Savoia Halvø (central East Greenland).

*Neogenisporis neogenicus* Krutzsch, *Neogenisporis* sp., *Radialisporis radiatus* (Krutzsch) Jansonius et Hills, *Toroisporis* sp., and *Verrucatosporites favus* (Potonié) Thomson et Pflug], occur rather occasionally. Some of them (*Cicatricosisporites* sp., *Corrugatisporites* cf. *graphicus*, *Leiotriletes wolffii*, *L. maxoides/maximus*, *Leiotriletes* sp., *Neogenisporis neogenicus*, *Neogenisporis* sp., *Radialisporis radiatus*, and *Toroisporis* sp.) represent the palaeotropical (P) geofloristic element.

**Pollen of gymnosperms.** — Bisaccate pollen grains are the most numerous among the sporomorphs in the sediment in question. The following taxa have been distinguished: *Pinus sylvestris* type [mainly *Pinuspollenites labdacus* (Potonié) Raatz ex Potonié], *Pinus haploxylon* type/*Cathayapollis* spp., *Picea* (*Piceapollis*), *Cedrus* [mainly *Cedripites parvisaccatus* (Zauer) Krutzsch, and *Cedripites* sp.], *Abies* (*Abiespollenites*), and others. Some bisaccate pollen grains are included into „small bisaccates” group, which includes corroded, difficult to determine specimens, probably, at least partly, recycled. Pollen grains of this group could represent the morphological genus *Pinuspollenites*, as well as *Cedripites*, *Cathayapollis* or others.

sample 811). **I.** *Mendicodinium* sp. A of Wrenn and Kokinos (1986; sample 811). **J.** *Operculodinium hirsutum* (sample 811). **K, L.** *Reticulatosphaera?* sp. (same specimen, various foci; sample 812). **M.** *Mendicodinium* sp. A of Wrenn and Kokinos (1986; sample 810). **N.** *Dapsilidinium* sp. (sample 814A). **O–Q.** *Cordosphaeridium minimum* (same specimen, various foci; sample 812). **R.** *Cordosphaeridium minimum* (sample 814A). **S.** *Cordosphaeridium minimum* (sample 811). **T.** *Cordosphaeridium minimum* (sample 812). **U, V.** *Cordosphaeridium minimum* (same specimen, various foci; sample 812). **W, X.** *Cordosphaeridium minimum* (same specimen, various foci; sample 811). **Y, Z<sub>1</sub>.** *Cordosphaeridium minimum* (same specimen, various foci; sample 810). **Z<sub>2</sub>.** *Cordosphaeridium minimum* (sample 814A). **Z<sub>3</sub>, Z<sub>4</sub>.** *Cordosphaeridium minimum* – specimen with apical archaeopyle (same specimen, various foci; sample 814A).

Pollen grains related to the family Pinaceae are well represented in the Cenozoic Arctic palynofloras (*e.g.* Boulter and Manum 1989, 1996), where at least 5 groups (biorecords) of bisaccate pollen are distinguished. Unfortunately, this morphological division is not synonymous with their botanical affinity (for example, “straight bisaccate” may include pollen grains of the genera *Pinus*, *Picea*, and *Cedrus* – see Boulter and Manum 1989). These most common pollen grains come from trees producing pollen in large quantities that are well equipped for long-distance dispersal in the air and water.

Among non-bisaccate pollen grains of conifers, including *Sciadopitys* [mainly *Sciadopityspollenites verticillatiformis* (Zauer) Krutzsch, and *Sciadopityspollenites* sp.], *Tsuga* (*Zonalapollenites* sp.), Cupressaceae [*Inaperturopollenites* spp., *Sequoia* (mainly *Sequoiapollenites rotundus* Krutzsch and *Sequoiapollenites* sp.) and others, are present. Pollen grains of *Sciadopitys* and *Tsuga* are well known from the Tertiary of the Arctic (Manum 1962; Head *et al.* 1989a; Boulter and Manum 1989, 1996; Jolley 1998).

Pollen grains of Cupressaceae are generally less frequent in the Tertiary Arctic palynofloras than in swamp spectra from lower latitudes, but (especially in the Palaeogene palynofloras) they are of various forms. In addition, macroremains of these plants [*e.g.* *Metasequoia occidentalis* (Newberry) Chaney, *Glyptostrobus dunoyeri* (Baily) Boulter *et* Kvaček, *Cupressoconus machenryi* (Baily) Boulter *et* Kvaček, and *Elatocladus campbellii* (Forbes) Seward *et* Holtum – close to *Sequoia* (Boulter and Kvaček 1989)] are also known from the former area. From the Arctic Tertiary, macroremains of *Pinus* are also known (Boulter and Kvaček 1989). Well preserved cones, leaves, twigs and wood fragments of *Metasequoia* and *Glyptostrobus*, accompanied by representatives of the Pinaceae family (*Pinus*, *Picea*, *Abies*, and *Larix*) were found in the Middle Eocene sediments on Axel Heiberg Island, Arctic Canada (Basinger *et al.* 1988; Jahren 2007). From the same locality numerous pollen grains of *Metasequoia* and *Glyptostrobus* types, as well as pollen of Pinaceae (*Picea*, *Abies*, and *Pinus*) were reported (Richter and LePage 2005). In addition, fossil *Cathaya* pollen (*Cathaya gaussenii* Sivak) from the Eocene of Axel Heiberg Island was reported, and its identification was confirmed by means of scanning electron microscopy (Liu and Basinger 2000). Pollen grains of this type of structure were often misidentified as *Abietineaepollenites*, *Pinus haploxylon* type, *Pityosporites*, *Podocarpus*, and *Podocarpidites* (Sivak 1976; Liu and Basinger 2000). In our material, pollen grains of the genus *Cathayapollis* were encountered in all studied samples.

**Pollen of angiosperms.** — In the studied material, pollen grains of angiosperms are very rare – only a few taxa were found. Ericaceous tetrads [*Ericipites ericius* (Potonié) Potonié, *E. callidus* (Potonié) Krutzsch, and *E. roboreus* (Potonié) Krutzsch] occur in five samples (810, 811, 812, 814A, and 815). The morphological genus *Ericipites* is well known from the Arctic Tertiary (*e.g.* Boulter and Manum 1989, 1996; Jolley 1998).

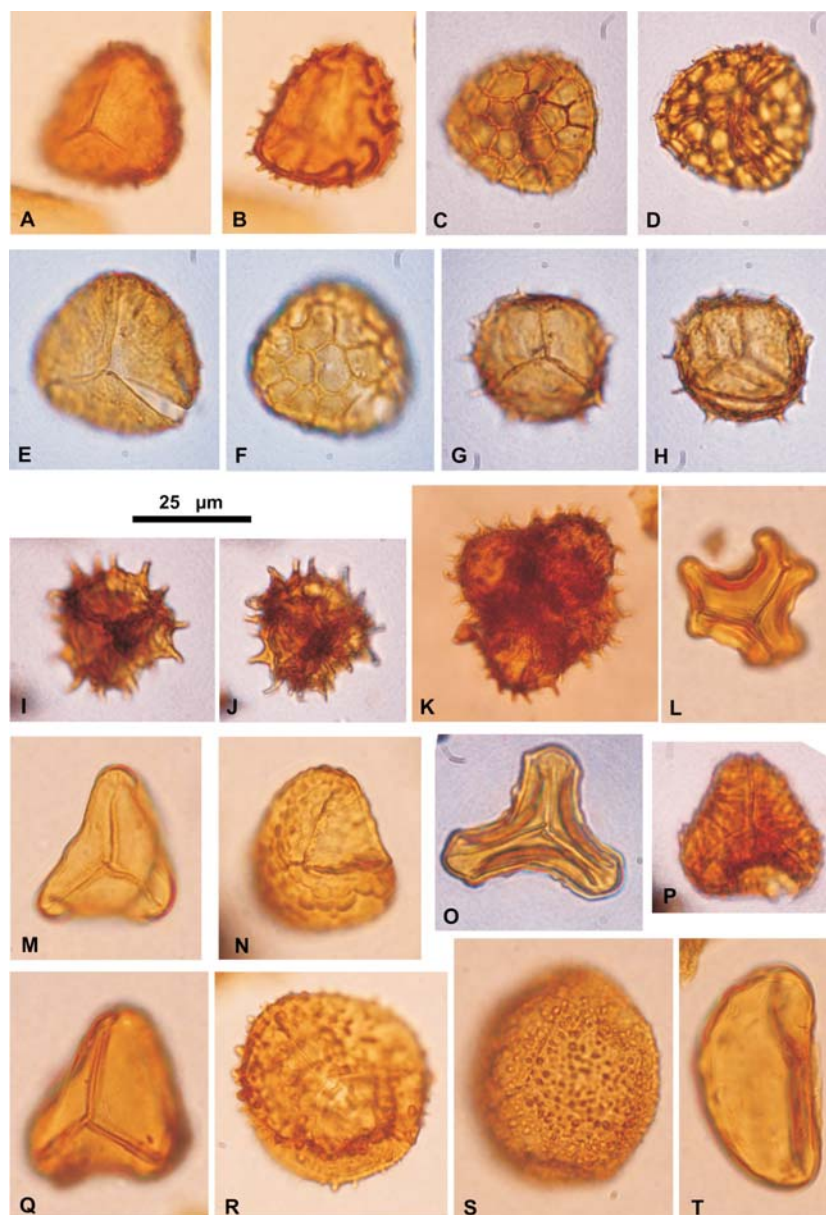


Fig. 13. Spores from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A, B.** *Retitriletes annotinioides* (same specimen, various foci; sample 812). **C, D.** *Retitriletes lusaticus* (same specimen, various foci; sample 815). **E, F.** *Retitriletes frankfurtensis* (same specimen, various foci; sample 813). **G, H.** *Echinatisporis* sp. (same specimen, various foci; sample 812). **I, J.** *Echinatisporis miocenicus* (same specimen, various foci; sample 812). **K.** *Echinatisporis* sp. – tetrad (sample 812). **L.** cf. *Concavisporites* sp. (sample 812). **M.** *Leiotriletes* sp. (sample 812). **N.** *Cryptogrammasporis* sp. (sample 812). **O.** *Neogenisporis* sp. (sample 812). **P.** *Radialisporis radiatus* (sample 815). **Q.** *Leiotriletes wolffii* (sample 812). **R.** *Baculatisporites primarius* (sample 811). **S.** *Rugulatisporites quintus* (sample 811). **T.** *Laevigatosporites nitidus* (sample 812).

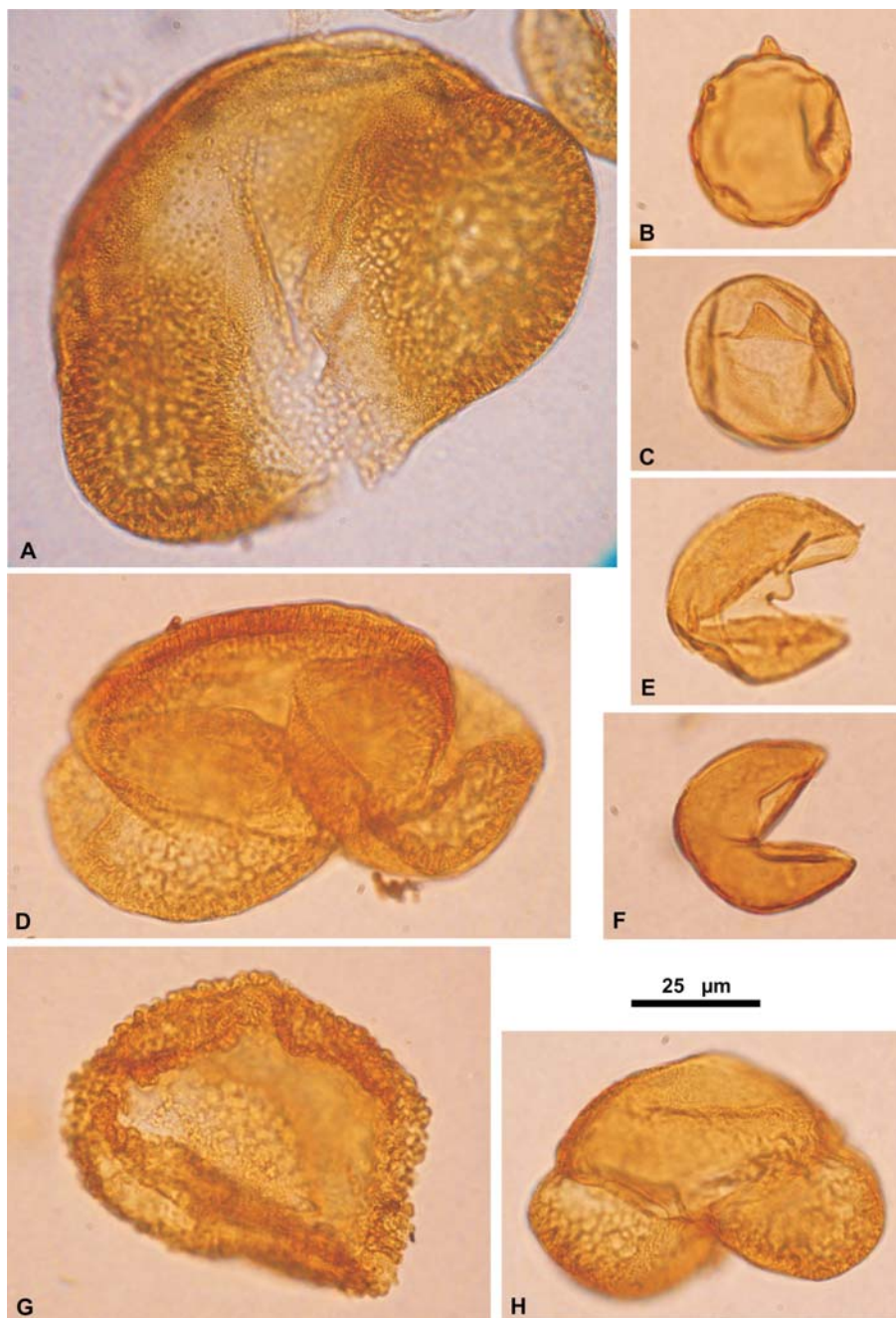


Fig. 14. Pollen grains from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A.** *Piceapollis tobolicus* (sample 812). **B.** *Sequoiapollenites rotundus* (sample 812). **C.** *Sequoiapollenites* sp. (sample 812). **D.** *Abiespollenites absolutus* (sample 812). **E.** *Inaperturopollenites verru-papillatus* (sample 812). **F.** *Inaperturopollenites dubius* (sample 812). **G.** *Zonalapollenites* sp. (sample 811). **H.** *Pinuspollenites labdacus* (sample 812).



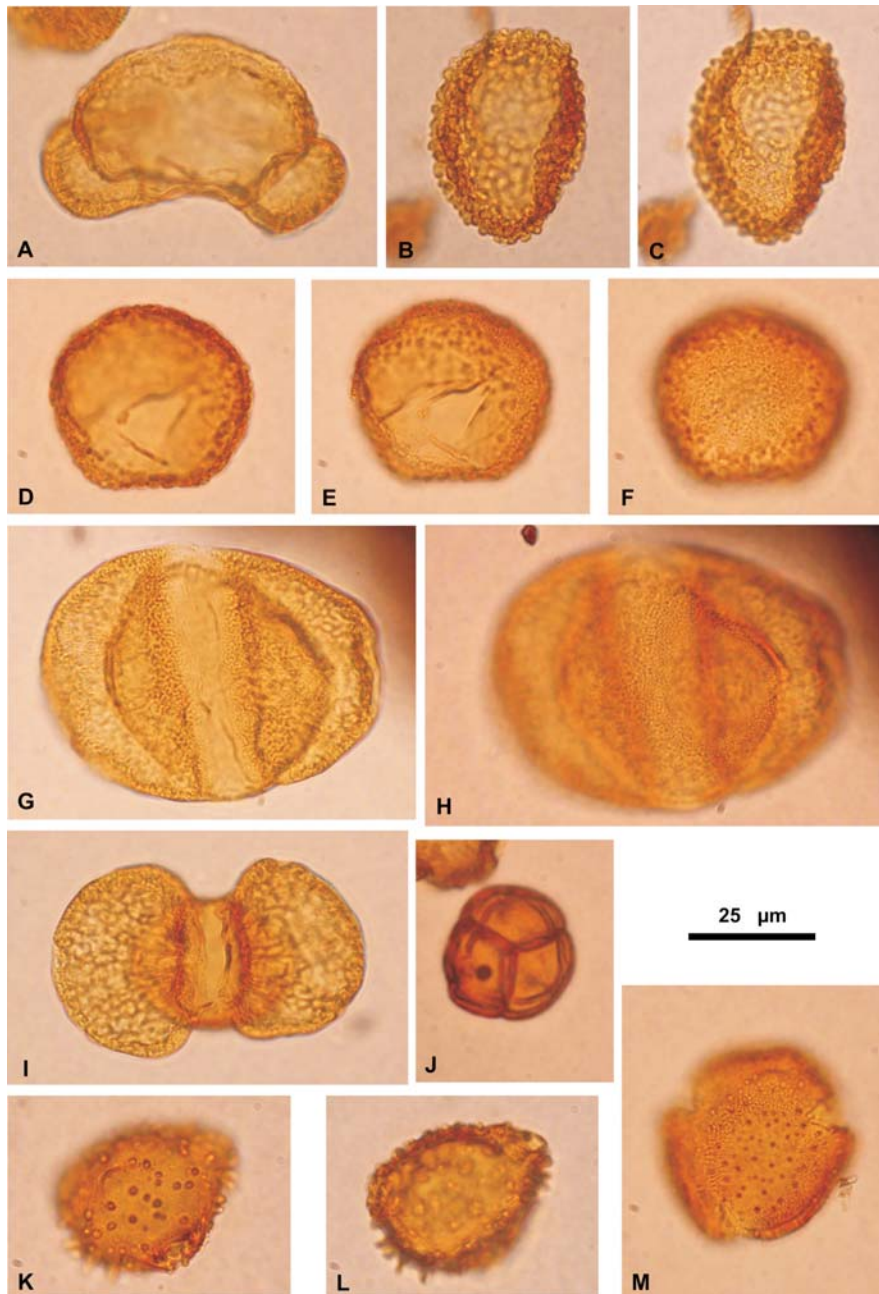


Fig. 15. Pollen grains from the Krabbedalen Formation at Savoia Halvø (central East Greenland). **A.** *Cedripites parvisaccatus* (sample 812). **B, C.** *Sciadopityspollenites verticillatiformis* (same specimen, various foci; sample 812). **D–F.** *Sciadopityspollenites tubulus* (same specimen, various foci; sample 812). **G, H.** *Cathayapollis wilsonii* (same specimen, various foci; sample 811). **I.** *Cathayapollis pulaensis* (sample 811). **J.** *Eriopites ericius* (sample 810). **K, L.** *Diervillapollenites* sp. (same specimen, various foci; sample 812). **M.** *Lonicerapollis gallwitzi* (sample 815).



**Fungi (Microthyriaceae).** — In the studied material, 3 various specimens of sporocarps of the Microthyriaceae epiphyllous fungi were found (in samples 811 and 812). Recently, these fungi are usually ectoparasites extended in tropical and subtropical regions. Some of them occur in sub-polar regions. Their presence is an important palaeoecological indicator of high total annual rainfall – above 1000 mm. They usually live on leaves of seed plants (conifers and others) as well as on ferns and mosses. Some of them could live on fallen leaves (Elsik 1978). According to Elsik (1978) and there cited authors, the oldest fossil microthyriaceous fungi were found in the Lower Cretaceous strata, being most numerous in the Eocene and Miocene ones.

### Palaeoflora and plant communities

It is difficult to reconstruct the type of northern subarctic palaeofloras, because there are no modern equivalents of the Tertiary palaeoenvironment of the Arctic (see Boulter and Manum 1996). According to earlier studies (Basinger *et al.* 1994; Boulter and Manum 1996), the climate was then temperate with periodic light reduction (a few months of reduced light and even darkness each year). These conditions surely demanded a special physiology and lifestyle for their inhabitants.

Composition of pollen spectra from sediment in question (dominated by bisaccate pollen) points at the presence of coniferous forests dominated by *Pinus* species, accompanied by *Picea*, Cupressaceae and others, with a minor share of angiosperms. Presence of spores shows an important role of ferns, Lycopodiaceae and Selaginellaceae. Probably the forests understory was composed of these plants, or they grew on open areas and at the edges of open water. Similar fossil plant communities were described from other Tertiary Arctic localities (Boulter and Fisher 1994 in Boulter and Manum 1996).

The state of preservation of some sporomorphs (*e.g.* spores *Echinatisporis* in tetrads) in our samples suggests that the distance to the terrestrial source was relatively short.

### Comparison with other palynofloras of Northern Subarctic

The studied palynoflora distinctly differs from the Paleocene–Eocene flora of Brito-Arctic Igneous Province, which is rich both in conifers and angiosperms (Boulter and Manum 1989). Also the Early Eocene palynofloras (Holes 916A and 918D) of East Greenland are distinctly richer, being dominated by *Inaperturopollenites hiatus* and various angiosperms. They contain some megatherm taxa and a high proportion of palaeotropical forms typical for the Eocene temperature maximum (Jolley 1998).

Spore-pollen assemblages from the Upper Paleocene and possibly Lower Eocene deposits from Spitsbergen are also dominated by conifers and ferns, with

moderate values of angiosperms. Although the conifers and ferns prevail, the angiosperm pollen are much more diverse – with taxa indicating a moderately warm-temperate climate (Norris and Head 1985). Similar Late Eocene spore-pollen assemblages (which point at warm-temperate climate) are also known from the Beaufort-Mackenzie Basin of western Arctic Canada (Norris and Head 1985).

The Middle Eocene palynoflora from Axel Heiberg Island, Canadian High Arctic (Richter and LePage 2005) is also distinctly richer in angiosperms (mainly *Alnus*, *Pterocarya*, *Juglans*, and *Quercus*). This site was studied using a high-resolution (detailed) palynological analysis. The pollen data show successional processes and suggest that the local vegetation reflected climatic and environmental changes. This palynoflora was dominated by members of the Pinaceae family (mainly *Picea* and *Abies*) when the area was relatively dry, whereas *Metasequoia* type (*Inaperturopollenites*) was predominant when local environmental conditions were more humid. So, fluctuations of share of the broad-leaved deciduous forests and *Metasequoia*-dominated swamp forest communities were observed (Richter and LePage 2005).

The share of angiosperms considerably decreased from the Eocene to the Oligocene. The declining climatic conditions and taxonomic decimation were caused by the global fall in temperature after the Terminal Eocene Event (Boulter and Manum 1996). The decrease of species diversity and disappearance of thermophilic taxa, indicating cooling of climate, is well recorded in many Arctic palynofloras.

The most similar to our results of pollen analysis have been shown by Boulter and Manum (1996) from the Oligocene and Miocene deposits from the Hovgård (Hovgaard) Ridge (Greenland Sea); especially from its Oligocene part. The pollen spectra are dominated there by bisaccate pollen (mainly of *Pinus*, *Picea*, and *Cedrus* types), accompanied by pollen of *Tsuga*, *Sciadopitys*, and some Taxodiaceae (= Cupressaceae). Angiosperms are represented by a few taxa and several specimens (mainly Ericaceae). In addition, spores are quite common (mainly *Baculatisporites*, *Polypodiaceasporites*, *Cyathidites*, *Lycopodiumsporites*, and *Gleicheniidites*). Spores from the same groups were found in our material.

Also the Middle Oligocene spore-pollen assemblages from Sarsbukta (Spitsbergen) are dominated by bisaccates, with a low share of angiosperms – both in terms of diversity and relative frequency (Manum 1962; Boulter and Manum 1996).

Similar pollen and spore assemblages are also described from the Miocene (Early and early Middle Miocene) of Baffin Bay (Head *et al.* 1989a). These pollen spectra consist mainly of coniferous tree pollen (*Pinus*, *Picea*, and *Tsuga* – making up about 50% of the sporomorphs) and trilete fern spores. Other pollen and spore taxa are present in small numbers. There are mainly warm-to-cool temperate forest species. In addition, isolated specimens of *Radialisporis radiatus*, *Reticulosporis* spp. (Lycopodiaceae), *Favoisporites trifavus*, *Saxonipollis* sp., and other taxa that range down into the Early Palaeocene of the Canadian Arctic occur. A similar situation was observed in the studied material. These sporomorphs might be reworked, although their state of preservation in both materials suggests that they are *in situ*.

During Pliocene and Pleistocene, the Arctic vegetation became enriched in non-arboreal plant pollen and spores. The Upper Pliocene to Holocene sediments, *e.g.* from Baffin Bay, contain more herbaceous pollen. These assemblages are largely dominated by *Pinus*, accompanied by *Betula* (probably shrub taxa), *Alnus* and Ericaceae, as well spores of Polypodiaceae ferns, *Lycopodium* and *Selaginella*. In addition, the high *Sphagnum* shares indicate the existence of extensive peatlands (de Vernal and Mudie 1989). Similar spore-pollen assemblages can be observed in the Pliocene–Pleistocene deposits from the Yermak Plateau, Arctic Ocean (Willard 1996). In contrast to our material, modern spore-pollen spectra from Spitsbergen, northern Greenland and Iceland are dominated by nonarboreal taxa, small angiosperms, with low percentages of such bisaccates as *Pinus* pollen (Willard 1996).

### Age interpretation

Pollen and spores found in our material are of limited biostratigraphic value. The marine spectra reflect changes of local vegetation (succession of plant communities, changes of climate – temperature, moisture, and light level), as well as distance from the source (forested) area, rather than their real age. Therefore we focused on age-interpretation of dinoflagellate cyst assemblages, which have been extensively studied for decades from the Tertiary of the northernmost Atlantic (*e.g.* Manum 1976; Manum *et al.* 1989; Firth 1996; Poulsen *et al.* 1996; Williams and Manum 1999; Nøhr-Hansen and Piasecki 2002; Eldrett *et al.* 2004; see also Damassa *et al.* 1990). Additionally, data of dinoflagellate cyst zonation schemes (*e.g.* Heilmann-Clausen and Costa 1990; Köthe 1990; Powell 1992; Van Simaey *et al.* 2005a) or stratigraphic ranges of particular species (*e.g.* Köthe and Piesker 2007) from north-western Europe can be compared, although due to significant differences in taxonomical composition between these two areas (see *e.g.* Williams and Manum 1999), their value may be slightly limited. Former studies on Palaeogene dinoflagellate cysts from the Greenland Sea and the Norwegian Sea were based mainly on material from mid-oceanic boreholes. Our material comes from exposures on Greenland, and may represent a different sedimentological setting than those mentioned above, since northernmost Atlantic area is believed to represent several isolated basins separated from oceanic circulation during early stages of its history (*e.g.* Thiede and Myhre 1996).

The majority of dinoflagellate cyst species from the Krabbedalen Formation at Savoia Halvø is known from Eocene (mainly Late Eocene) and Early Oligocene of lower latitudes. This refers to *e.g.* *Phthanoperidinium comatum* (Fig. 10B–H), *Cribooperidinium tenuitabulatum* (Fig. 11C, D), *Pentadinium laticinctum* (Fig. 5R–U), *Glaphyrocysta semitecta* (Fig. 4A–K), and *Lentinia serrata* (Fig. 9I–P). Comparison of taxonomical composition of our assemblages to those from North Atlantic, also shows some similarities to assemblages described from both Eocene

and Oligocene sites by previous authors, and makes unanimous age interpretation difficult. Moreover, some of our dinoflagellate cysts are also known from Oligocene–Miocene of northern Atlantic. Thus, a Miocene age of the Krabbedalen Formation, although less precisely documented, cannot be excluded. The sporomorph data do not contradict such a young age.

Two basal samples, 810 and 811, yielded frequent specimens of well preserved *Glaphyrocysta semitecta* (Fig. 4A–K). This species so far have not been reported from Oligocene strata of the North Atlantic. It is known to have occurred in lower latitudes during Bartonian–early Rupelian (Bujak *et al.* 1980; Brinkhuis 1992, 1994). In the same basal interval (samples 810, 811), *Corrudinium incompositum* (Fig. 7U–Y) occurs. This species is known from the Greenland–Norwegian seas from Eocene only (Manum *et al.* 1989; Firth 1996), while it is present in Oligocene strata in lower latitudes (*e.g.* Haq *et al.* 1987).

Another species present in our material and reported from the Eocene of higher latitudes is *Lentinia serrata* (Fig. 9I–P), being also known from Bartonian–mid Rupelian strata of lower latitudes (Bujak *et al.* 1980; Brinkhuis 1992, 1994). Manum *et al.* (1989) reported *Lentinia serrata* and *Lentinia wetzelii* from Lower Eocene strata of the Norwegian Sea (possibly one of these species represents *Deflandrea* sp. 1 from Lower Eocene, figured by Manum 1976, pl. 4.21). Also Firth (1996) reports both species from Eocene strata of the Greenland Sea only, but in that case, Oligocene interval was very poorly sampled.

Much younger, Oligocene age of the basal sample 810, could be suggested by the presence of *Spiniferella cornuta* (Fig. 6C–E) known from Rupelian– Chattian of the northernmost Atlantic (Poulsen *et al.* 1996; Williams and Manum 1999; see also Benedek 1972). However, Damassa *et al.* (1990) report Priabonian age range of this species in the North Atlantic.

Oligocene age of our Krabbedalen Formation section could be assumed on the base of occurrence of a species Dinoflagellate cyst sp. A (Fig. 10I–L) in samples 810, 811, and 814A. This species resembles Dinoflagellate cyst 3 (*?Evittosphaerula* sp. 1) of Manum *et al.* (1989, pl. 8.3, 4) described from Rupelian strata of the Norwegian Sea (see also Williams and Manum 1999). *?Evittosphaerula* sp. 1 of Manum *et al.* (1989) was later synonymized with a newly described species *Piccoladinium fenestratum* by Versteegh and Zevenboom (1995). Interestingly, this species was formally described from Upper Pliocene of Sicily, Italy (Versteegh and Zevenboom 1995) whereas *?Evittosphaerula* sp. 1 (and, possibly representing the same species, our Dinoflagellate cyst sp. A) was described from (mid?) Oligocene of the Norwegian Sea (Manum *et al.* 1989) and Greenland (this paper). No record of similar morphotype has so far been reported from the interval between Oligocene and Pliocene.

Another species, which also frequently occurs in our material, is *Cordosphaeridium minimum*. It possesses a precingular archaeopyle and processes that are not united distally, showing only indistinct ridges connecting process bases (Fig. 11O–Q, T–V). Some specimens, however, are larger. They possess massive pro-

cesses and low membranes that proximally connect the processes (Fig. 11R, Z<sub>2</sub>). Moreover, one specimen (Fig. 11Z<sub>3</sub>, Z<sub>4</sub>) possesses an apical archaeopyle. This makes this taxon similar to the *Labirynthodinium truncatum* subs. *truncatum* described by de Verteuil and Norris (1996) from Middle Miocene of eastern USA. However, Manum (1976) described similar morphotypes, with both apical (Dinocyst V; Manum 1976, pl. 4.5) and presumably precingular archaeopyle (Dinocyst II; Manum 1976, pl. 2.19), from “mid” Oligocene–Middle Miocene and Middle Eocene–Lower Miocene intervals, respectively.

*Batiacasphaera minuta* (Fig. 7A–E) is another species that is frequently described from Miocene strata (see Matsuoka and Head 1992). However, this species is not a good age indicator due to its similarity to other taxa. It has been presumably described also from Palaeogene strata under other taxonomical names, e.g. *Tectatodinium* sp. of Matsuoka (1974) or some representatives of the *Batiacasphaeral Cerebrocysta* group A *sensu* Head *et al.* (1989b; see Matsuoka and Head 1992, p. 168). Manum *et al.* (1989) described *Batiacasphaera minuta* from Oligocene–Lower Miocene interval of the Norwegian Sea.

*Pyxidinospis* sp. 1 *sensu* Manum *et al.* (1989), a species found in samples 810 and 814A (Fig. 7F–J), was described from “mid” Oligocene–Lower Miocene (Manum *et al.* 1989, pl. 3.7) and Rupelian–Burdigalian (Williams and Manum 1999, p. 106, pl. 2.9a–b) strata of the Norwegian Sea.

An indirect clue leading to acceptance of an Oligocene age of the Krabbedalen Formation could be the rarity of Wetzelielloideae in our material (frequently occurring in Palaeogene strata of lower latitudes), which resembles their scarcity in Oligocene of the northernmost Atlantic (e.g. Costa and Downie 1979; Firth 1996). Only two specimens of *Wetzeliella* sp. and *Charlesdowniea* sp. (Fig. 8E and Fig. 8A, B, respectively) have been found in sample 813. Three specimens of *Apectodinium* sp. (Fig. 8N, O) occur in samples 811–813 (Table 2). Representatives of *Deflandrea*, a typical Palaeogene genus, occur as single, poorly preserved specimens only (Fig. 8C, D, F; Table 2). This genus is also rare in Oligocene sequences previously studied from the northernmost Atlantic (e.g. Manum *et al.* 1989; Firth 1996).

Another characteristic feature of our assemblage from the Krabbedalen Formation is the lack of *Chiropteridium*, a genus, which was frequently reported from higher Rupelian–Chattian strata of north Atlantic (Manum *et al.* 1989; Poulsen *et al.* 1996). Its absence may indicate both Eocene and/or earliest Rupelian age of the studied assemblage. However, it should be noted that Upper Eocene and presumably lowermost Oligocene strata were missing or strongly impoverished in the material studied by Manum *et al.* (1989, p. 615), Firth (1996, p. 203) and Poulsen *et al.* (1996). This may explain an “absence” of several species in basal Oligocene sequence of the Norwegian and Greenland seas.

The age-interpretation of sporomorph assemblages suggest a wide time-span for the Krabbedalen Formation, spanning Oligocene through Middle Miocene. The studied pollen spectra are largely dominated by bisaccate pollen (mainly



*Pinuspollenites*), which are always over-represented in marine sediments due to high pollen productivity of *Pinus* trees, and because its morphology is favourable for long-distance atmospheric and hydrologic (buoyancy) transportation. In addition, plant evolution and migration during Tertiary at high latitudes were less active than farther south, and the changes of flora and vegetation were more gradual. As a consequence, the differences between spectra of different ages are less distinct at higher latitudes (Boulter and Manum 1996).

The studied spectra are most similar to the Middle Oligocene spectra from Sarsbukta, Spitsbergen (Manum 1962), the Oligocene–Miocene spectra from the Hovgård Ridge on the Greenland Sea (Boulter and Manum 1996), and the Miocene (Early and early Middle Miocene) spectra from the Baffin Bay (Head *et al.* 1989a). They are dominated by conifers (mainly *Pinus*), with very low share of angiosperms, and are relatively rich in spores (including some palaeotropical taxa). They also lack such elements as *Sphagnum*, herbaceous angiosperms, as well as *Betula* and *Alnus* pollen. Therefore, the results of the spore-pollen analysis point at an Oligocene to Middle Miocene age-range of the studied material.

A supposition of a Lower Miocene age of the described section, would mean that a majority of the described specimens, especially frequently occurring species such as *Glaphyrocysta semitecta*, *Lentinia serrata*, *Phthanoperidinium comatum*, and also less common species *Spiniferella cornuta*, and *Corrudinium incompositum*, could be treated as recycled. This would indicate an intense reworking of Palaeogene strata in Greenland, similar to the one noted by Williams and Manum (1999) from Oligocene–Lower Miocene of the Norwegian Sea. However, this age-interpretation is based on a vague material composed of taxa known also from the Oligocene. We did not find any true Miocene indicators among the species determined from the Krabbedalen Formation.

### Pre-Tertiary recycled taxa

The Krabbedalen Formation yielded a few recycled Cretaceous dinoflagellate cysts. These are single specimens of *Litosphaeridium* sp., *Subtilisphaera* sp., *Circulodinium* sp. and *Oligosphaeridium* sp., all found in sample 813. Additionally, poorly preserved *Palaeoperidinium?* sp. (Fig. 10M, N) was found in sample 814A. Their presence indicates erosion of Cretaceous strata in Greenland (see, *e.g.* Nøhr-Hansen 1993, 1996). Recycling of Cretaceous species was also reported by Williams and Manum (1999) from Oligocene–Lower Miocene strata of the Norwegian Sea.

### Palaeoenvironment and palaeogeography

Our results show overwhelming domination of terrestrial palynomorphs over marine ones in the sediments in question. The latter, represented almost exclu-

sively by dinoflagellate cysts, do not exceed 1–2% of palynofacies, being virtually absent in samples 813 and 815. So, infrequent occurrence of dinoflagellate cysts make them out of use in sense of statistical analysis. Nevertheless, their presence suggests a marine sedimentary setting with high influx of terrestrial organic matter, which may indicate land proximity. However, this interpretation contrasts with occurrence of the genus *Impagidinium*, which is known to prefer oceanic waters (*e.g.* Harland 1983; Marret and Zonneveld 2003). The sediments in question were deposited close to sea shore, in an environment with relatively narrow shelf area, within reach of oceanic water currents. This assumption may be supported by the fact that our material is completely devoid of *Homotryblum* specimens. This genus is believed to have been associated with very proximal shelf areas, lagoonal, often with increased salinity (*e.g.* Brinkhuis 1992). However, lack of *Homotryblum* in our material may be caused by East Greenland palaeo-shoreline and oceanic circulation during deposition of sediments in question. Early Oligocene cold water masses of the East Greenland Current evidenced by Birkenmajer and Jednorowska (1997) could cause unfavourable conditions for motile stage of this genus. Cold-water conditions are evidenced by the presence of *Svalbardella* (Fig. 100–Q), a genus believed to had cold-water preferences (*e.g.* Van Simaeys *et al.* 2005b). *Homotryblum* is also rare (*e.g.* Firth 1996) or absent (*e.g.* Poulsen *et al.* 1996) in Oligocene strata of the northern Atlantic basins.

Changes of dinoflagellate cyst frequency in our section may reflect slight fluctuations in shore proximity and/or terrestrial matter influx. Both may be associated with sea level fluctuations: the lowermost part of the section (samples 810–812) and the one represented by sample 814A, could be deposited during relative high-sea level phases. Intervals represented by samples 813 and 815, in turn, were presumably deposited during sea-level drop, followed by increased terrestrial influx due to increased land erosion that is indicated by appearance of recycled, presumably Cretaceous dinoflagellate cysts.

Tertiary strata of the Greenland and Norwegian seas, studied in more offshore settings, yielded differentiated palynological organic matters. In most cases, they contain much richer and more taxonomically diversified dinoflagellate cyst assemblages, especially in approximately coeval intervals (Manum 1976, fig. 2; Firth 1996).

## Selected dinoflagellate cyst taxonomy

In this chapter, several species have been described, with uncertain taxonomical position. This refers especially to small holocavate specimens, which resemble *Chlamydophorella* and *Habibacysta* in general morphology and wall features, but differ in archaeopyle type.

*Chlamydothorella?* sp. A

(Fig. 7K–O)

**Description.** — Cyst subspherical, slightly ovoidal, holocavate. Cyst wall composed of thin and solid endophragm covered by regularly distributed, closely spaced tiny processes, which seem to be united distally by thin ectophragm. Archaeopyle apical; operculum always attached. No expressions of paratabulation except of archaeopyle margin.

**Discussion.** — This species is assigned to the genus *Chlamydothorella* on the base of general morphology and wall structure; however, its always attached archaeopyle makes this assignment tentative. *Chlamydothorella?* sp. A shows similarity in cyst wall structure to the genus *Habibacysta*. Closely spaced tiny processes of the former species resemble columellate periphragm of *Habibacysta*.

*Habibacysta?* sp. A

(Fig. 7P–R)

**Description.** — Cyst subspherical, holocavate, with hardly distinguishable thin endophragm and thick columellate periphragm, distally united by rather discontinuous periphragm. Archaeopyle type uncertain, presumably formed by disruption of a single precingular paraplate, which remains attached. No indication of paratabulation.

**Comparison.** — This species diagnosis is similar to the generic diagnosis of *Habibacysta* as given by Head *et al.* (1989b), except of archaeopyle type, which in original diagnosis is formed by loss of a single precingular paraplate. Specimens described in this paper as *Habibacysta?* sp. A, similarly as *H.?* sp. B, possess archaeopyle of uncertain type, possibly formed by loss of precingular paraplate; opercula of both species remain attached. Thus, the discussed specimens from Savoia Halvø are tentatively assigned to the genus *Habibacysta*.

*Habibacysta?* sp. B

(Fig. 7S, T)

**Description.** — Cyst small, spherical, holocavate. Cyst wall composed of thin solid endophragm covered with irregularly spaced clusters. Archaeopyle type not certain, presumably precingular; operculum attached.

*Achomosphaera* sp. A

(Fig. 6I–K)

**Description.** — Tiny subspherical chorate cyst with central body bearing numerous processes connected proximally by very indistinct, partially not developed ridges. Cyst wall consists of slightly thicker, rather smooth or very finely granular endophragm, and thin and smooth periphragm. Wall layers remain in contact except of process bases. Processes presumably in gonal positions, mainly hollow, relatively wide at base, narrowing upwards, distally bifurcated. Some processes, especially in parasulcal area, may be solid. Archaeopyle not visible.

**Discussion.** — This species was included in the genus *Achomosphaera*, although it possesses proximal but not fully developed ridges.

*Reticulosphaera?* sp.  
(Fig. 11K, L)

**Remarks.** — This species resembles *Reticulosphaera actinocoronata* in general arrangement. Distal terminations of processes also show branching typical for *R. actinocoronata*. Processes in *Reticulosphaera?* sp. are hollow, whereas the ones in typical *Reticulosphaera* are solid.

*Alterbidinium* sp. A  
(Fig. 9A–E, G, H)

**Description.** — Dorso-ventrally compressed peridinioid cyst, rhomboidal pericyst, and ovoidal endocyst with one apical and two asymmetrical antapical horns. Endocyst remains in close contact with periphragm in hypocyst (except of antapical horns, where it is cornucavate). They are widely separated from each other in epicyst, forming a large epicavation. Endophragm without ornamentation, periphragm densely covered with granules, which frequently fuse with each other. Paracingulum and parasulcus developed as faint depressions, the former showing linear alignment of granules. Archaeopyle intercalary formed by loss of anterior intercalary paraplate, which remains attached.

Peridinioid sp. A  
(Fig. 9Q, R)

**Description.** — Small, elongated, dorso-ventrally compressed peridinioid, with rounded apical horn and two asymmetrical antapical horns. Large epipericoel present. On hypocyst, periphragm and endophragm are pressed except of horns. Periphragm finely striated. Archaeopyle not observed.

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## References

- BASINGER J.F., GREENWOOD D.R. and SWEDA T. 1994. Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. *In*: M.C. Boulter and H.C. Fisher (eds) *Cenozoic Plants and Climates of the Arctic. NATO Advanced Science Institutes Series 127*: 175–213.
- BASINGER J.F., MCIVER E.E. and LEPAGE B.A. 1988. The fossil forests of Axel Heiberg Island. *Musk-Ox* 36: 50–55.
- BENEDEK P.N. 1972. Phytoplankton aus dem Mittel- und Oberoligozän von Tönisberg (Niederrheingebiet). *Palaeontographica* B137: 1–71.
- BIRKENMAJER K. 1972. Report on investigations of Tertiary sediments at Kap Brewster, Scoresby Sund, East Greenland. *Grønlands geologiske undersøgelse, Rapport* 48: 85–91.



- BIRKENMAJER K. 2000. Faulting of Tertiary lavas and sediments at Savoia Halvø, East Greenland. *Polish Polar Studies, 27th International Polar Symposium* (Toruń): 153–158.
- BIRKENMAJER K. and JEDNOROWSKA A. 1977. Foraminiferal evidence for the East Greenland Current during the Oligocene. *Grønlands geologiske undersøgelse, Rapport 85*: 86–89.
- BIRKENMAJER K. and JEDNOROWSKA A. 1997. Early Oligocene foraminifera from Kap Brewster, East Greenland. *Annales Societatis Geologorum Poloniae* 67: 155–173.
- BOULTER M.C. and FISHER H.C. (eds) 1994. *Cenozoic Plants and Climates of the Arctic*. Springer Verlag, Heidelberg: 401 pp.
- BOULTER M.C. and KVAČEK Z. 1989. The Palaeocene flora of the Isle of Mull. *Special Papers in Palaeontology* 42: 1–149.
- BOULTER M.C. and MANUM S.B. 1989. The Brito-Arctic Igneous Province flora around the Palaeocene/Eocene boundary. In: O. Eldholm, J. Thiede, E. Taylor *et al.* (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 104: 663–680.
- BOULTER M.C. and MANUM S.B. 1996. Oligocene and Miocene vegetation in high latitudes of the north Atlantic: Palynological evidence from the Hovgård Ridge in the Greenland Sea (site 908). In: J. Thiede, A.M. Myhre, J.V. Firth, G.L. Johnson and W.F. Ruddiman (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 151: 289–296.
- BRINKHUIS H. 1992. *Late Eocene to Early Oligocene dinoflagellate cysts from central and northeast Italy*. Ph.D. thesis, University of Utrecht: 169 pp.
- BRINKHUIS H. 1994. Late Eocene to Early Oligocene dinoflagellate cysts from the Priabonian type-area (northeast Italy); biostratigraphy and palaeoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 121–163. [http://dx.doi.org/10.1016/0031-0182\(94\)90168-6](http://dx.doi.org/10.1016/0031-0182(94)90168-6)
- BUJAK J.P., DOWNIE C., EATON G.L. and WILLIAMS G.L. 1980. Dinoflagellate cysts and acritarchs from the Eocene of southern England. *Special Papers in Palaeontology* 24: 1–100.
- COSTA L.I. and DOWNIE C. 1979. Cenozoic dinocyst stratigraphy of Sites 403 to 406 (Rockall Plateau), IPOD, Leg 48. In: L. Montadert and D.G. Roberts (eds) *Initial Reports of the Deep Sea Drilling Project* 48: 513–529.
- DAMASSA S.P., GOODMAN D.K., KIDSON E.J. and WILLIAMS G.L. 1990. Correlation of Paleogene dinoflagellate assemblages to standard nannofossil zonation in North Atlantic DSDP sites. *Review of Palaeobotany and Palynology* 65: 331–339. [http://dx.doi.org/10.1016/0034-6667\(90\)90083-U](http://dx.doi.org/10.1016/0034-6667(90)90083-U)
- DE VERNAL A. and MUDIE P.J. 1989. Late Pliocene to Holocene palynostratigraphy at ODP Site 645, Baffin Bay. In: S.P. Srivastava, M. Arthur, B. Clement *et al.* (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 105: 387–399.
- DE VERTEUIL L. and NORRIS G. 1996. Miocene dinoflagellate stratigraphy and systematics of Maryland and Virginia. *Micropaleontology* 42, Supplement: 1–172.
- ELDRETT J.S., HARDING I.C., FIRTH J.V. and ROBERTS A.P. 2004. Magnetostratigraphic calibration of Eocene–Oligocene dinoflagellate cyst biostratigraphy from the Norwegian–Greenland Sea. *Marine Geology* 204: 91–127. [http://dx.doi.org/10.1016/S0025-3227\(03\)00357-8](http://dx.doi.org/10.1016/S0025-3227(03)00357-8)
- ELSIK W.C. 1978. Classification and geologic history of the microthyriaceous fungi. *Proceedings of the IV International Palynological Conference, Lucknow (1976–77)* 1: 331–342.
- FENSOME R.A. and WILLIAMS G.L. 2004. The Lentin and Williams index of fossil dinoflagellates 2004 edition. *American Association of Stratigraphic Palynologists Contributions Series* 42: 1–909.
- FIRTH J.V. 1996. Upper Middle Eocene to Oligocene dinoflagellate biostratigraphy and assemblage variations in Hole 913B, Greenland Sea. In: J. Thiede, A.M. Myhre, G.L. Johnson and W.F. Ruddiman (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 151: 203–242.
- HAQ B.U., HARDENBOL J. and VAIL P.R. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235: 1156–1167. <http://dx.doi.org/10.1126/science.235.4793.1156>
- HARLAND R. 1983. Dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. *Palaeontology* 26: 321–387.
- HASSAN M.Y. 1953. Tertiary faunas from Kap Brewster, East Greenland. *Meddelelser om Grønland* 111 (5): 42 pp.

- HEAD M.J., NORRIS G. and MUDIE P.J. 1989a. Palynology and dinocyst stratigraphy of the Miocene in ODP Leg 105, Hole 645E, Baffin Bay. *In: S.P. Srivastava, M. Arthur, B. Clement et al. (eds) Proceedings of the Ocean Drilling Program, Scientific Results 105: 467–514.*
- HEAD M.J., NORRIS G. and MUDIE P.J. 1989b. Palynology and dinocyst stratigraphy of the Upper Miocene and lowermost Pliocene, ODP Leg 105, Site 646, Labrador Sea. *In: S.P. Srivastava, M. Arthur, B. Clement et al. (eds) Proceedings of the Ocean Drilling Program, Scientific Results 105: 423–451.*
- HEILMANN-CLAUSEN C. and COSTA L.I. 1990. Dinoflagellate zonation of the uppermost Paleocene? to lower Miocene in the Wursterheide Research Well, NW Germany. *Geologisches Jahrbuch A111: 431–521.*
- JAHREN A.H. 2007. The Arctic Forest of the Middle Eocene. *Annual Review of Earth and Planetary Sciences 35: 509–540.* <http://dx.doi.org/10.1146/annurev.earth.35.031306.140125>
- JOLLEY D.W. 1998. Early Eocene palynofloras from Holes 915A, 916A, 917A and 918D, East Greenland. *In: A.D. Saunders, H.C. Larsen and S.W. Jr. Wise (eds) Proceedings of the Ocean Drilling Program, Scientific Results 152: 221–231.*
- KORENEVA E.V., ZAKLINSKAYA E.D., BRATSEVA G.M. and KARTASHOVA G.G. 1976. Palynology studies of Sites 336, 338, 345, 346 and 348, DSDP Leg 38. *In: S.M. White (ed.) Initial Reports of the Deep Sea Drilling Project 38: 1169–1193.*
- KÖTHE A. 1990. Paleogene dinoflagellates from northwest Germany. *Geologisches Jahrbuch A118: 1–111.*
- KÖTHE A. and PIESKER B. 2007. Stratigraphic distribution of Paleogene and Miocene dinocysts in Germany. *Revue de Paléobiologie, Genève 26: 1–39.*
- LIU Y-S. and BASINGER J.F. 2000. Fossil *Cathaya* (Pinaceae) pollen from the Canadian High Arctic. *International Journal of Plant Sciences 161: 829–847.* <http://dx.doi.org/10.1086/314296>
- MANUM S.B. 1962. Studies in the Tertiary flora of Spitsbergen, with notes on Tertiary floras of Ellesmere Island, Greenland, and Iceland. A palynological investigation. *Norsk Polarinstittut Skrifter 125: 1–127.*
- MANUM S.B. 1976. Dinocysts in Tertiary Norwegian-Greenland Sea sediments (Deep Sea Drilling Project Leg 38), with observations on palynomorphs and palynodebris in relation to environment. *In: M. Talwani, G. Udintsev et al. Initial Reports of the Deep Sea Drilling Project 38: 897–919.*
- MANUM S.B., BOULTER M.C., GUNNARSDOTTIR H., RANGNES K. and SCHOLZE A. 1989. Eocene to Miocene palynology of the Norwegian Sea (ODP Leg 104). *In: O. Eldholm, J. Thiede, E. Taylor et al. (eds) Proceedings of the Ocean Drilling Program, Scientific Results 104: 611–662.*
- MATSUOKA K. 1974. Some plant microfossils from the Miocene Fujiwara Group, Nara, Central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan 94: 319–340.*
- MATSUOKA K. and HEAD M.J. 1992. Taxonomic revision of the Neogene marine palynomorphs *Cyclopsiella granosa* (Matsuoka) and *Batiacasphaera minuta* (Matsuoka), and a new species of *Pyxidiniopsis* Habib (Dinophyceae) from the Miocene of the Labrador Sea. *In: M.J. Head and J.H. Wrenn (eds) Neogene and Quaternary Dinoflagellate Cysts and Acritarchs.* American Association of Stratigraphic Palynologists Foundation, Dallas: 165–180.
- MARRET F. and ZONNEVELD K.A.F. 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology 125: 1–200.*
- NORRIS G. and HEAD M.J. 1985. Climatic interpretation of Paleogene and Early Neogene spore-pollen floras from Spitsbergen and Arctic Canada. *Geological Society of America, Abstracts with Programs, 17, Annual Meeting of the Geological Society of America: 679.*
- NØHR-HANSEN H. 1993. Dinoflagellate cyst stratigraphy of the Barremian to Albian, Lower Cretaceous, North-East Greenland. *Grønlands geologiske undersøgelse, Bulletin 166: 1–171.*
- NØHR-HANSEN H. 1996. Upper Cretaceous dinoflagellate cyst stratigraphy, onshore West Greenland. *Grønlands geologiske undersøgelse, Bulletin 170: 1–104.*
- NØHR-HANSEN H. and PIASECKI S. 2002. Paleocene sub-basaltic sediments on Savoia Halvø, East Greenland. *Geology of Greenland Survey Bulletin 191: 111–116.*
- POULSEN N.E., MANUM S.B., WILLIAMS G.L. and ELLEGAARD M. 1996. Tertiary dinoflagellate biostratigraphy of Sites 907, 908, and 909 in the Norwegian-Greenland Sea. *In: J. Thiede, A.M.*

- Myhre, G.L. Johnson and W.F. Ruddiman (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 151: 255–287.
- POWELL A.J. 1992. Dinoflagellate cysts of the Tertiary System. In: A.J. Powell (ed.) *A Stratigraphic Index of Dinoflagellate Cysts. British Micropaleontological Society Publication Series*. Chapman & Hall, London: 155–249.
- RICHTER S.L. and LEPAGE B.A. 2005. A high-resolution palynological analysis, Axel Heiberg Island, Canadian High Arctic. In: B.A. LePage, C.J. Williams and H. Yang (eds) *The Geobiology and Ecology of Metasequoia*. Springer, The Netherlands: 137–158.
- SIVAK J. 1976. Nouvelles espèces du genre *Cathaya* d'après leurs grains de pollen dans le tertiaire du sud de la France. *Pollen et Spores* 18: 243–288.
- SOPER N.J. and COSTA L.I. 1976. Palynological evidence for the age of Tertiary basalts and post-basaltic sediments at Kap Dalton, central East Greenland. *Grønlands geologiske undersøgelse, Rapport* 80: 123–127.
- SOPER N.J., DOWNIE C., HIGGINS A.C. and COSTA L.I. 1976a. Biostratigraphic ages of Tertiary basalts of the East Greenland continental margin and their relationship to plate separation in the Northeast Atlantic. *Earth and Planetary Science Letters* 32: 149–157.  
[http://dx.doi.org/10.1016/0012-821X\(76\)90053-4](http://dx.doi.org/10.1016/0012-821X(76)90053-4)
- SOPER N.J., HIGGINS A.C., DOWNIE C., MATTHEWS D.W. and BROWN P.E. 1976b. Late Cretaceous–early Tertiary stratigraphy of the Kangerdlugssuaq area, East Greenland, and the age of opening of the north-east Atlantic. *Journal of the Geological Society London* 132: 85–104.  
<http://dx.doi.org/10.1144/gsjgs.132.1.0085>
- THIEDE J. and MYHRE A.M. 1996. The paleoceanographic history of the North Atlantic-Arctic Gateways: synthesis of the Leg 151 drilling results. In: J. Thiede, A.M. Myhre, G.L. Johnson and W.F. Ruddiman (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 151: 645–658.
- VAN SIMAEYS S., MUNSTERMAN D. and BRINKHUIS H. 2005a. Oligocene dinoflagellate cyst biostratigraphy of the southern North Sea Basin. *Review of Palaeobotany and Palynology* 134: 105–128. <http://dx.doi.org/10.1016/j.revpalbo.2004.12.003>
- VAN SIMAEYS S., BRINKHUIS H., PROSS J., WILLIAMS G.L. and ZACHOS J.C. 2005b. Arctic dinoflagellate migrations mark the strongest Oligocene glaciations. *Geology* 33: 709–712.  
<http://dx.doi.org/10.1130/G21634.1>
- VERSTEEGH G.J.M. and ZEVENBOOM D. 1995. New genera and species of dinoflagellate cysts from the Mediterranean Neogene. *Review of Palaeobotany and Palynology* 85: 213–229.  
[http://dx.doi.org/10.1016/0034-6667\(94\)00127-6](http://dx.doi.org/10.1016/0034-6667(94)00127-6)
- WILLARD D.A. 1996. Pliocene–Pleistocene pollen assemblages from the Yermak Plateau, Arctic Ocean: Sites 910 and 911. In: J. Thiede, A.M. Myhre, J.V. Firth, G.L. Johnson and W.F. Ruddiman (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 151: 297–305.
- WILLIAMS G.L. and MANUM S.B. 1976. Oligocene–Early Miocene dinocyst stratigraphy of Hole 985A (Norwegian sea). In: M.E. Raymo, E. Jansen, P. Blum and T.D. Herbert (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 162: 99–109.
- WILLIAMS G.L. and MANUM S.B. 1999. Oligocene–Early Miocene dinocyst stratigraphy of hole 985A (Norwegian Sea). *Proceedings of the Ocean Drilling Program, Scientific Results* 162: 99–109.
- WRENN J.H. and KOKINOS J.P. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico. *American Association of Stratigraphic Palynologists, Contribution Series* 17: 169–225.
- ZIEMBIŃSKA-TWORZYDŁO M., GRABOWSKA I., KOHLMAN-ADAMSKA A., SADOWSKA A., SŁODKOWSKA B., STUHLIK L. and WAŻYŃSKA H. 1994. Checklist of selected genera and species of spores and pollen grains ordered in morphological system. In: L. Stuchlik (ed.) *Neogene pollen flora of Central Europe. Part 1. Acta Palaeobotanica, Supplement* 1: 31–56.

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## Appendix 1 – dinoflagellate cysts

An alphabetic listing of dinoflagellate cysts from the Krabbedalen Formation at Savoia Halvø (Central East Greenland) is provided below. Full taxonomic citations are given in Fensome and Williams (2004). Numbers in parentheses refer to Table 2, followed by reference to the appropriate photomicrographs in Figs 4 to 11.

- Achomosphaera alcornu* (2; Fig. 6A)  
*Achomosphaera ramulifera* (28; Fig. 6B)  
*Achomosphaera* sp. A (42; Fig. 6I–K)  
*Achomosphaera* sp. (29)  
*Alterbidinium* sp. A (35; Fig. 9A–E, G, H)  
*Alterbidinium* sp. (25; Fig. 9F)  
*Apectodinium* sp. (34; Fig. 8N, O)  
*Batiacasphaera minuta* (1; Fig. 7A–E)  
*Charlesdownia* sp. (48; Fig. 8A, B)  
*Chlamydophorella?* sp. A (11; Fig. 7K–O)  
*Cordosphaeridium cantharellum* (55; Fig. 11E)  
*Cordosphaeridium minimum* (1; Fig. 11O–Z<sub>4</sub>)  
*Corrudinium incompositum* (13; Fig. 7U–Y)  
*Cribooperidinium tenuitabulatum* (52; Fig. 11C, D)  
*Dapsilidinium* sp. (54; Fig. 11N)  
*Deflandrea heterophlycta* (23; Fig. 8F)  
*Deflandrea* sp. (14; Fig. 8C, D)  
Dinoflagellate cyst sp. A (19; Fig. 10I–L)  
*Glaphyrocysta semitecta* (26; Fig. 4A–K)  
*Glaphyrocysta* sp. (9; Fig. 4L)  
*Habibacysta?* sp. A (21; Fig. 7P–R)  
*Habibacysta?* sp. B (37; Fig. 7S, T)  
*Impagidinium aculeatum* (36; Fig. 5D, E)  
*Impagidinium japonicum* (6; Fig. 5A–C)  
*Impagidinium sphaericum* (31; Fig. 5F–J)  
*Impagidinium velorum* (10; Fig. 5K)  
*Impagidinium* sp. (30; Fig. 5L–N, Q)  
*Kallosphaeridium* sp. (40; Fig. 4T)  
*Lentinia serrata* (39; Fig. 9I–P)  
*Lingulodinium machaerophorum* (7; Fig. 4M–S)  
*Litosphaeridium* sp. (46; Fig. 8G)  
*Membranophoridium* sp. (15; Fig. 8P)  
*Mendicodinium* sp. A of Wrenn and Kokinos (1986) (27; Fig. 11I, M)  
*Nematosphaeropsis* sp. (32; Fig. 5O, P, V, W)  
*Oligosphaeridium* sp. (45; Fig. 8H–L)  
*Operculodinium centrocarpum* (18; Fig. 11F–H)  
*Operculodinium hirsutum* (38; Fig. 11J)  
*Palaeoperidinium?* sp. (53; Fig. 10M, N)  
*Pentadinium laticinctum* (5; Fig. 5R–U)  
*Pentadinium taeniagerum* (24; Fig. 11A, B)  
Peridinioid sp. A (43; Fig. 9Q, R)  
*Phthanoperidinium ameonum* (33; Fig. 10A)  
*Phthanoperidinium comatum* (12; Fig. 10B–H)  
*Pseudoceratium* sp. (47; Fig. 4U, V)



*Pyxidinospis* sp. 1 of Manum *et al.* 1989 (3; Fig. 7F–J)  
*Reticulatosphaera?* sp. (41; Fig. 11K, L)  
*Spiniferella cornuta* (16; Fig. 6C, D, E)  
*Spiniferites pseudofurcatus* (8; Fig. 6G, H)  
*Spiniferites* sp. (20; Fig. 6F, L–U)  
*Stoveracysta* sp. (22; Fig. 7Z<sub>1</sub>–Z<sub>5</sub>)  
*Subtilisphaera* sp. (50; Fig. 8M)  
*Svalbardella* sp. (17; Fig. 10O–Q)  
*Trithyrodinium* sp. (51; Fig. 9U)  
*Vozzhemikovia* sp. (44; Fig. 9S, T)  
*Wetzeliella* sp. (49; Fig. 8E)

## Appendix 2 – sporomorphs and fresh-water phytoplankton

This is a systematical listing of spores, pollen grains and fresh-water phytoplankton from the Krabbedalen Formation at Savoia Halvø (Central East Greenland).

### Lycophytina

*Echinatisporis miocenicus* Krutzsch *et* Sontag (Fig. 13I, J)  
*Echinatisporis* sp. (Fig. 13G, H)  
*Retitriletes annotinioides* Krutzsch (Fig. 13A, B)  
*Retitriletes frankfurtensis* Krutzsch (Fig. 13E, F)  
*Retitriletes lusaticus* Krutzsch (Fig. 13C, D)  
*Retitriletes pseudoclavatus* Krutzsch  
*Retitriletes punctoides* Krutzsch  
*Retitriletes* sp.

### Pterophytina

*Baculatisporites major* (Raatz) Krutzsch  
*Baculatisporites nanus* (Wolff) Krutzsch  
*Baculatisporites primarius* (Wolff) Pflug *et* Thomson (Fig. 13R)  
*Cicatricosisporites* sp.  
 cf. *Concavisporites* sp. (Fig. 13L)  
*Corrugatisporites* cf. *graphicus* Nagy  
*Cryptogrammasporis* sp. (Fig. 13N)  
 cf. *Favoisporis* sp.  
*Foveotriletes megafovearis* (Krutzsch) Grabowska  
*Foveotriletes* sp.  
*Intrapunctisporis* sp.  
*Laevigatosporites haardti* (Potonié *et* Venitz) Thomson *et* Pflug  
*Laevigatosporites major* Cookson *ex* Krutzsch  
*Laevigatosporites nitidus* (Mamczar *ex* Krutzsch) Krutzsch (Fig. 13T)  
*Laevigatosporites* sp.  
*Leiotriletes maxoides/maximus* type  
*Leiotriletes wolffii* Krutzsch (Fig. 13Q)  
*Leiotriletes* sp. (Fig. 13M)  
*Monoleiotriletes gracilis* Krutzsch  
*Neogenisporis neogenicus* Krutzsch  
*Neogenisporis* cf. *plicatoides* Krutzsch  
*Neogenisporis* sp. (Fig. 13O)

*Perinomonoletes* sp.*Radialisporis radiatus* (Krutzsch) Jansonius *et* Hills (Fig. 13P)*Rugulatisporites quintus* Pflug *et* Thomson (Fig. 13S)*Toroisporis* sp.*Verrucatosporites favus* (Potonié) Thomson *et* Pflug**Gymnosperms***Abiespollenites absolutus* Thiergart *ex* Potonié (Fig. 14D)*Abiespollenites latisaccatus* (Trevisan) Krutzsch *ex* Ziemińska-Tworzydło*Abiespollenites* sp.*Cathayapollis pulaensis* (Nagy) Ziemińska-Tworzydło (Fig. 15I)*Cathayapollis wilsonii* (Sivak) Ziemińska-Tworzydło (Fig. 15G, H)*Cathayapollis* sp.*Cedripites* cf. *miocaenicus* Krutzsch*Cedripites parvisaccatus* (Zauer) Krutzsch (Fig. 15A)*Cedripites* sp.*Inaperturopollenites concedipites* (Wodehouse) Krutzsch*Inaperturopollenites dubius* (Potonié *et* Venitz) Thomson *et* Pflug (Fig. 14F)*Inaperturopollenites verrupapillatus* Trevisan (Fig. 14E)cf. *Keteleeriapollenites* sp.*Laricispollenites* sp.*Piceapollis sacculiferoides* Krutzsch *ex* Hochuli*Piceapollis tobolicus* (Panova) Krutzsch (Fig. 14A)*Piceapollis* sp.*Pinuspollenites labdacus* (Potonié) Raatz *ex* Potonié (Fig. 14H)*Pinuspollenites macroinsignis* (Krutzsch *ex* Ollivier-Pierre) Planderová*Pinuspollenites* sp.*Sciadopityspollenites quintus* Krutzsch *ex* Ziemińska-Tworzydło*Sciadopityspollenites serratus* (Potonié *et* Venitz) Raatz *ex* Potonié*Sciadopityspollenites tubulus* Krutzsch *ex* Ashraf *et* Mosbrugger (Fig. 15D–F)*Sciadopityspollenites verticillatiformis* (Zauer) Krutzsch (Fig. 15B, C)*Sciadopityspollenites* sp.*Sequoiapollenites polyformosus* Thiergart*Sequoiapollenites rotundus* Krutzsch (Fig. 14B)*Sequoiapollenites* sp. (Fig. 14C)*Zonalapollenites* sp. (Fig. 14G)**Angiosperms***Diervillapollenites* sp. (Fig. 15K, L)*Ericipites callidus* (Potonié) Krutzsch*Ericipites ericius* (Potonié) Potonié (Fig. 15J)*Ericipites roboreus* (Potonié) Krutzsch*Intratriporopollenites microreticulatus* Mai*Lonicerapollis gallwitzi* Krutzsch (Fig. 15M)? *Pistillipollenites mcgregori* Rouse*Quercoidites* sp.? *Saxonipollis* sp.*Tricolporopollenites* sp.**Fresh-water phytoplankton***Botryococcus* cf. *neglectus* (West *et* West) Komarek *et* Marven*Sigmopollis* sp.