

Dinoflagellate stratigraphy and echinoid distribution in Upper Maastrichtian and Danian deposits from Denmark

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A dinoflagellate stratigraphy of the Upper Maastrichtian and Danian of Denmark is proposed. The zonation based on species of *Tylocidaris* generally used in the Danish Basin is found to be diachronous relative to the dinoflagellate zonation. A general sedimentary model of the Danian of the Danish Basin is presented.

10 new species are described of which 5 belong to a new genus *Hafniasphaera*.

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In 1967–1972 several boreholes were drilled in Copenhagen, the majority of which include strata of Danian age. The geological results from the cores retrieved from these drillings have been published by Stenestad (1976). One of the cores, TUBA 13, penetrated strata of Selandian, Danian and Upper Maastrichtian age. Since the core seemed to comprise the most complete Danian sequence in the type area of the Danian (E. Stenestad & I. Bang, pers. comm. 1974) it was chosen as a reference section for the present study.

In addition samples from several other localities were processed and studied for comparison. These localities (fig. 1) include Kjølby Gård, Stevns Klint, Dania (Maastrichtian/Danian boundary), Karleby Klint, Skovvad Bro, Råsted, Voldum, Katrinegård, Tustrup, Krogsager, Mønsted, Klostergård, Fakse, Bulbjerg, Nyvang Gård (Danian), Klintholm and Hvalløse (Danian/Selandian boundary); fig. 1. Most of these localities yielded well-preserved dinoflagellate assemblages. The localities mentioned were chosen since they have all been the subject of other types of biostratigraphical studies by Ravn (1902, 1903, 1928), Nielsen (1909, 1937), Ødum (1926, 1966), Rosenkrantz (1924a, 1924b, 1930, 1937, 1939, 1966), Troelsen (1937, 1955, 1957), Rasmussen (1950), Wind (1953, 1954, 1959), Birkelund (1957), Berthelsen (1962), Bang (1967), Hansen (1968), Surlyk (1970, 1972), Wilson

(1971a, 1974 MS), Stenestad (1972). These localities thus offer the possibility of correlation between dinoflagellate stratigraphy and other types of biostratigraphical divisions. Special emphasis has been laid on localities studied by Ødum

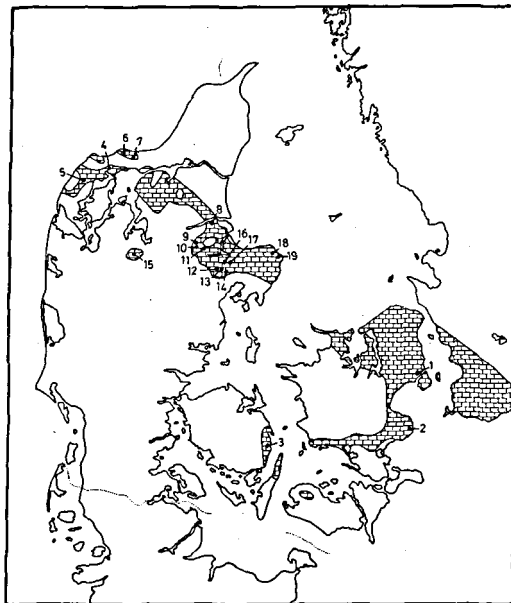


Fig. 1. Geological map of the Danian showing position of localities. 1: Copenhagen (TUBA 13). 2: Stevns Klint. 3: Klintholm. 4: Kjølby Gård. 5: Klostergård. 6: Bulbjerg. 7: Klim Bjerg. 8: Dania. 9: Nyvang Gård. 10: Skovvad Bro. 11: Råsted. 12: Hvalløse. 13: Klausholm. 14: Voldum. 15: Mønsted. 16: Tustrup. 17: Krogsager. 18: Sangstrup Klint. 19: Karleby Klint.

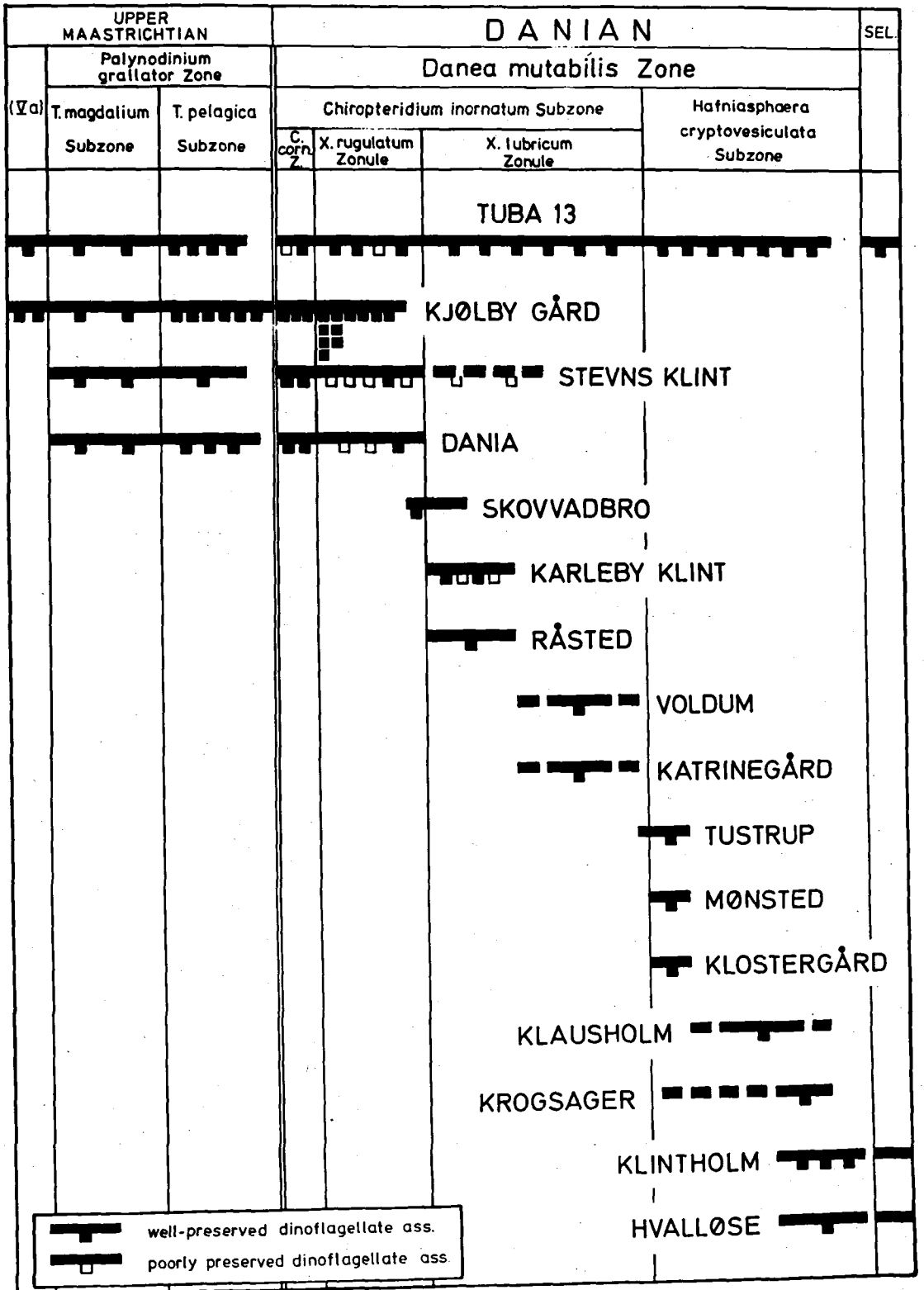


Fig. 2. Stratigraphical range of the localities.

(1926), Rosenkrantz (1937) and Wind (1953, 1954).

Sedimentological studies from some of the localities mentioned above have further been published by Bromley (1968, 1975), Rasmussen (1971), Håkansson (1971), Christensen & al. (1973), Håkansson, Bromley & Perch-Nielsen (1974), Jørgensen (1975) and Thomsen (1976). Nielsen (1976) made a detailed study of the petrology of TUBA 13.

Using standard palynological preparation techniques (Wilson 1971b) 115 samples have been processed. Of these 27 samples were from TUBA 13 (fig. 2). A total of 80 samples yielded well-preserved dinoflagellate assemblages; several hundred slides containing 1,000 – 25,000 specimens each have been studied.

A detailed sample list, reference samples and the figured specimens are deposited in the Geological Museum of the University of Copenhagen (MGUH).

Stratigraphy

On the basis of dinoflagellates TUBA 13 can be divided into 7 zones including 3 Upper Maastrichtian and 4 Danian zones (figs 3 & 4). This zonation, which appears to be applicable throughout the Danish Basin, may prove useful in other areas as well. Wilson (1971a, 1974 MS) and Kjellström (1973) described Upper Maastrichtian dinoflagellates from north-western Europe. Drugg (1967, 1970) described Upper Maastrichtian and Danian dinoflagellates from North America. Morgenroth (1968) described Danian dinoflagellates from Denmark, Sweden and Germany. Unfortunately, many papers dealing with Upper Cretaceous and Lower Tertiary dinoflagellates in general cannot with any certainty be referred to the Upper Maastrichtian or the Danian.

Maastrichtian

Upper Maastrichtian dinoflagellates from the white chalk of TUBA 13, Stevns Klint, Dania and Kjølby Gård have been investigated. At these localities the Upper Maastrichtian can be divided into 3 zones. The lowest of these (Zone

Va, Wilson 1974 MS) is found in TUBA 13 and Kjølby Gård. According to Wilson (1974 MS) this zone corresponds to the upper part of the *Belemnitella junior* Zone (Birkelund 1957) and to brachiopod Zone 9 (Surlyk 1970, 1972). Above this zone *Palynodinium grallator* Gocht, 1970 is found (Zone Vb, Wilson 1974 MS) at all localities comprising the Maastrichtian/Danian boundary. With the present material it has been possible to divide Wilson's Zone Vb, characterized by *Palynodinium grallator*, into 2 subzones, both of which are included in the *Belemnella casimirovensis* Zone (Birkelund 1957) and brachiopod Zone 10 (Surlyk 1970, 1972). In TUBA 13 the *Palynodinium grallator* Zone comprises 19 m, at Stevns Klint more than 8 m, at Dania more than 20 m, and at Kjølby Gård 10 m of chalk.

Danian

In general the Maastrichtian/Danian boundary is strongly marked by the sudden occurrence of many characteristic Danian species. Most important for correlation purposes is the occurrence of *Danea mutabilis* Morgenroth, 1968, *Chiropteridium inornatum* Drugg, 1970, *Lanterosphaeridium ovale* sp. nov., *Hafniasphaera hyalospinosa* gen. & sp. nov., *Carpatella cornuta* Grigorovitch, 1969, and *Membranilarnacia tenella* Morgenroth, 1968. At the boundary, however, only few species disappear. Most important is the extinction of *Spiniferites ramosus cavipinosus* subsp. nov. and *Palynodinium grallator*. At all localities studied there is a sedimentary break at the base of the Danian (conglomerates, hardgrounds). At Kjølby Gård, however, the upper c. 0.5 m of the chalk contain typical Maastrichtian dinoflagellates together with dinoflagellates restricted to the Danian at other localities. This feature is considered primary, since other typical Danian species as *Danea mutabilis*, *Carpatella cornuta* and *Membranilarnacia tenella* first appear at higher levels. This concurrent range indicates a more complete sequence in the Kjølby Gård area, and the presence of a smaller hiatus across the Maastrichtian/Danian boundary in the central part of the basin than in the other areas studied.

The Danian can be divided into 2 subzones and 3 zonules, all of which are included in the *Danea mutabilis* Zone.

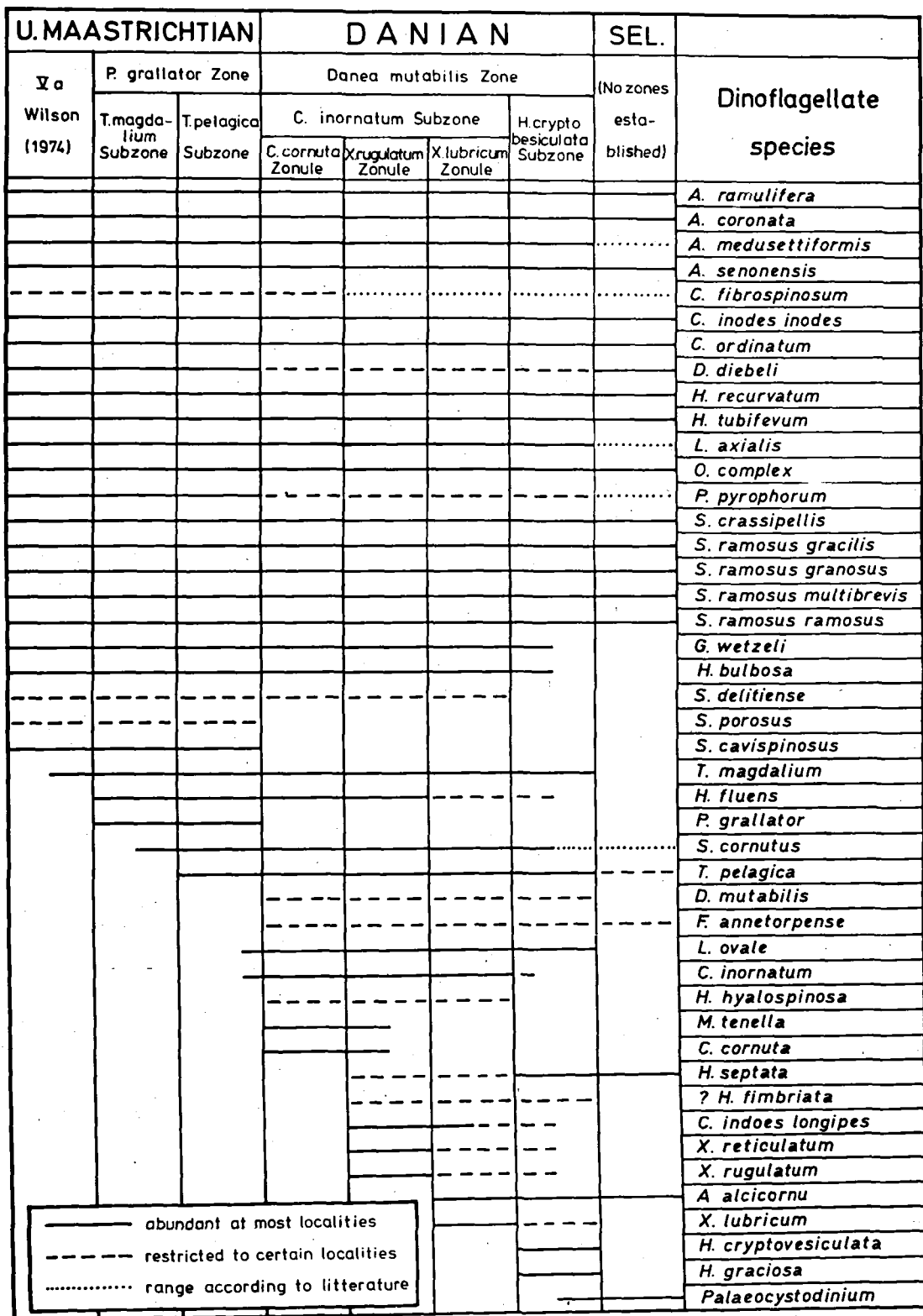


Fig. 3. Stratigraphical range of 45 common species.

Stratigraphically significant species	Localities																																					
	TUBA 13	KJØLBY GÅRD	TUBA 13	STEVNS KLINT	DANIA	KJØLBY GÅRD	TUBA 13	DANIA	KJØLBY GÅRD	TUBA 13	STEVNS KLINT	DANIA	KJØLBY GÅRD	KJØLBY GÅRD	TUBA 13	STEVNS KLINT	DANIA	SKOVVAD BRO	KARLEBY KLINT	RÅSTED	TUBA 13	VOLDUM	KATRINEGÅRD	TUSTRUP	MØNSTED	KLOSTERGÅRD	TUBA 13	KLAUSHOLM	KROGSAGER	KLINTHOLM	HVALLØSE	TUBA 13						
<i>S. ram. cavispinosus</i>	•	•																																				
<i>H. fluens</i>			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
<i>P. grallator</i>			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
<i>S. cornutus</i>																																						
<i>T. magdali</i>		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
<i>T. pelagica</i>																																						
<i>D. mutabilis</i>																																						
<i>F. anetorpense</i>																																						
<i>? H. fimbriata</i>																																						
<i>L. ovale</i>																																						
<i>C. inornatum</i>																																						
<i>H. hyalospinosa</i>																																						
<i>M. tenella</i>																																						
<i>C. cornuta</i>																																						
<i>H. septata</i>																																						
<i>C. inodes longipes</i>																																						
<i>X. reticulatum</i>																																						
<i>X. rugulatum</i>																																						
<i>A. allicornu</i>																																						
<i>X. lubricum</i>																																						
<i>H. cryptovesiculata</i>																																						
<i>H. graciosa</i>																																						
<i>Palaeocystodinium</i>																																						
WIND, 1954 (1-9)	(9)	(9)	(10)	10	10	(10)	(10)	10	(10)		I	I	I	I		II	II	III	II	II		III	III	III	III	III	III	IV	IV	IV	IV	IV	IV	IV	IV			
SURLYK, 1970 (9-10)																																						
DINOFLAGELLATE STRATIGRAPHY	Va Wilson (1974)		T. magdali Subzone				T. pelagica Subzone				C. cornuta Zonule				X. rugulatum Zonule				X. lubricum Zonule				Hafniasphaera cryptovesiculata Subzone															
	P. grallator Zone										Danea mutabilis Zone																											

Fig. 4. Scheme showing the occurrences of 23 stratigraphically significant species at different localities. It is seen, that species like *Spiniferites ramosus cavispinosus*, *Palynodinium grallator*, *Tanyosphaeridium magdali*, *Thalassiphora pelagica*, *Lantanosphaeridium ovale*, *Chiropteridium inornatum*, *Membranilarnacia tenella*, *Carpatella cornuta* and *Hafniasphaera cryptovesiculata* occur at most localities within their stratigraphical range, whereas species like *Hafniasphaera hyalospinosa* and *?Hystrichokolpoma fimbriata* seem more or less restricted to basin marginal and basin central localities respectively.

Dinoflagellate zonation

The dinoflagellate zones defined below comprise zones, which are divided into subzones. The Lower and Middle Danian *Chiropteridium inornatum* Subzone is further divided into 3 zonules. Zones are defined by the stratigraphical range of one species, whereas subzones and zonules are defined by the first occurrences of two or more species.

The use of first occurrences in dinoflagellate stratigraphy has lately been shown to yield a high level of biostratigraphical resolution in the Palaeogene of north-western Europe (Costa & Downie 1976).

Palynodinium grallator Zone

Definition: Sediments containing *Palynodinium grallator* Gocht, 1970.

Stratigraphical range: Uppermost Maastrichtian above Zone Va (Wilson 1974 MS) and below *Danea mutabilis* Zone nov.

Reference section: Kjølbj Gård; from 10 m below the Maastrichtian/Danian boundary to the top of the Maastrichtian.

Correlations: This zone corresponds to Zone Vb (Wilson 1974 MS), which according to Wilson is

equivalent to the *Belemnella casimirovensis* Zone (Birkelund 1957) and brachiopod Zone 10 (Surlyk 1970). In TUBA 13 the lower limit of this zone seems almost coincident with the upper limit of the *Pseudouigerina rugosa* Zone (Stenestad 1976: 21, 149).

Remarks: The lower limit of the zone has been located in TUBA 13 (19 m below the Maastrichtian/Danian boundary) and at Kjølby Gård.

Tanyosphaeridium magdali Subzone.

Definition: Sediments containing *Palynodinium grallator*, but excluding sediments containing *Thalassiphora pelagica* Eisenack, 1954.

Stratigraphical range: Lower part of the *Palynodinium grallator* Zone.

Reference section: Kjølby Gård; from 10 to 7.5 m below the Maastrichtian/Danian boundary.

Remarks: Named after the common species *T. magdali* (Drugg, 1967). This species, however, has a much longer range. This subzone comprises c. 14 m in TUBA 13, more than 3 m in Stevns Klint, c. 10 m in Dania.

Thalassiphora pelagica Subzone

Definition: Sediments containing both *Palynodinium grallator* and *Thalassiphora pelagica*.

Stratigraphical range: Upper part of the *Palynodinium grallator* Zone.

Reference section: Kjølby Gård; upper 7.5 m of the Maastrichtian.

Remarks: This subzone comprises c. 5 m in TUBA 13, c. 10 m in Dania and c. 5 m at Stevns Klint (Wilson 1971).

Danea mutabilis Zone

Definition: Sediments containing *Danea mutabilis* Morgenroth, 1968.

Stratigraphical range: Danian.

Reference section: TUBA 13; from -103.5 to -11.1 m.

Correlations: *Globoconusa daugbjergensis* Zone, Danian A, B, C, D (Ødum 1926), Zones of *Tylocidaris oedumi*, *T. abildgaardi*, *T. bruennichi*, *T. vexillifera* (Rosenkrantz 1937). Danian I, II, III, IV (Wind 1953, 1954). *Markalius inversus* Zone and lower part of *Cruciplacolithus tenuis* Zone (Perch-Nielsen 1969).

Remarks: The range of *D. mutabilis* is almost identical with the range of the more common species *Lanternosphaeridium ovale* nov. However, the latter species is also found in the uppermost 0.5 m of the Maastrichtian at Kjølby Gård.

Chiropteridium inornatum Subzone

Definition: Sediments containing *Chiropteridium inornatum* Drugg, 1970, but excluding sediments containing *Palynodinium grallator* and *Hafniasphaera cryptovesiculata* gen. & sp. nov.

Stratigraphical range: Lower part of the *Danea mutabilis* Zone.

Reference section: TUBA 13; from -103.5 to -55.5 m.

Local correlations: In Danish localities this subzone includes sediments belonging to the Zones of *Tylocidaris oedumi*, *T. abildgaardi*, *T. bruennichi* (Rosenkrantz 1937).

Remarks: At all localities comprising the Maastrichtian/Danian boundary *Chiropteridium inornatum* is present in high quantities in the Danian as is *Palynodinium grallator* in the Maastrichtian. Thus these two fossils are excellent guide fossils with respect to establishment of the Maastrichtian/Danian boundary. The range of *C. inornatum* is almost identical with the range of *Hafniasphaera hyalospinosa* gen. & sp. nov. The disappearance of *C. inornatum* from the Danish Basin is almost coincident with the appearance of *Hafniasphaera cryptovesiculata*. At Kjølby Gård *C. inornatum* and *Lanternosphaeridium ovale* are found together with *Palynodinium grallator* in the uppermost 0.5 m of the Maastrichtian. At all other localities studied *C.*

inornatum and *L. ovale* have their lowest occurrence at the base of the Danian.

Carpatella cornuta Zonule

Definition: Sediments containing *Carpatella cornuta* Grigorovitch, 1969, *Membranilarnacia tenella* Morgenroth, 1968, but excluding sediments containing *Palynodinium grillator* or *Hafniasphaera septata* gen. & comb. nov., *Xenicodinium rugulatum* sp. nov., *Xenicodinium reticulatum* sp. nov., *Cordosphaeridium inodes longipes* subsp. nov.

Stratigraphical range: Lower part of the *Chiropteridium inornatum* Subzone.

Reference section: TUBA 13; from -103.5 to c. -102 m.

Local correlations: At Stevns Klint this zonule comprises at least the Fish Clay at the base of the Danian corresponding to the lower part of Danian A (Ødum 1926) and the lower part of Danian I (Wind 1954). However, no samples from the Cerithium Limestone above the Fish Clay yielded dinoflagellates. At Kjølby Gård sediments belonging to this zonule are also referred to the lower part of Danian A (Ødum 1926).

Remarks: This zonule is present at Stevns Klint (0-0.3 m of marl), at Dania (0.2 m of marl) and Kjølby Gård (lower part of the marl layer). The 1.5 m present in TUBA 13 includes partly hardened and partly marly limestones.

Xenicodinium rugulatum Zonule

Definition: Sediments containing *Xenicodinium rugulatum* sp. nov., *Xenicodinium reticulatum* sp. nov., *Hafniasphaera septata* gen. & comb. nov., *Cordosphaeridium inodes longipes* subsp. nov., but excluding sediments containing *Achomosphaera alcornu* (Eisenack, 1954), *Xenicodinium lubricum* Morgenroth, 1968.

Stratigraphical range: Middle part of the *Chiropteridium inornatum* Subzone.

Reference section: TUBA 13; from - c. 102 to c. -92 m.

Local correlations: At Stevns Klint the lowermost part of the bryozoan limestone (*T. oedumi* Zone, Rosenkrantz 1937) belongs to this zonule. Samples from the *T. abildgaardii* and *T. bruennichi* Zones yielded no satisfactorily preserved dinoflagellates. At Kjølby Gård sediments belonging to this zonule are referred to Danian A (Ødum 1926). A sample from Skovvad Bro dated by Wind to Zone III belongs to this zonule.

Remarks: This zonule comprises c. 10 m partly hardened and partly bryozoan limestone in TUBA 13, more than 1 m of bryozoan limestone in Stevns Klint, more than 10 m of partly bryozoan limestone in Dania, and more than 5 m of marl and coccolith limestone in Kjølby Gård.

Xenicodinium lubricum Zonule

Definition: Sediments containing *Xenicodinium lubricum* Morgenroth, 1968, *Achomosphaera alcornu* (Eisenack, 1954), but excluding sediments containing *Hafniasphaera cryptovesiculata* gen. & sp. nov.

Stratigraphical range: Upper part of *Chiropteridium inornatum* Subzone.

Reference section: TUBA 13; from c. -92 to -55.5 m.

Local correlations: Samples from Karleby Klint (Zone B of Ødum 1926), Råsted (Zone II of Wind 1953), Voldum (Zone III of Wind, Zone C-D of Ødum), and Katrinegård (Zone III of Wind) belong to this zonule.

Remarks: This zonule comprises c. 37 m of mainly bryozoan limestone in TUBA 13, and more than 10 m of bryozoan limestone and marl in Karleby Klint. Samples from the upper part of Stevns Klint, which probably belongs to this zonule, yielded no satisfactorily preserved dinoflagellates.

Hafniasphaera cryptovesiculata Subzone

Definition: Sediments containing *Hafniasphaera cryptovesiculata* gen. & sp. nov. and commonly also *Hafniasphaera graciosa* gen. & sp. nov.

Stratigraphical range: Upper part of the *Danea mutabilis* Zone.

Reference section: TUBA 13; from -55.5 to -11.1 m.

Local correlations: This subzone is found in Tustrup (Zone D of Ødum, 1926, Zone III of Wind, 1953), Mønsted (Zone C of Ødum), Klostergård (Zone III of Wind), Klausholm (Zone C-D of Ødum, Zone IV of Wind), Krogsager (Zone D of Ødum, Zone IV of Wind), Klintholm (Zone IV of Wind) and Hvalløse (Zone D of Ødum, Zone IV-V of Wind).

Remarks: At Klintholm and Hvalløse, localities belonging to the uppermost part of this subzone, species of *Palaeocystodinium* Alberti, 1961 occur. Yet these species have not been found in other parts of the Danian indicating the presence of very young Danian deposits at Klintholm and Hvalløse, and also indicating the presence of a major hiatus below the base of the Selandian in TUBA 13.

Discussion and conclusions

It is generally accepted amongst stratigraphers that a high level of stratigraphical accuracy is obtained in dinoflagellate zonations. According to their planktic mode of life even restricted communities become widespread in the palaeogeographical record. This may be due to the extreme high number of motile dinoflagellates typically present in the seas, but it is, of course, only the occurrence of dinoflagellate cysts that is recorded in fossil assemblages. However, since encystment is mainly a response to deteriorating environment (Sarjeant 1974: 48), the proportional production of cysts from a given population is likely to increase away from the main habitat area and, thus, greatly improve the stratigraphical potential of the group. In good accordance with this argument, such important species as *Danea mutabilis*, *Chiropteridium inornatum*, *Lanternosphaeridium ovale*, *Hafniasphaera cryptovesiculata*, *Cordosphaeridium inodes longipes*, *Carpatella cornuta*, *Xenicodinium rugulatum* and *Xenicodinium lubricum* are found in all lithologies represented in the Danish Basin and

several of them also in clastic sediments in North America, the Soviet Union, and central West Greenland. Dependence upon environment is rather reflected by the relative numbers of specimens in species like *Hystriochosphaeridium tubiferum* (Ehrenberg, 1838), *Spiniferites ramosus ramosus* (Davey & Williams, 1966) and *Spiniferites ramosus gracilis* (Davey & Williams, 1966). The relative number of *Spiniferites ramosus* varies from 30 to 50% of the total number of dinoflagellates in the lower and middle parts of the Danian, and from 20 to 34 % in the upper part of the Danian. *Hystriochosphaeridium tubiferum* varies from 0 to 9 % throughout the Danian of TUBA 13, but at selected localities in Jylland such extremely high percentages as 95 and 98 % are obtained. But even at such localities it is possible to find satisfactory numbers of stratigraphically significant dinoflagellates.

In consequence the stratigraphical range of dinoflagellates is much more reliable with reference to chronostratigraphy than benthic species, which furthermore are found in much smaller numbers.

The dinoflagellate succession found in TUBA 13 seems to agree well with the dinoflagellate successions found in Kjølbj Gård, Dania and Stevns Klint. At Kjølbj Gård the most complete Upper Maastrichtian sequence is found. Here *Chiropteridium inornatum* and *Lanternosphaeridium ovale*, which at other localities first occur in the Danian, are found together with the typically Upper Maastrichtian species *Palynodinium grallator* below the *Carpatella cornuta* Zone in the upper 0.5 m of the white chalk.

No major discrepancy between the dinoflagellate zonation and earlier Upper Maastrichtian biozonations is obvious in the area studied. Apparently, Upper Maastrichtian dinoflagellate distribution is in good agreement with the belemnite and brachiopod zones (Wilson 1974 MS), and with the foraminiferal zones (Stenestad, pers. comm. 1977).

The biostratigraphical zonations of the Danian of the Danish Basin have traditionally mainly been based on the regular echinoid *Tylocidaris*. The *Tylocidaris* zonation was established on the basis of outcrops in eastern Denmark, especially Stevns Klint and the Copenhagen area (Nielsen 1909, 1937; Rosenkrantz 1924b, 1937). The zones established by Ødum (1926) at Fyn and in

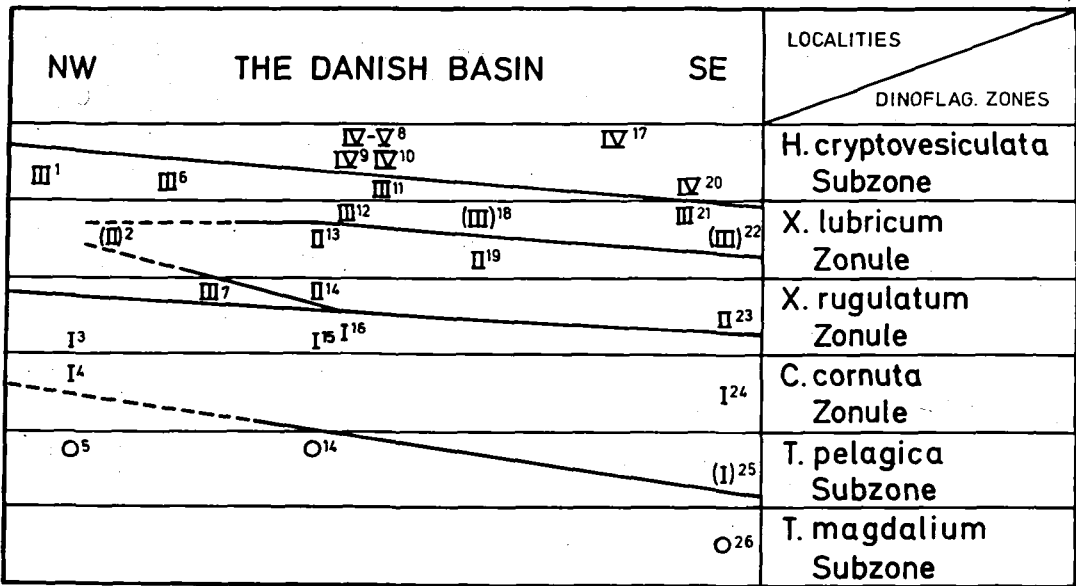


Fig. 5. I: *Tylocidaris oedumi* zone. II: *Tylocidaris abildgaardii* zone. III: *Tylocidaris bruennichi* zone. IV: *Tylocidaris vexillifera* zone. V: Zone without *Tylocidaris*. O: *Tylocidaris baltica* zone.

1: Klostergård; sample collected and dated by Wind. 2: Klim Bjerg and Bulbjerg; no well-preserved dinoflagellate assemblage yet recovered. 3 & 4: Kjølbj Gård; according to Ødum (1926: 196) this locality belongs to the older Danian. 5: Kjølbj Gård; Ødum (1926: 196) found *T. baltica* in the lowermost Danian, but considered the specimens to be reworked. 6: Mønsted; sample collected by Rosenkrantz in the lower part of the mine. 7: Skovvad Bro; sample collected and dated by Wind. 8: Hvalløse; sample collected and dated by Wind. 9: Klausholm; sample collected and dated by Wind. 10: Krogsager; according to Wind (1953) this locality belongs to zone IV.

11: Tustrup; sample collected and dated by Wind. 12: Voldum; sample collected and dated by Wind. 13: Råsted; sample collected and dated by Wind. 14: Dania; according to Ødum (1966) the uppermost Danian of this locality belongs to the *T. abildgaardii* zone. 15 & 16: Nyvang Gård; samples collected and dated by Wind; only few dinoflagellates. 17: Klintholm; according to Wind (1953) the Danian of this locality belongs to zone IV. 18: Sangstrup Klint; Ravn (1928) found *T. bruennichi* at this locality. 19: Karleby Klint; Ødum (1926: 35) refers this locality to zone B. 20 & 21: In the Copenhagen area the *T. bruennichi* - *T. vexillifera* boundary is almost coincident with the lower limit of the Hafniasphaera cryptovesiculata Subzone. 21, 22, 23, 24, 25 & 26: Stevns Klint; according to Wind (1953, 1954), Rosenkrantz (1937) and Ravn (1928).

Jylland were correlated with the *Tylocidaris* zones by Rosenkrantz (1937). In 1953, 1954 and 1959 Wind extended the *Tylocidaris* zones to a great number of small localities in Jylland. It should be emphasised that Wind revised the names of most of the *Tylocidaris* species. For convenience the names that are well-established in the stratigraphical literature are used in this work.

In the area around Randers, localities within the *T. abildgaardii* Zone comprise both the *X. rugulatum* and *X. lubricum* Zonules, whereas localities within the *T. bruennichi* Zone comprise the *X. rugulatum* and the *X. lubricum* Zonules and the *H. cryptovesiculata* Subzone, which demonstrates the diachronous nature of the *T. abildgaardii*/*T. bruennichi* boundary compared to dinoflagellate zones (fig. 5).

In the Copenhagen area the *T. bruennichi*/*T. vexillifera* boundary is almost coincident with the *X. lubricum*/*H. cryptovesiculata* boundary. However, at northwestern localities (Mønsted, Klostergård and Tustrup) the *T. bruennichi* Zone is found at rather high levels in the *H. cryptovesiculata* Subzone.

Wind (1953, 1954: 482) found *T. oedumi* in the Maastrichtian of Stevns Klint, which may indicate a diachronous nature of the first occurrence of *T. oedumi* also.

Considering the geographical distribution of the *Tylocidaris* zones there is a trend showing progressively younger occurrences of the *Tylocidaris* zones towards the northwest (fig. 5). The internal diachrony of the two types of biostratigraphy may be explained by the benthic mode of life of *Tylocidaris*. Since a general regression is

believed to have taken place during the Danian (Ødum 1926; Rosenkrantz 1937), it is hard to believe that the regression should not affect benthic faunas. Numerous studies on recent and fossil echinoids show the environmental dependence of echinoids. Thus it is striking that *T. abildgaardi* most frequently occur in typical bryozoan limestones, *T. baltica* in coccolith limestones and *T. vexillifera* in calcarenites.

During a simple regression these communities characterized by species of *Tylocidaris* would be forced towards the centre of the Danish Basin. On the other hand a regression resulting from infill of the basin would result in a vertical succession of *Tylocidaris* spp. covering extensive parts of the Danish Basin, and would further result in a lithological succession corresponding to the lithological sequences actually formed in the Upper Maastrichtian and Danian of the Danish Basin. However, this succession does not reflect chronostratigraphical events.

This is supported by the investigations of Nielsen (1976), who concluded that the lower part of the Danian limestone in TUBA 13 (including the *C. cornuta* Zonule and the lower part of the *H. cryptovesiculata* Subzone) accumulated in low energy environments, whereas the upper part (upper part of *H. cryptovesiculata* Subzone) accumulated under high current and wave intensity.

A striking feature of the Maastrichtian/Danian boundary is the presence of a marl layer at all localities studied (fig. 6). Worsley (1971) suggested that the marl layer was formed as a result of a rise in the CaCO₃-compensation depth (CCD) in late Maastrichtian and early Danian times, and tried (Worsley 1974) to support this hypothesis by aid of nannoplankton stratigraphy. Unfortunately, however, the stratigraphical resolution established with nannoplankton is quite insufficient for this purpose and, furthermore, it appears to be based only on Maastrichtian evidence.

Several other reasons for not using coccoliths in discerning the events leading to the formation of the marl layer can be mentioned. Due to their calcite skeleton primary coccoliths should not be present in the marl layer if Worsley's hypothesis is accepted and, positive correlations of the marl layer therefore, are inconceivable. Furthermore, a stratigraphical separation of the marl layer and the hiatus below on the basis of coccoliths is impossible; reworked coccoliths occur through

extensive parts of the Danian of the Danish Basin (cf. Perch-Nielsen 1969) and it is difficult to distinguish between reworked and primary coccoliths.

However, in spite of these arguments several features observed in the sedimentary sections and in the dinoflagellate distribution may support Worsley's hypothesis.

Christensen & al. (1973) studied the Fish Clay at Stevns Klint in detail and observed a remarkable decrease in noncarbonate constituents towards the boundaries of the marl layer. Jørgensen (1975) observed the same trend in the marl layer at Dania. Furthermore, the absolute number of dinoflagellates in the marl layer is extremely high compared to the surrounding limestones. At Dania the number of dinoflagellates in the white chalk slowly decreases from 11,000 /gm sediment 17 m below the marl layer to 1,900 /gm sediment 1 m below the marl layer. In the lower part of the marl layer the number is 15,000 /gm sediment, in the middle part 47,000 /gm sediment. In the Danian limestone at this locality the highest number of dinoflagellates is 1,900 /gm sediment 10 m above the marl layer.

These features may imply that the non-carbonates of the marl layer can be interpreted as a concentrate of the small amounts of non-carbonates (excluding flints) known from the surrounding sediments (cf. Håkansson et al. 1974). In consequence of this the formation of the marl layer could not have been caused by any abrupt event, but rather resulted from a gradual development such as would be expected if a short term rise in the level of the CCD took place.

At Stevns Klint, TUBA 13, Dania and Kjølbj Gård the marl layer belongs to the *Carpatella cornuta* Zonule. At Kjølbj Gård the upper part of the marl layer extends into the *Xenicodinium rugulatum* Zonule (fig. 6). This zonation demonstrates that the top of the marl layer is youngest in the central part of the Danish Basin and similarly, as indicated by the symmetrical distribution of non-carbonates (including dinoflagellates) around the middle of the marl layer, that the lower boundary of the marl layer is probably oldest in the central part of the basin.

The conclusions drawn above enable the presentation of a sedimentary model of the Maastrichtian/Danian transition and Danian of the Danish Basin (fig. 6):

At the Maastrichtian/Danian transition conti-

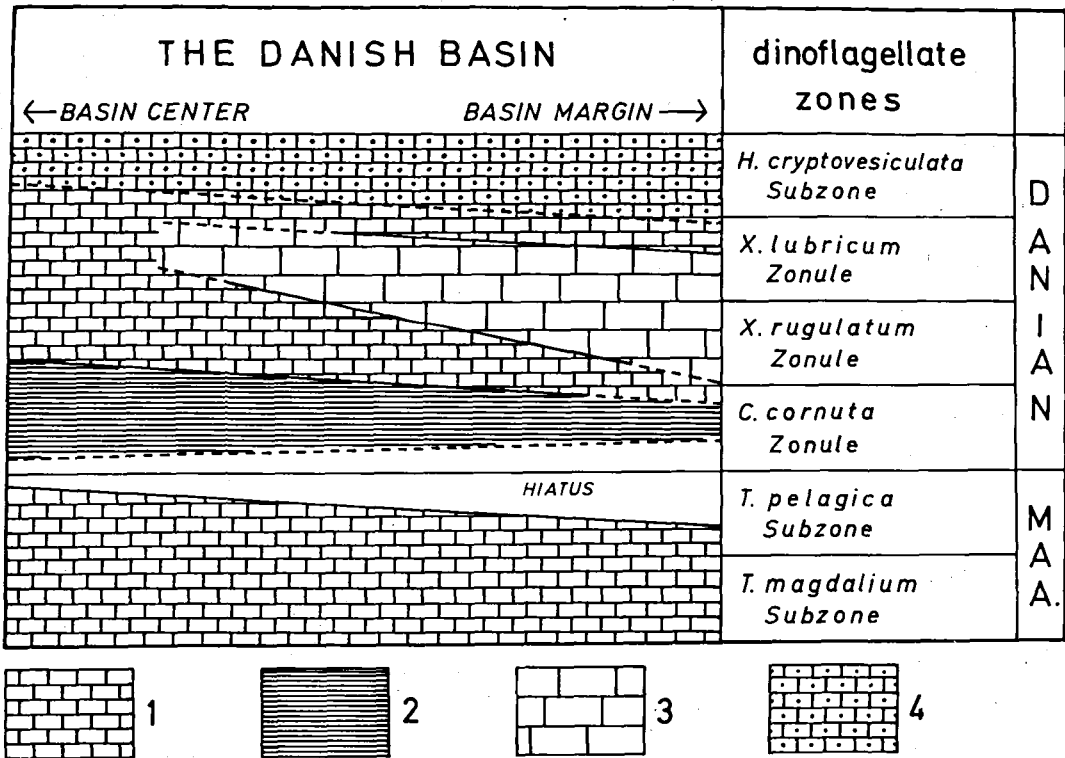


Fig. 6. Sedimentary model of the Maastrichtian/Danian transition and Danian of the Danish Basin. 1: coccolith limestones. 2: marl. 3: bryozoan limestone, locally with ahermatypic corals. 4: calcarenites.

nuous accumulation of coccoliths was prevented, resulting in the formation of a marl layer. Whether the non-deposition of coccoliths resulted from a rise in the CCD remains uncertain. Gradually the accumulation of coccoliths was resumed. In marginal parts of the basin bryozoan limestones, locally with corals, were deposited and eventually, through the infill of the basin, the bryozoans were forced towards the centre. Ultimately the entire basin was covered by calcarenites, rapidly spreading inwards from the margins of the basin.

Acknowledgements. Thanks are given to E. Håkansson for many inspiring discussions, to G. Kjellström, H. J. Hansen, K. Raunsgaard Pedersen, Tove Birkelund, N. O. Jørgensen, E. Stenestad and Inger Bang for encouragement and much good advice. L. Gudmundsson skillfully processed many of the samples and E. Max Andersen and H. Egelund made the drawings. H. Wienberg Rasmussen kindly pinpointed several of the localities and B. Holland improved the language.

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Dansk sammendrag

På grundlag af en kerneboring fra København kan der opstilles en dinoflagellat-stratigrafi omfattende 3 Øvre Maastrichtien zoner og 4 Danien zoner. Boringen omfatter en næsten ubrudt serie af sedimenter fra og med Øvre Maastrichtien til og med Nedre Selandien. Dinoflagellat-zonerne, som defineres ved hjælp af en eller flere dinoflagellat-arters første stratigrafiske optræden, genfindes på en række andre danske lokaliteter, der tidligere har været dateret ved hjælp af *Tylocidaris*-pigge. Imidlertid viser det sig, at *Tylocidaris*-zonerne er diakrone, idet de i forhold til dinoflagellat-zonerne findes på stratigrafisk højere niveau i den centrale del af det danske basin end i randområderne. Dette tolkes som udtryk for, at *Tylocidaris*-piggen i højere grad afspejler bundsedimentets beskaffenhed end stratigrafisk bestemte begivenheder.

På de fleste steder, hvor Maastrichtien-Danien grænsen er blottet, markeres Danienets undergrænse af et mergellag. Da dette mergellag 1) generelt indeholder ekstremt mange dinoflagellater i forhold til det omliggende sediment, og 2) da mergellaget overalt falder indenfor den samme dinoflagellat-zone, og 3) da toppen af mergellaget på en lokalitet i den centrale del af det danske basin desuden rækker ind i den påfølgende dinoflagellat-zone, kan det konkluderes, at der til dannelsen af mergellaget er medgået et betragteligt tidsrum, muligvis op imod ¼ af Danien tid, og at mergeldannelsen har stået på i længst tid i den centrale del af basinet. Da disse forhold udmærket kan forklares med, at en opløsning af coccolitherne eller en fortrængning af coccolithophoriderne har fundet sted på overgangen mellem

Maastrichtien og Danien, kan det ikke udelukkes, at en væsentlig årsag til mergellagets dannelse har været en voldsom hævnning af calciumkarbonats kompensationsdybde.

På grundlag af den observerede fordeling af sedimenttyper i forhold til dinoflagellat-zonerne kan der skitseres en sedimentationsmodel for det danske basins udvikling i Danien:

På grund af en brat ændring af det sedimentære miljø, muligvis en hævnning af kalk-kompensationsdybden, forhindredes en kontinuert akkumulation af coccolither på overgangen mellem Maastrichtien og Danien. Specielt i den centrale del af basinet blev coccolith-akkumulationen derpå genoptaget, mens der i basinets randområder skete en akkumulation af bryozokalk. Efterhånden som basinet opfyldtes blev dannelsen af bryozokalk fortrængt til mere centrale dele af basinet, mens der i randområderne blev dannet kalksandsten, som efterhånden bredte sig over hele basinet.

Systematic Palaeontology

Division *Pyrrhophyta*.

Class *Dinophyceae* Fritsch, 1935.

Order *Peridiniales* Haeckel, 1894.

Family *Aptediniaceae* Eisenack, 1961, *emend.* Sarjeant & Downie, 1972.

Genus *Xenicodinium* Klement, 1960.

Xenicodinium reticulatum sp. nov.

Fig. 20 D, E, F, G.

Diagnosis: *Xenicodinium* Klement, 1960 with a clearly reticulate surface.

Holotype: slide 13122 sil. 1, (46.1–101.5). Dimensions: Diameter 48–50 μm . Wall 5 μm .

Description: Egg-shaped cysts. Wall composed of two layers, endophragm and periphragm. Endophragm smooth c. 0.5 μm , periphragm composed of a tight reticulum of membranes (4–5 μm high) orthogonal to the surface. The reticulum thus formed has a mesh-size from 4 to 10 μm . The reticulum may be orientated. In optical sections the outer margin of the reticulum is always sharp. The membranes forming the reticulum are solid. Archaeopyle angular with (3-) 5 sides, probably precingular, situated below the less rounded pole of the cyst.

Remarks: *Xenicodinium reticulatum* sp. nov. resembles *Xenicodinium lubricum* Morgenroth, 1968, but differs by the structure of the periphragm, which in *X. lubricum* is not or only weakly reticulate and possessing small cavities in the basal part of the membranes, giving rise to a more irregular surface than in *X. reticulatum*.

Type locality and type stratum: TUBA 13, –99.2 m, *Xenicodinium lubricum* Zonule.

Stratigraphical occurrence: TUBA 13: from c. 1.5 to c. 32 m above the Maastrichtian/Danian boundary. Stevns Klint: above the *Cerithium* Limestone. Kjølbj Gård: 0.05 m above Maastrichtian/Danian boundary (in a complex marl layer) and upwards. Localities of Katrinegård and Klostergård.

Xenicodinium rugulatum sp. nov.

Fig. 20 H, J.

Diagnosis: *Xenicodinium* Klement, 1960 with a thick wall and possessing a strongly rugulate surface.

Holotype: Slide 13122 sil 1, (40.5–104.5). Dimensions: Diameter 45–50 μm . Wall: 4–5 μm .

Description: Egg-shaped, thick-walled cysts (4–5 μm). Wall composed of two layers, endophragm and periphragm. Endophragm smooth c. 0.5 μm thick, periphragm 4–5 μm thick seemingly built up by numerous less than 0.5 μm granules giving rise to a spongy structure. Archaeopyle angular with (3-)5 sides, probably precingular, situated below the less rounded pole of the cysts.

Remarks: *Xenicodinium rugulatum* resembles *Batiacasphaera compta* Drugg, 1970, but differs clearly from this species by the precingular archaeopyle.

Type locality and type stratum: TUBA 13, –99.2 m, *Xenicodinium lubricum* Zonule.

Stratigraphical occurrence: TUBA 13: from c. 1.5 to c. 32 m above Maastrichtian/Danian boundary. Stevns Klint: above the *Cerithium* Lime-

stone. Kjølbj Gård: 0.05 m above Maastrichtian/Danian boundary (in a complex marl layer) and upwards. Localities of Skovvad Bro, Katri-negård and Klostergård.

Family *Spiniferitaceae* Sarjeant, 1970, *emend.* Sarjeant & Downie, 1974.

Genus *Spiniferites* Mantell, 1850, *emend.* Sarjeant, 1970.

Spiniferites ramosus (Ehrenberg, 1838)
cavispinosus subsp. nov.

Fig. 21 D, E.

Hystriosphera ramosa. – Gocht, 1970, pl. 3, fig. 2, 3.

Spiniferites ramosus var. *granosus*. – Kjellström, 1973, fig. 37.

Diagnosis: *Spiniferites ramosus* with hollow processes and a composite granulation of the central body, i.e. 10–15 small granules are grouped together forming larger granules with almost no spacing giving rise to a structure resembling a cauliflower.

Holotype: Slide 17/7 (Stevns Klint). Dimensions: Diameter of central body 60 μm . Overall diameter 120 μm . Thickness of wall 1.5 μm .

Description: Spherical central body with long and very thin-walled processes. Processes hollow to the tips of furcae, unbranched, or branched in the cingular region, trifurcate and with bifid tips. Processes circular or rounded triangular in cross-section, distally closed. Sutural processes not present. Process bases are connected by low double-membranes or by tubiform bulges of the periphram. At the central body the endophragm and periphram are in close contact and cannot be distinguished except below processes and sutures where the composite granulation is seen to be attributed to the endophragm. At plate areas the composite granulation is seen on the surface of the periphram. This may be explained by the extremely thin periphram,

which may form an external cast of the endophragm structure.

Type locality and type stratum: Stevns Klint, 8 m below Maastrichtian/Danian boundary, *Tanyosphaeridium magdaliium* Subzone.

Stratigraphical occurrence: TUBA 13, Stevns Klint, Kjølbj Gård: below Maastrichtian/Danian boundary. Dania: from bottom of quarry to 3 m below Maastrichtian/Danian boundary. Scania, Southern Sweden: Middle and Upper Maastrichtian.

Genus *Hafniasphaera* nov.

Diagnosis: Chorate cysts with a subspherical or ovoid central body composed of two layers, endophragm and periphram. One or both of these layers contain numerous evenly distributed vesicles (vacuoles). The vesicles are spherical or, if interconnected, they may form a fine reticulum internal in the cyst wall. Processes intertabular, formed by the periphram, with or without vesicles, solid or hollow, closed or open distally. Simple processes trifurcate (gonal processes) or bifurcate (sutural processes). Composite processes ramifying in more complex ways. Tips of furcae bifid. Archaeopyle type P, formed by loss of paraplate 3''. Operculum becomes typically completely detached.

Paratabulation indicated by presence of sutural crests, weak bulges of the periphram, by alignment of the vesicles, or by the arrangement of the processes only. Paratabulation of plates 1'–3'(4'), 1''–6'', 1c–6c, (1''') 2'''–6''', (ps), (1p), 1'''''. Paraplate 6'' is triangular, 1'''' very little if not absent. If present paraplate 4' is situated between 1'' and 5'', above 6'' and parasulcus. Suture between 3''' and 4''' is situated a little to the left of suture between 2'' and 3'', whereas suture between 4'''' and 5'''' is aligned with or slightly to the right of suture between 3'' and 4''. Paracingulum disposed in a laevorotary spiral.

Type species: *Hafniasphaera hyalospinosa* sp. nov.

Stratigraphical occurrence of the genus: Upper

Maastrichtian, Denmark; Danian, Denmark and U.S.A.; Upper Palaeocene, Australia and U.S.A.

Hafniasphaera hyalospinosa sp. nov.

Fig. 7, 8; fig. 18 A.

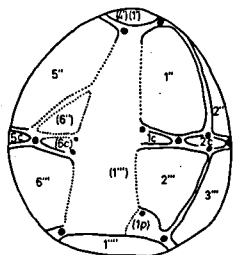


Fig. 7. *Hafniasphaera hyalospinosa*, ventral view.

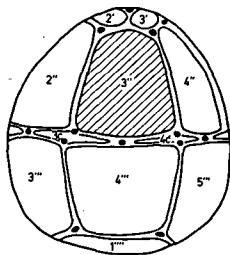


Fig. 8. *Hafniasphaera hyalospinosa*, dorsal view.

Type species of *Hafniasphaera* gen. nov.

? *Cannosphaeropsis* sp. B. – Drugg, 1967, p. 26, pl. 4, fig. 18.

? *Spiniferites* sp. – Wilson, 1971, pl. 4, fig. 16.

Diagnosis: *Hafniasphaera* gen. nov. with ovoid, thick-walled central body. Cyst wall contains numerous evenly distributed 0.5–1.0 μm vesicles at the paraplate areas. Boundaries between paraplates indicated by weak alignment of vesicles, or by a weak bulge of the periphragm. Processes distally closed, centrally containing a variable number of vesicles generally larger than vesicles in the cyst wall. Simple processes unbranched, trifurcate, bifid. Composite processes ramifying in more complex ways.

Holotype: Slide 13124II A1. Dimensions: Diameter of central body 62–68 μm . Length of processes 30–35 μm .

Description: Central body more or less translucent dependent on the density of the vesicles. Paratabulation of plates 1'–3', 1''–6'', 1c–6c, 2'''–6''', (1p), 1'''''. Cingular paraplates very narrow. No sulcal paraplates visible. A notch in the lower left side of 2''' indicates the presence of 1p. Archaeopyle often enlarged. Processes solid (except for the vesicles). Simple processes

subcircular in cross-section. Composite processes more irregular. Some processes provided with a basal cavity. Process material seems brighter than wall material. Number of vesicles in the processes varies greatly within the same specimen. Small processes may be free of vesicles, whereas large processes may contain 30 vesicles. A few specimens contain no vesicles in the processes at all. In general 5–20 vesicles are present in each process. Size of vesicles in processes varies greatly within the same specimen from 1/10 of the process diameter to more than average process diameter, which gives rise to balloon-like thickenings of the processes. Distally two processes may be interconnected by trabeculae (rare).

Range (20 specimens measured): Central body: Short diameter 42–62 μm , average 53.0 μm . Long diameter 50–74 μm , average 60.2 μm . Overall diameter: Short diameter 90–120 μm , average 105.8 μm . Long diameter 92–140 μm , average 116.2 μm .

Type locality and type stratum: TUBA 13, –103.1 m, *Carpatella cornuta* Zonule.

Stratigraphical occurrence: TUBA 13: the lower 53 m of the Danian. Stevns Klint: from the base of the Danian. California: Upper Dos Palos Shale (Upper Moreno Formation), Danian (Drugg, 1967). The quarries at Skovvad Bro, Råsted and Voldum.

Hafniasphaera cryptovesiculata sp. nov.

Fig. 9, 10; fig. 18 C, E, F, 19 A, B.

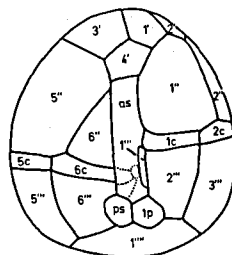


Fig. 9. *Hafniasphaera cryptovesiculata*, ventral view.

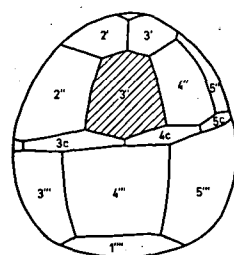


Fig. 10. *Hafniasphaera cryptovesiculata*, dorsal view.

Diagnosis: *Hafniasphaera* gen. nov. with subspherical, thick-walled central body provided with numerous evenly distributed vesicles with a diameter of 0.5 μm or less. Boundaries between paraplates clearly marked by folds of periphragm. Processes strong, solid, Y-shaped in cross-section, trifurcate, bifid. If present the vesicles in the processes generally are smaller than those of the central body.

Holotype: Slide 13047 Euk. 1 (32.2–104.0). Dimensions: Diameter of central body 80–84 μm . Overall diameter 120–140 μm .

Description: Central body with a clear paratabulation of plates 1'–4', 1''–6'', 1c–6c, 1'''–6''', ps, 1p, 1'''''. Paraplate 1'''' is very little, 4' is situated above parasulcus, between 1'' and 5''. Paracingulum is rather narrow. Vesicles are most abundant in the inner part of the cyst wall (endophragm). The vesiculation of the outer layer and the processes (periphragm) varies greatly from absent to almost as dense as in the endophragm. Processes often provided with a basal cavity with the shape of a tetrahedron. Sutural processes have not been observed.

Range: Central body: Short diameter 76–88 μm , average 84.6 μm . Long diameter 80–100 μm , average 88.3 μm . Overall diameter: Short diameter 108–142 μm , average 124.0 μm . Long diameter 120–146 μm , average 130.7 μm .

Type locality and type stratum: TUBA 13, –25.8 m, *Hafniasphaera cryptovesiculata* Subzone.

Stratigraphical occurrence: TUBA 13: from 55 to 78 m above the Maastrichtian/Danian boundary. The localities of Tustrup, Mønsted, Klostergård, Klausholm, Krogsager, Klintholm and Hvalløse.

Hafniasphaera graciosa sp. nov.

Fig. 11, 12; fig. 18 B, D.

Diagnosis: *Hafniasphaera* gen. nov. with subspherical, thin-walled central body containing

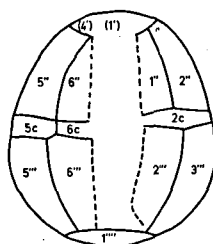


Fig. 11. *Hafniasphaera graciosa*, ventral view.

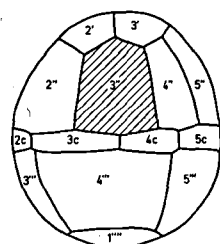


Fig. 12. *Hafniasphaera graciosa*, dorsal view.

numerous evenly distributed vesicles with a diameter less than 0.5 μm . Simple processes circular in cross-section, hollow, distally open, trifurcate, bifid.

Holotype: Slide 13076 Euk. 1 (36–103). Dimensions: Diameter of central body 68–72 μm . Overall diameter 115–117 μm . **Paratype:** Slide 13041 B6. Dimensions: Diameter of central body 68–80 μm . Overall diameter 108–115 μm . **Paratype:** Slide MPA 71 B (41.2–106.2). Dimensions: Diameter of central body 48–55 μm . Overall diameter 83–100 μm .

Description: Central body with a very weak paratabulation, generally only visible on the dorsal side, of plates 1'–3', 1''–6'', 1c–6c, 2'''–6''', 1'''''. Paracingulum narrow. Sutures indicated as extremely fine folds of the periphragm. Cyst wall two-layered. Vesicles mostly confined to the endophragm, but processes may also contain vesicles. Simple processes trumpet-shaped below the trifurcation. Cingular processes often complex and branched.

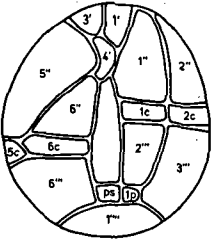
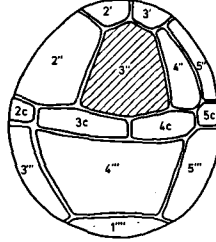
Range: Central body: Short diameter 48–68 μm , average 57.6 μm . Long diameter 55–80 μm , average 65.4 μm . Overall diameter: Short diameter 83–108 μm , average 95.8 μm . Long diameter 92–115 μm , average 104.6 μm .

Type locality and type stratum: TUBA 13, –48.3 m, *Hafniasphaera cryptovesiculata* Subzone.

Stratigraphical occurrence: TUBA 13: from 55 to 78 m above the Maastrichtian/Danian boundary. The localities of Mønsted, Klostergård, Klausholm, Klintholm and Hvalløse.

Hafniasphaera fluens sp. nov.

Fig. 13, 14; fig. 19 C, D.

Fig. 13. *Hafniasphaera fluens*, ventral view.Fig. 14. *Hafniasphaera fluens*, dorsal view.

Diagnosis: *Hafniasphaera* gen. nov. with subspherical, thin-walled central body. Cyst wall contains numerous evenly distributed vesicles with a diameter of c. 0.5 μm . Vesicles may be confluent giving rise to an internal fine reticulum. Processes similar to those in *Spiniferites ramosus*, but provided with a variable number of vesicles of approx. same size or, less frequently, larger when compared to vesicles of central body. Sutures, which may contain one row of vesicles, are clearly marked by folds of periphragm.

Holotype: Slide D1 (3omy) Euk. 1 (25.3–99.7). Dimensions: Diameter of central body 32–37 μm . Overall diameter 55–57 μm .

Description: Central body with a clear paratabulation of plates 1'–4', 1''–6'', 1c–6c, 2'''–6''', ps, 1p, 1'''. Paraplate 4' is C-shaped (interior view) and situated between 1'' and 5'' above parasolcus, but in contact with the anterior corner of 6''. Paracingulum rather broad. Cyst wall 1–2 μm thick, two-layered. Vesicles seemingly confined to the boundary between endophragm and periphragm. Gonol processes triangular in cross-section, trifurcate, bifid. Sutural processes taeniate, bifurcate, bifid. Number of vesicles varies from 0 (rare) to 20 per process. Distally processes may contain large vesicles (3–4 μm), which gives rise to balloon-like thickenings.

Range: Central body: Short diameter 30–34 μm , average 31.8 μm . Long diameter 32–41 μm , average 36.3 μm . Overall diameter: Short diameter 46–63 μm , average 53.5 μm . Long diameter 54–64 μm , average 59.0 μm .

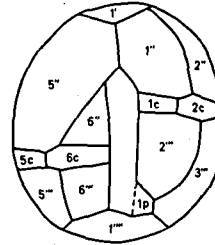
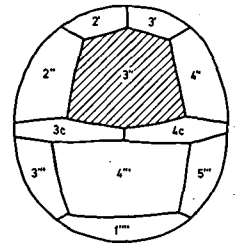
Type locality and type stratum: Dania, 20 m below the Maastrichtian/Danian boundary, *Tanyosphaeridium magdali* Subzone.

Stratigraphical occurrence: TUBA 13: Upper 18 m of the Maastrichtian, lower 1 m of the Danian. Stevns Klint: a few specimens found 1 m below the Maastrichtian/Danian boundary. Dania: Upper Maastrichtian and lower 1 m of the Danian. Kjølbj Gård: A few specimens found 10.5 m below the Maastrichtian/Danian boundary.

Remarks: *Hafniasphaera fluens* is the only species of *Hafniasphaera* occurring in the Maastrichtian. It is in shape, tabulation and morphology of the processes very close to *Spiniferites ramosus* (Ehrenberg, 1838), and may show that *Hafniasphaera* has evolved from *Spiniferites*.

Hafniasphaera septata
(Cookson & Eisenack, 1967)
comb. nov.

Fig. 15, 16; fig. 22 A, B, C, D, E.

Fig. 15. *Hafniasphaera septata*, ventral view.Fig. 16. *Hafniasphaera septata*, dorsal view.

Baltisphaeridium septatum. – Cookson & Eisenack, 1967, p. 253, pl. 42, figs. 6–10.

Spiniferites septatus. – McLean, 1971, p. 729–730, figs. 1–9.

Remarks: Danian and Lower Selandian specimens fit well with the description by Mc Lean (1971). Most specimens studied possess a well defined paratabulation of plates 1'–3', 1''–6'', 1c–6c, 2'''–6''', (1p), 1'''. Cyst wall composed of a very thin (less than 1 μm), compact inner layer (endophragm) and a typically extremely

thick (3–7 μm) outer layer (periphragm) with a characteristic bubble-like (vacuolate) structure. The bubbles are closely appressed and range in size from 1 to 3 μm .

Stratigraphical occurrence: TUBA 13: from 1.5 m above Maastrichtian/Danian boundary and throughout the Danian and Selandian. Kjølby Gård: 0.05 m above the Maastrichtian/Danian boundary (in a complex marl layer) and upwards. The localities of Skovvad Bro, Voldum, Mønsted, Klostergård, Krogsager and Hvalløse. Maryland, U.S.A.: Aquia glauconite quartz sand (Aquia Formation): from the base of the Tertiary section. Victoria, Australia: Rivernook Member of Dilwyn Clay, Upper Palaeocene.

Family *Exocosphaeridiaceae* Sarjeant & Downie, 1966.

Genus *Lanternosphaeridium* Morgenroth, 1966.

Lanternosphaeridium ovale
sp. nov.

Fig. 19 F, G.

Diagnosis: *Lanternosphaeridium* Morgenroth, 1967 with an oval central body and with a variable number of similar processes.

Holotype: Slide 13105 E2. Dimensions: Diameter of central body 70–86 μm . Overall diameter 120–126 μm . Thickness of wall 4 μm .

Description: The oval central body consists of an inner, seemingly structureless layer (endophragm) and an outer very finely fibrous layer (periphragm). Processes intratabular, solid, circular in cross-section and formed by numerous hardly visible coalescent fibres. More than one process per plate area. There is a tendency to a circular arrangement of the processes in the cingular region. Archaeopyle type P. Operculum becomes typically completely detached.

Type locality and type stratum: TUBA 13, –71.8 m, *Xenicodinium lubricum* Zonule.

Stratigraphical occurrence: TUBA 13, Dania,

Stevns Klint: throughout the Danian. Kjølby Gård: upper 0.5 m of the Maastrichtian and throughout the Danian. Localities of Skovvad Bro, Karleby Klint, Råsted, Voldum, Katrinegård, Tustrup, Klostergård, Klausholm, Mønsted, Krogsager, Klintholm and Hvalløse.

Family *Cordosphaeridiaceae* Sarjeant & Downie, 1974.

Genus *Cordosphaeridium* Eisenack, 1963, *emend.* Davey, 1969.

Cordosphaeridium inodes
(Klumpp, 1953)
longipes subsp. nov.

Fig. 17 C, D, E.

Cordosphaeridium inodes. – Drugg, 1967, pl. 5, figs. 8–9.

Cordosphaeridium inodes. – Morgenroth, 1968, pl. 46, figs. 4–8.

Diagnosis: *Cordosphaeridium inodes* (Klumpp, 1953) with an antapical process longer than all other processes.

Holotype: Slide 13086 E1. Dimensions: Diameter of central body: 84–90 μm . Overall diameter 124–138 μm . Length of antapical process 32 μm . Thickness of wall 2.5–5.0 μm .

Description: Central body ovoid and strongly fibrous. The periphragm consists of numerous 0.2–0.4 μm thick anastomosing fibres. The endophragm seems almost without structures. Processes strongly fibrous and taeniate except the antapical process, which is circular in cross-section. Distally the fibres are split up into single fibres or bundles of fibres. They may be branched, or in few cases fenestrate. Processes clearly arranged in 3 circles corresponding to the precingular-, cingular- and postcingular regions. In the cingular region processes may be placed on low thickenings of the periphragm. Endophragm extruded into the base of the antapical process. Archaeopyle type P, generally enlarged. Operculum typically becomes completely detached.

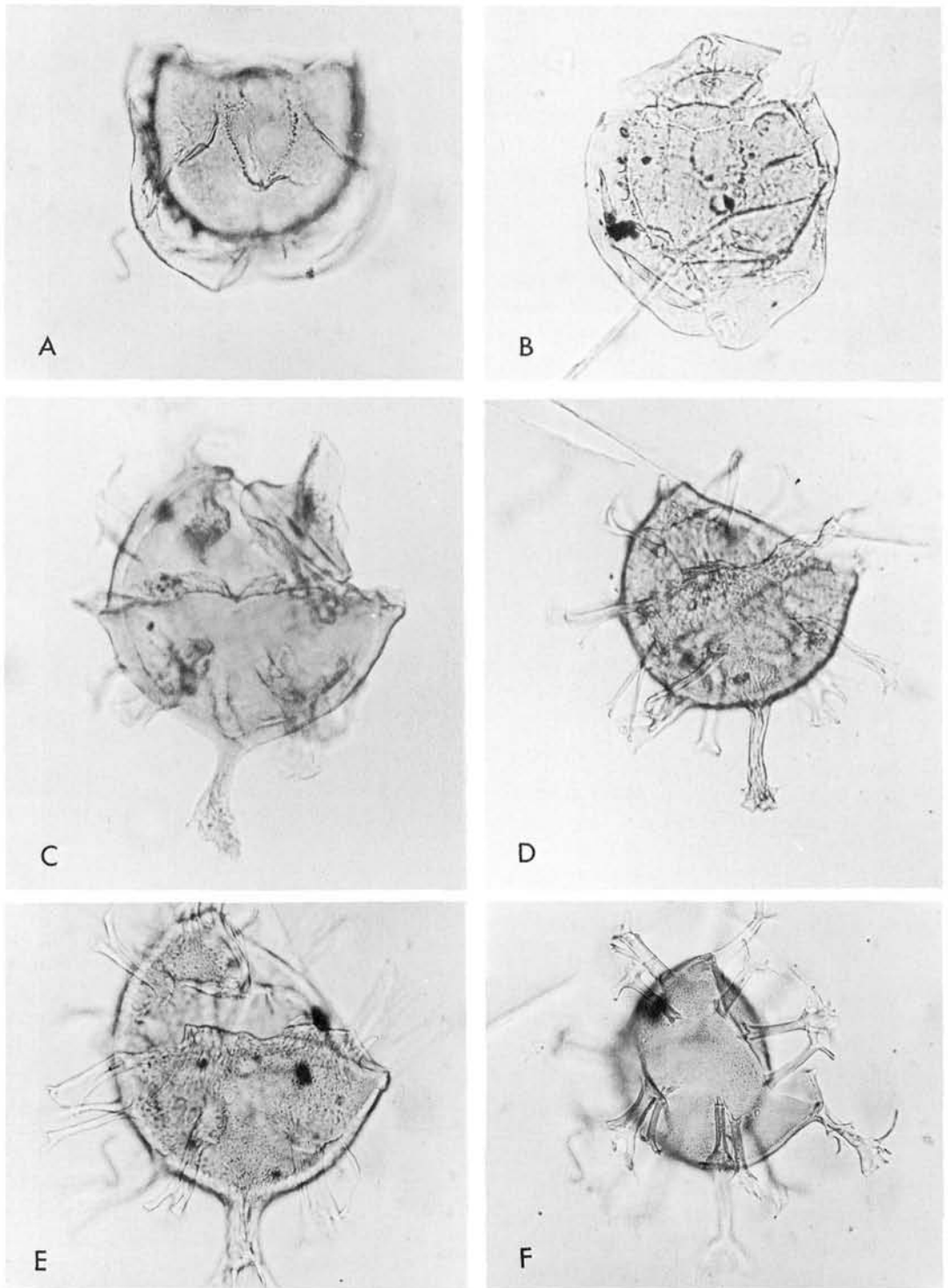


Fig. 17. All figures $600\times$: A: *Chiropteridium inornatum*, ventral view. MGUH 13, 946. B: *Chiropteridium inornatum*, specimen with attached operculum. MGUH 13, 947. C: *Cordosphaeridium inodes longipes* ssp. nov. 13, 948. D: *Cordosphaeri-*

dium inodes longipes ssp. nov. 13, 949. E: *Cordosphaeridium inodes longipes* ssp. nov., holotype. MGUH 13, 950. F: *Achromosphaera alcornu*, specimen with faint sutures between process bases. MGUH 13, 951.

Type locality and type stratum: TUBA 13, -56 m, *Xenicodinium lubricum* Zonule.

Stratigraphical occurrence: TUBA 13: from 4 to 48.5 m above the Maastrichtian/Danian boundary. Dania: 10 m above the Maastrichtian/Danian boundary. Kjølby Gård: from 0.05 m above the Maastrichtian/Danian boundary (upper part of a complex marl layer) to the top of the section. Localities of Skovvad Bro, Karleby Klint, Råsted, Tustrup, Klausholm. California: Upper Dos Palos Shale (Upper Moreno Formation), Danian.

Dinoflagellate list

Dinoflagellates not treated in the systematic part are listed below. The list only includes specimens that are believed not to have been reworked. Thus many occurrences of Maastrichtian and Danian species in the Lower Selandian greensand are excluded from the list. UM = Upper Maastrichtian, D = Danian, LS = Lower Selandian.

Achomospaera alaicornu (Eisenack, 1954). D. Fig. 17 F.

Achomospaera ramulifera (Deflandre, 1937). UM, D, LS.

Areoligera coronata (Wetzel, 1932). UM, D.

? *Areoligera danica* (Wetzel, 1952). D.

Areoligera medusettiformis (Wetzel, 1932). UM, D.

Areoligera senoniense Lejeune-Carpentier, 1939. UM, D.

Areoligera volata Drugg, 1967. D.

? *Batiacasphaera* sp. D.

Carpatella cornuta Grigorovitch, 1969. D. Fig. 21 F.

Cordosphaeridium filosum Davey & Williams, 1966. UM.

Cordosphaeridium inodes inodes (Klumpp, 1953). UM, D.

Cordosphaeridium inodes gracilis Eisenack, 1963. D.

Cordosphaeridium inodes robustum Gocht, 1969. D.

Chiropteridium inornatum Drugg, 1970. D. Fig. 17 A, B.

Cleistosphaeridium sp. D.

Danea mutabilis Morgenroth, 1968. D. Fig. 21 B, C.

Deflandrea diebeli Alberti, 1959. UM, D.

Dictyopyxidina sp. UM, D.

Duosphaeridium rugosum Drugg, 1970. D.

Fibradinium annetorpense Morgenroth, 1968. UM, D.

Gonyaulacysta wetzeli (Lejeune-Carpentier, 1939). UM, D.

Hystrichokolpoma bulbosa (Ehrenberg, 1838). UM, D.

? *Hystrichokolpoma fimbriata* Morgenroth, 1968. D.

Hystrichosphaeridium difficile Manum & Cookson, 1964. UM, D.

Hystrichosphaeridium recurvatum (White) Lejeune-Carpentier, 1940. UM, D.

Hystrichosphaeridium tubiferum (Ehrenberg, 1838). UM, D, LS.

Hystrichosphaeropsis ovum Deflandre, 1935. UM.

Lanternosphaeridium axiale (Eisenack, 1965). UM, D, LS.

Lejeunia sp. UM, D.

Lithosphaeridium siphonophorum (Cookson & Eisenack, 1958). D.

Membranilarnacia tenella Morgenroth, 1968. D. Fig. 21 G.

Oligosphaeridium complex (White, 1842). UM, D.

Ophiobulus lapidaris Wetzel, 1932. D.

Palaeocystodinium sp. D, LS.

Palaeoperidinium basilium (Drugg, 1967). S.

Palaeoperidinium pyrophorum (Ehrenberg, 1838). UM, D.

Palaeotetradinium silicorum Deflandre, 1934. D.

Palynodinium grillator Gocht, 1970. UM. Fig. 20 K, L.

Rhenidinium membraniferum Morgenroth, 1968. UM, D.

Spiniferites cornutus (Gerlach, 1961). UM, D. Fig. 21 A.

Spiniferites crassipellis (Deflandre & Cookson, 1955). UM, D.

Spiniferites porosus (Manum & Cookson, 1964). UM.

Spiniferites pterotus (Cookson & Eisenack, 1958). UM, D.

Spiniferites ramosus gracilis (Davey & Williams, 1966) UM, D, LS.

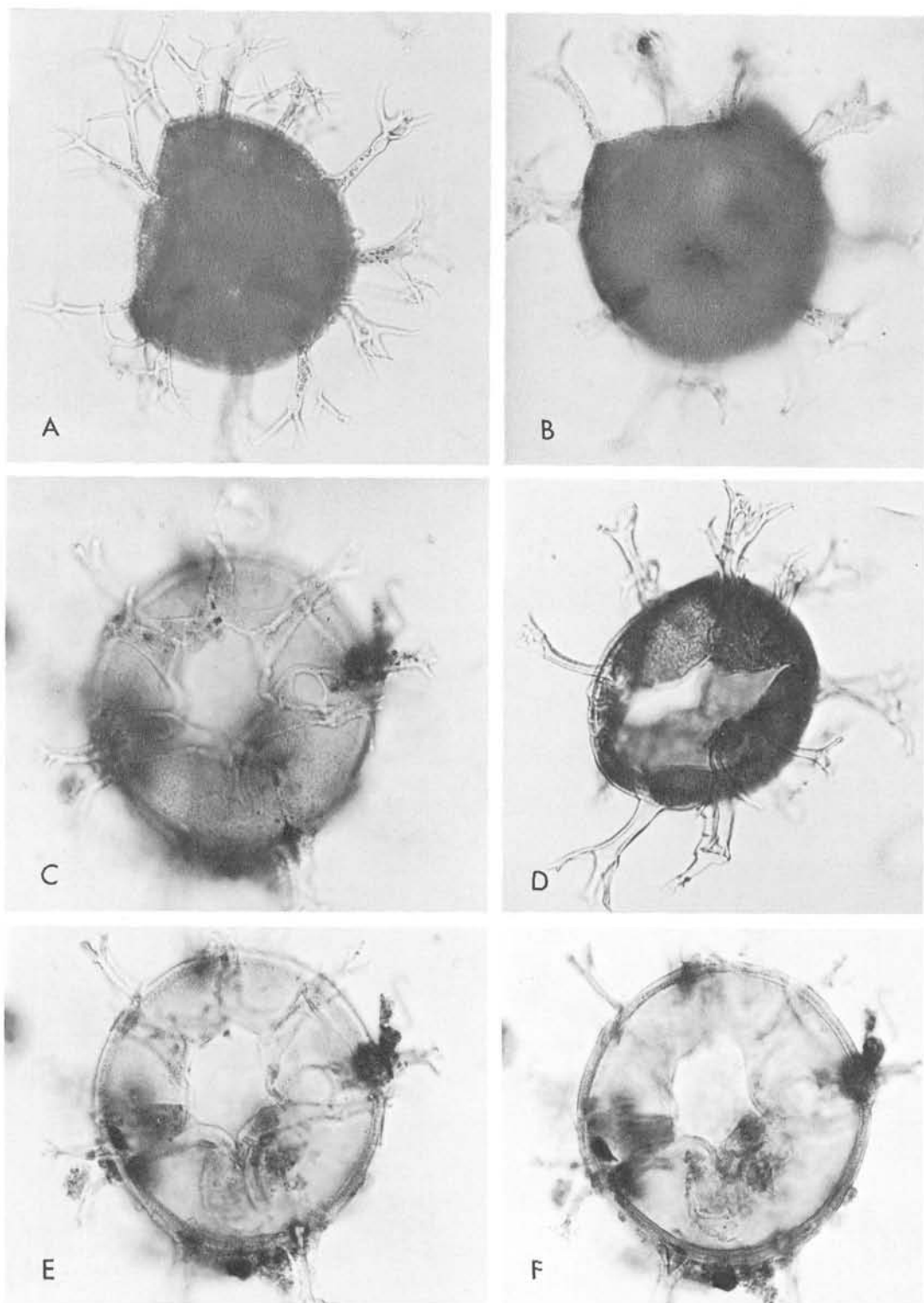


Fig. 18. All figures 600 \times . A: *Hafniasphaera hyalospinosa* gen. & sp. nov., holotype. MGUH 13, 952. B: *Hafniasphaera graciosa* gen. & sp. nov., holotype. MGUH 13, 953. C: *Hafniasphaera cryptovesiculata* gen. & sp. nov., holotype. MGUH 13,

954. D: *Hafniasphaera graciosa* gen. & sp. nov., paratype MGUH 13, 955. E: *Hafniasphaera cryptovesiculata* gen. & sp. nov., holotype. MGUH 13, 954. F: *Hafniasphaera cryptovesiculata* gen. & sp. nov., holotype. MGUH 13, 954.

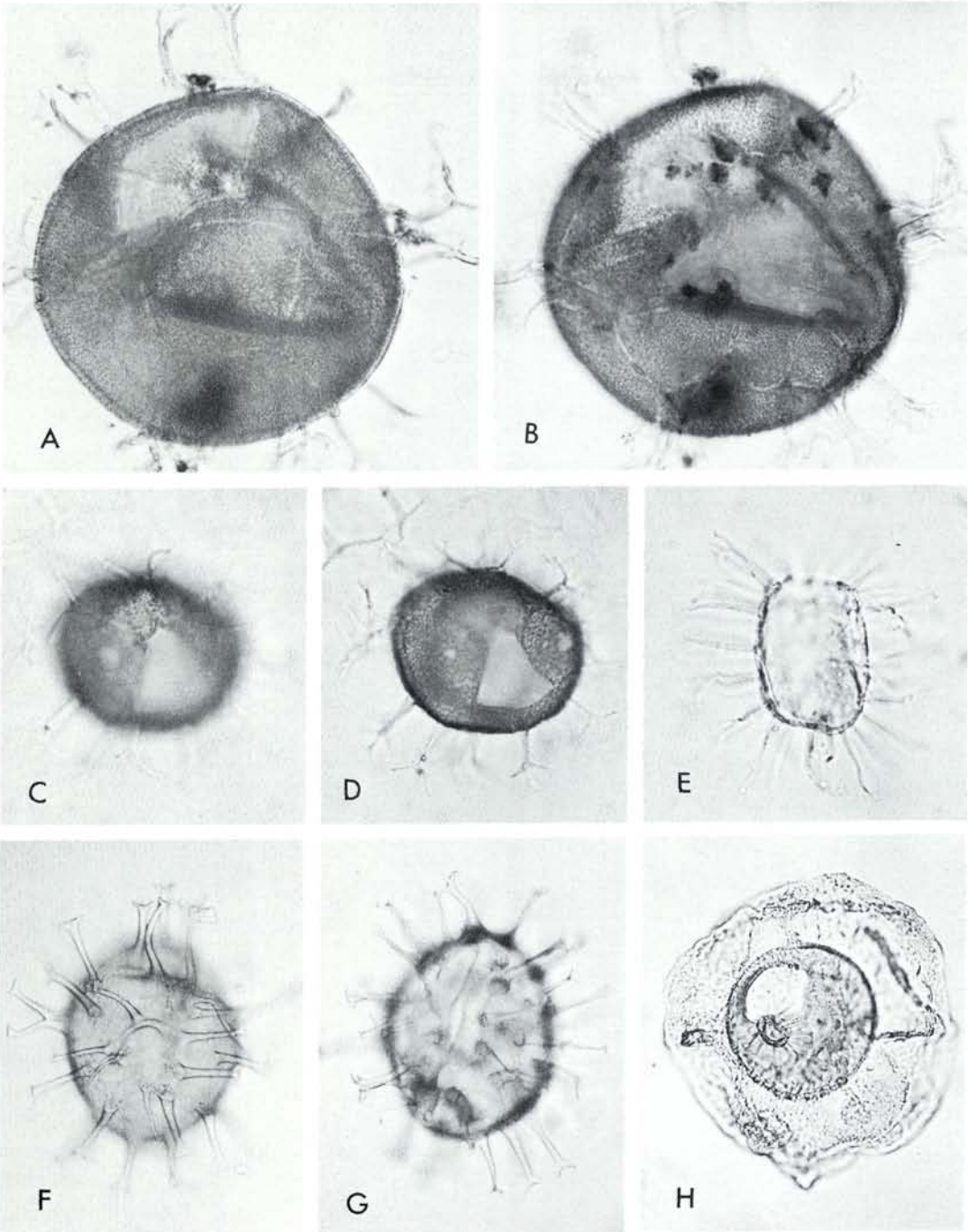


Fig. 19. A: *Hafniasphaera cryptovesiculata* gen. & sp. nov., 600 ×. MGUH 13, 956. B: *Hafniasphaera cryptovesiculata* gen. & sp. nov., 600 ×, same as fig. A, showing paraplates ps and lp. MGUH 13, 956. C: *Hafniasphaera fluens* gen. & sp. nov., 800 ×, holotype. MGUH 13, 957. D: *Hafniasphaera fluens* gen. & sp. nov., 800 ×, holotype. MGUH 13, 957. E:

Tanyosphaeridium magdali, 800 ×. MGUH 13, 958. F: *Lanternosphaeridium ovale* sp. nov., 320 ×, holotype. MGUH 13, 959. G: *Lanternosphaeridium ovale* sp. nov., 320 ×, holotype. MGUH 13, 959. H: *Thalassiphora pelagica*, 320 ×. MGUH 13, 960.

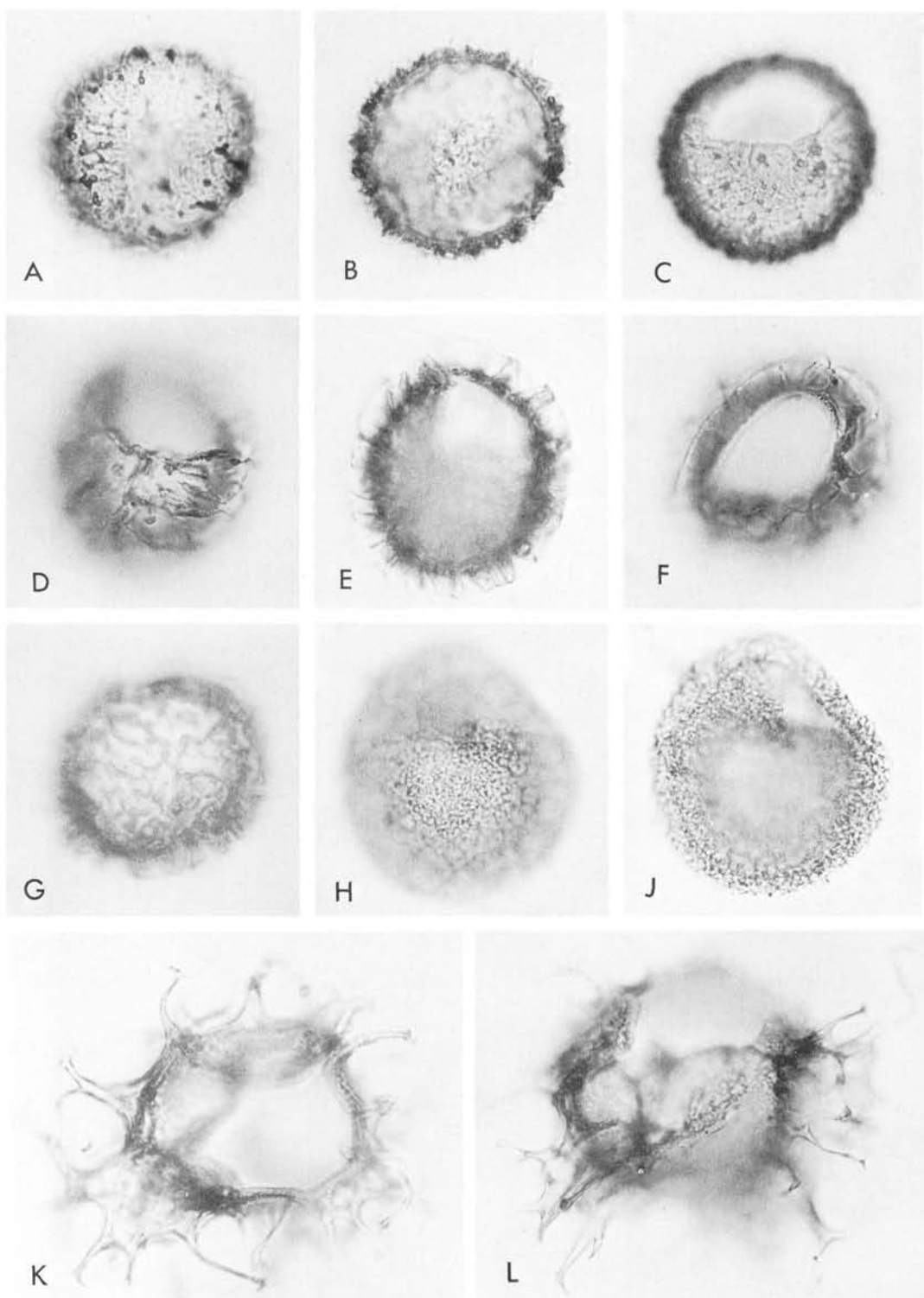


Fig. 20. All figures 800 \times . A: *Xenicodinium lubricum*. MGUH 13, 961. B: *Xenicodinium lubricum*, optical section. MGUH 13, 961. C: *Xenicodinium lubricum*, focus on archaeopyle. MGUH 13, 961. D: *Xenicodinium reticulatum* sp. nov., holotype. MGUH 13, 962. E: *Xenicodinium reticulatum* sp. nov., holotype, optical section. MGUH 13, 962. F: *Xenicodinium reticulatum* sp. nov., holotype, specimen turned, focus on ar-

chaeopyle. MGUH 13, 962. G: *Xenicodinium reticulatum* sp. nov., holotype, internal view. MGUH 13, 962. H: *Xenicodinium rugulatum* sp. nov., holotype, focus on surface. MGUH 13, 963. J: *Xenicodinium rugulatum* sp. nov., holotype, focus on archaeopyle. MGUH 13, 963. K: *Palynodinium grallator*, apical view, optical section. MGUH 13, 964. L: *Palynodinium grallator*, ventral view. MGUH 13, 964.

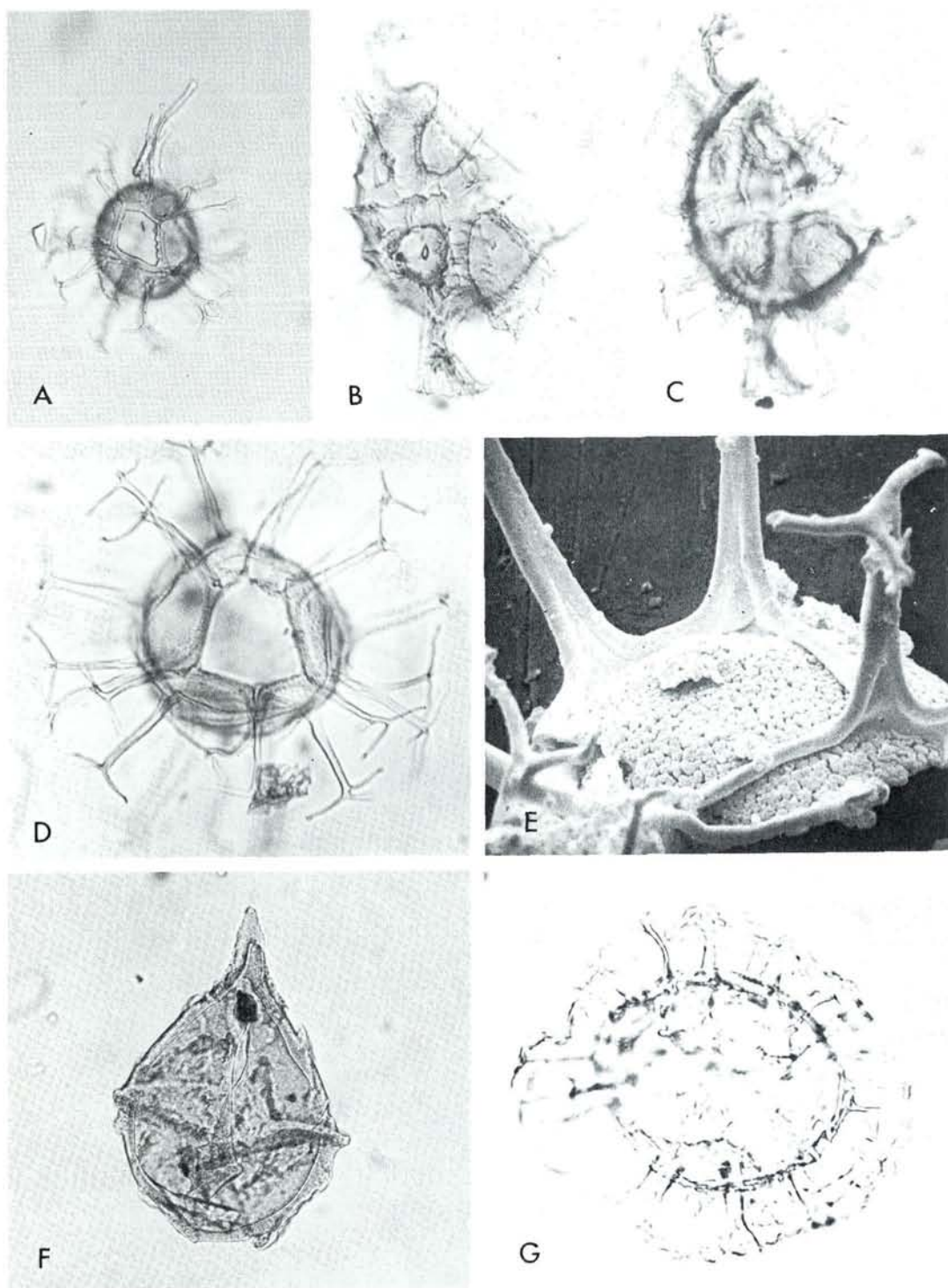


Fig. 21. A: *Spiniferites cornutus*, 420 \times . MGUH 13, 965. B: *Danaea mutabilis*, 420 \times , focus on surface. MGUH 13, 966. C: *Danaea mutabilis*, 420 \times , optical section. MGUH 13, 966. D: *Spiniferites ramosus cavispinosus* ssp. nov., Holotype, 500 \times . MGUH 13, 967. E: *Spiniferites ramosus cavispinosus* ssp.

nov., 1,500 \times , SEM photograph showing surface structures clearly different from *Spiniferites ramosus granosus* (cf. fig. 22 F). MGUH 13, 968. F: *Carpatella cornuta*, 420 \times . MGUH 13, 969. G: *Membranilarnacia tenella*, 800 \times , compiled from two photographs. MGUH 13, 970.

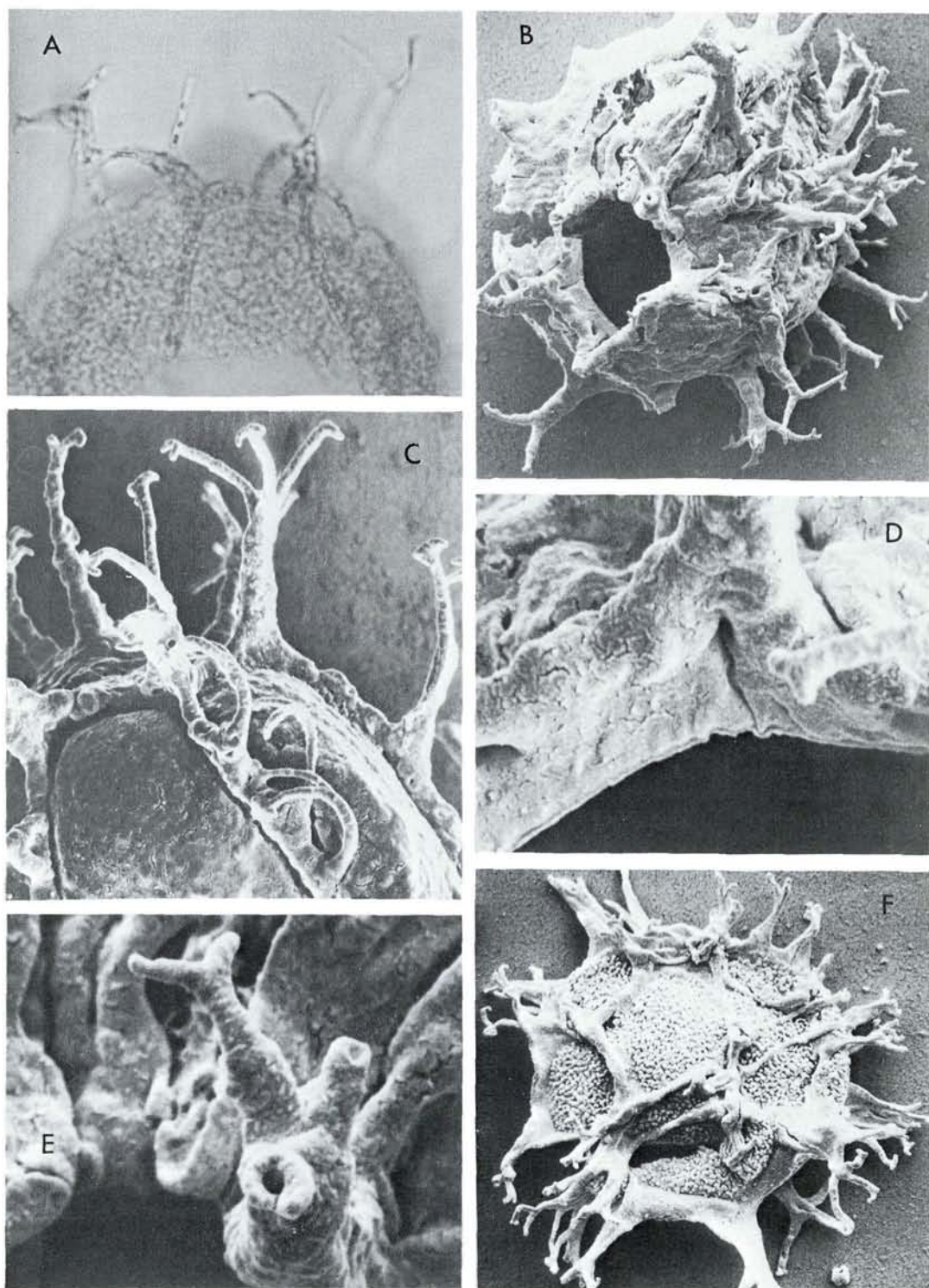


Fig. 22. A: *Hafniasphaera septata* comb. nov., 1,500 \times , same specimen as fig. C. MGUH 13, 971. B: *Hafniasphaera septata* comb. nov., 1,000 \times , specimen showing poorly developed paratabulation. MGUH 13, 972. C: *Hafniasphaera septata* comb. nov., 1,500 \times , same specimen as fig. A, showing clear paratabulation of hypotract. MGUH, 13, 971. D: *Hafniasphaera septata* comb. nov., 4,500 \times , same specimen as fig. B, showing

border of archaeopyle. Inner layer (endophragm) c. 0.2 μ m, outer layer (periphragm) excluding sutures 2.5 μ m. Notice that vesicles do not penetrate the archaeopyle border. MGUH 13, 972. E: *Hafniasphaera septata* comb. nov., 4,500 \times , same specimen as fig. B, showing cross-sections of vesicles in broken processes. MGUH 13, 972. F: *Spiniferites ramosus granosus*, 800 \times , cf. fig. 21 E. MGUH 13, 973.

Spiniferites ramosus granomembraneus (Davey & Williams, 1966) UM, D.

Spiniferites ramosus granosus (Davey & Williams, 1966). UM, D, LS.

Spiniferites ramosus ramosus (Davey & Williams, 1966). UM, D, LS.

Spiniferites supparus (Drugg, 1967). D.

Spongodinium delitiense (Ehrenberg, 1838). D.

Subtilidinium minutum Morgenroth, 1968. ?
UM, D.

Tanyosphaeridium magdaliu (Drugg, 1967).
UM, D. Fig. 19 E.

Thalassiphora pelagica Eisenack, 1954. UM, D.
Fig. 19 H.

Xenicodinium lubricum Morgenroth, 1968. D.
Fig. 20 A, B, C.

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