CENOZOIC DINOFLAGELLATE CYSTS FROM THE NAVARIN BASIN,
NORTON SOUND AND ST. GEORGE BASIN, BERING SEA

Kazumi MATSUOKA and Jonathan P. BUJAK

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Abstract

Biostratigraphic studies in the Navarin Basin COST No. 1 well, Norton Sound COST No. 1 well and St. George Basin COST No. 2 well in the Bering Sea were carried out based on dinoflagellate cyst and acritarch assemblages. Several local dinoflagellate cyst zones are independently proposed for each well, and then the composite dinoflagellate cyst zones are established for the central to eastern Bering Sea based on the composite ranges of dinoflagellate cysts obtained from the three wells. These zones are follows in descending order; Filisphaera filifera Zone (late Pliocene to early Pleistocene), Filisphaera pilosa Zone (early to late Pliocene), Hystrichosphaeropsis variabile Zone (late Miocene), Heteraulacacysta campanula Zone (latest late Oligocene to early Miocene), Impagidinium velorum Zone (early Oligocene) and Areosphaeridium diktyoplokus Zone (late Eocene). Correlation of these zones with other Cenozoic dinoflagellate zonations are also discussed.

Totally thirty-four genera and seventy species of dinoflagellates including one new genus (Algidasphaeridium) and twenty new species, and three genera and three species of acritarchs containing one new genus and species (Joviela magnifica) are recorded from the three wells.

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1) Department of Geology, Faculty of Liberal Arts, Nagasaki University ; 1–14 Bunkyomachi, Nagasaki, 852, Japan
2) Bujak Davies Group ; 1–2835 19th Street, N.E. Calgary, Alberta, Canada, T2E 7A2
I Introduction

This publication discusses the palynological results of analyses undertaken on three of the six Continental Offshore Stratigraphic Tests (COST) drilled in the Bering Sea (Text-fig. 1). The six COST wells which have been drilled are:

- Aleutian COST No. 1 well
- Navarin Basin COST No. 1 well
- Norton Sound COST No. 1 well
- Norton Sound COST No. 2 well
- St. George Basin COST No. 1 well
- St. George Basin COST No. 2 well

Data and samples have been released to the public on all of these wells, except for the Aleutian COST No. 1 well which will remain confidential until after the Aleutian Basin Lease Sales.

Three of the five released wells were therefore selected for study, including one well from each of the three basins:

- Navarin Basin COST No. 1 well
- Norton Sound COST No. 1 well
- St. George Basin COST No. 2 well

Several biostratigraphic studies have been previously undertaken on these wells (excluding in-house oil company studies) as discussed in three open file reports published by the Department of the Interior, United States Geological Survey, Minerals Management Service (Turner, 1983; 1984a; 1984b).
These previous biostratigraphic studies mostly include data from diatoms, Foraminifera and palynomorphs. The former are particularly useful in the upper Miocene and younger sections of all three wells. However, conclusions regarding the age of the sections below the upper Miocene are based mainly on palynology and so the ages assigned to those sections by the present study are discussed in particular detail.

The following paper is divided into sections on biostratigraphy with depositional environment on each well, composite zonation, and taxonomy. The degree to which the proposed Bering Sea zones can be correlated with other dinoflagellate zonations varies. The zones are therefore also calibrated against the diatoms zones assigned to the wells in Turner (1983, 1984a, 1984b) for the upper Miocene and younger sections which contain common diatoms. Older rocks contain fewer or no siliceous microfossils,
and also have little age control based on Foraminifera and calcareous nannofossils. The assigned ages for the pre-late Miocene zones therefore rely heavily on their calibration with stratigraphic ranges determined for various taxa in other areas.

II Material and Methods

Totally three hundred and thirty-five samples from the Navarin Basin COST No. 1 well, Norton Sound COST No. 1 well and St. George Basin No. 2 well in the central to eastern Bering Sea were examined palynologically. Text-fig. 1 shows the locations of these wells. Most samples from the wells are rotary drill bit cuttings, and a few samples, which are marked in Text-

Text-figure 2 Lithology of three COST wells and occurrences of diatoms (from Turner (ed.) 1983, 1984a, 1984b) and dinoflagellate cysts.
Dinoflagellate cysts from the Bering Sea

fig. 22 are collected from conventional and sidewall cores of the Norton Sound COST No. 1 well. Ditch samples in the wells were analysed at 90-foot interval excepting biostratigraphically important horizons. The lithology and other physical features of the wells are given by the Department of the Interior, United States Geological Survey, Mineral Management Service (Turner, 1983; 1984a, b).

The samples were processed in order to extract organic-walled microfossils such as dinoflagellate cysts, acritarchs, pollen and spores with the standard techniques described by Bass and Williams (1983). Dinoflagellate cyst and acritarch taxa were identified under the phase contrast, interference contrast and fluorescence optics. The abundances of these taxa are shown

Text-figure 3 Published Neogene dinoflagellate cyst studies in the northern hemisphere and generalized modern current systems.
in the following categories; Present (1 specimen), Rare (2 to 4 specimens), Common (5 to 19 specimens); Abundant (more than 20 specimens). Their stratigraphic distributions in each well are shown in Text-figs. 22, 23 and 24.

All slides including the type specimens observed in this study are kept in the palynology collection of the Bujak-Davies Group in Calgary, Canada.

### III BIOSTRATIGRAPHY IN EACH WELL

#### 1 NAVARIN BASIN COST NO. 1 WELL: BIOSTRATIGRAPHIC SUMMARY

- **1536-2730ft:** *Filisphaera pilosa* Zone (Pliocene)
- **2730-5370ft:** *Hystrichosphaeropsis variabile* Zone (late Miocene)
- **5370-11,000ft:** *Heteraulacacysta campanula* Zone (latest late Oligocene to early Miocene)
- **11,000-12,680ft:** *Impagidinium velorum* Zone (early Oligocene)
- **12,680-12,770ft:** *Trinovantedinium boreale* Zone (early Oligocene)
- **12,770-12,920ft:** *Areosphaeridium diktyoplokus* Zone (late Eocene)
- **12,920-13,280ft:** Late Cretaceous unnamed Zone (late Campanian to early Maastrichtian)
- **13,280-16,400ft:** no age determination

#### NAVARIN BASIN COST NO. 1 WELL: DINOFLAGELLATE CYST ZONATION

**1536-2730ft:** *Filisphaera pilosa* Zone (Pliocene)

Remarks: The presence of the marine dinoflagellates *Filisphaera filifera* and *Impagidinium japonicum* suggests that the depositional environment for the lower part of this interval was middle to outer shelf. The upper part of this interval from approximately 1536-1830ft was probably deposited in a nearshore marine or brackish water environment based on the presence of undescribed brackish or freshwater algal cysts. The Pliocene age assignment for the upper part of this interval is based on the associated miospores.

The *F. pilosa* Zone occurs in the Navarin COST No. 1 well from 1536-2730ft and correlates with the *D. seminae* var. *fossilis*, *D. seminae* var. *fossilis* - *D. kamtschatica* and the upper part of the *Thalassiosira oestrupii*
Dinoflagellate cysts from the Bering Sea

Diatom Zones which occur from 1536-3180 ft according to Turner (1984b). This indicates an early to late Pliocene age based on the diatom zonal scheme of Koizumi (1985).

2730-5370 ft: *Hystrichosphaeropsis variabile* Zone (late Miocene)

Remarks: Marine dinoflagellate cysts including *Brigantedinium* spp., *Selenopemphix nephroides*, *Xandarodinium variabile* and *Spiniferites* spp. occur in upper part of this zone, and reflect a middle to outer shelf environment. The upper part of the *H. variabile* Zone occurs in the Navarin Basin COST No. 1 well from 2730-3750 ft and correlates with the lower *T. oestrupii*, *D. kamtschatica*, and approximate *Rouxia californica* diatom Zones according to Turner (1984b). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

The middle part of the *H. variabile* Zone occurs in the Navarin Basin COST No. 1 well from 3750-4350 ft and according to Turner (1984b) correlates with the middle part of the *Denticulopsis hustedtii* diatom Zone (approximately equal to the *Thalassionema schraderi* diatom Zone). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985). Marine dinoflagellate cysts do not occur in the middle part of this zone except for the rare occurrence of *Impagidinium manumii*. The low species diversity of dinoflagellate cysts probably reflects a regressive phase and relative lowering of sea level. The absence of protoperidiniacean dinoflagellate cysts probably also reflects an oceanographic change that occurred between this interval and the upper part of the *H. variabile* Zone. This may have involved an increase in primary productively in the overlying zone relative to the upper part of the *H. variabile* Zone based on the observations of Bujak (1984a).

The lower part of the *H. variabile* Zone is characterized by the latest occurrence of the dinoflagellate *Spiniferites reductus*. The presence of marine dinoflagellate cysts such as *Impagidinium japonicum*, *Spiniferites reductus* and *Operculodinium* sp. indet. in this interval suggests that the depositional environment was middle to outer shelf. The lower part of the *H. variabile* Zone occurs in the Navarin Basin COST No. 1 well from 4350-5370 ft, and the upper part correlates with the lower *Denticulopsis hustedtii* diatom Zone (approximately equals the *Denticulopsis katayamae* diatom
Zone), according to Turner (1984b). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

5370-11,000ft: Heteraulacacysta campanula Zone (latest late Oligocene to early Miocene)

Remarks: The species diversity of palynomorphs is highest in this interval in the Navarin Basin COST No. 1 well, with many marine gonyaulaccean dinoflagellate cysts occurring.

The dinoflagellate cyst assemblages in the upper part of this interval are characterized by common specimens of species assignable to Spiniferites and Operculodinium which probably reflect a middle to outer neritic environment. Spiniferites pseudofurcatus, which has been recorded from the late Paleocene to middle Miocene, occurs abundantly from 6570 to 6930 feet. Diphyes sp. cf. colligerum is abundant in the middle part of this subzone. Tuberculodinium rossignoliae also occur in this subzone and was first recorded from the Miocene of Sumatra by Drugg (1970), but this species also occurs in upper Oligocene strata as discussed later in this paper. Another species of Tuberculodinium, T. vancampoae, occurs and has a worldwide range extending up into the Recent in warm oceanographic areas (Wall et al., 1977; Matsuoka, 1985a), and has its earliest occurrence in the late Oligocene (Ioannides and Colin, 1977; Williams, 1978; Powell, 1986a). Lingulodinium machaerophorum, which also occurs in this zone, is known from warm-water regions of the western Pacific (Matsuoka, 1985a). The stratigraphic ranges of these taxa are discussed further in this paper in the section on composite zonation. The presence of these warm-water species and the high species diversity of marine dinoflagellate cysts suggest that the paleoceanic temperature was warmer than in the overlying sections of the well.

Marine dinoflagellate cysts are rare in the lower part of the H. campanula Zone from 8190-11,000ft and only Operculodinium sp. cf. centrocarpum and Systematophora ancyrea were observed. This may reflect a nearshore depositional environment.

11,000-12,680ft: Impagidinium velorum Zone (probably early Oligocene)
Remarks: Several marine dinoflagellate cysts occur in the interval, including *Lejeunecysta granosa* which was described from the Oligocene of Nigeria by Biffi and Grigagni (1983). *Chiropteridium mespilatum*, which has been described from the Oligocene of the northern North Pacific by Bujak (1984a), is also present.

The depositional environment may have been middle to outer shelf based on the dinoflagellates that occur in this zone.

**12,680-12,770ft: Trinovantedinium boreale Zone (early Oligocene)**

Remarks: The dinoflagellate cyst assemblages in this interval are characterized by an abundance of *Trinovantedinium boreale* and *Phthanooperidinium bennettii*. *T. boreale* indicates an early Oligocene age because this species which was first reported from the late Eocene of the northern North Pacific by Bujak (1984a) has a range extending into the early Oligocene in the Bering Sea (Bujak and Matsuoka, 1986a).

The low diversity and high dominance of dinoflagellate cyst assemblages, and abundance of *Phthanooperidinium bennettii* indicate an inner to middle shelf environment, possibly with some brackish water influence.

**12,770-12,920ft: Areosphaeridium diktyoplokus Zone (late Eocene)**

Remarks: The association of *Trinovantedinium boreale* and *Areosphaeridium diktyoplokus* indicates a late Eocene age, similar to that observed in DSDP sections from the northern Pacific by Bujak (1984a).

**12,920-13,280ft: Late Cretaceous unnamed zone (late Campanian-early Maastrichtian)**

Remarks: A single specimen of the pollen species *Aquilapollenites quadrilobus* was observed in the sample at 13,280ft. This species occurs in the *Hystrichosphaeridium difficile* and *Isabelidinium amphiatum* Zones of Bujak (1984b), assigned to the late Campanian and early Maastrichtian respectively based on data from McIntyre (1974, 1975).

**13,280-16,400ft: No age determination**
Remarks: No palynomorphs were observed in this section of the well, so that it was not possible to determine the age based on the present palynological study.

2 NORTON SOUND COST NO. 1 WELL: BIOSTRATIGRAPHIC SUMMARY

1230-1410ft: *Filisphaera filifera* Zone (late Pliocene to early Pleistocene)

1410-2850ft: *Filisphaera pilosa* Zone (Pliocene)

2850-5012.2ft: *Hystrichosphaeropsis variabile* Zone (late Miocene)

5012.2-7920ft: *Heteraulacacysta campanula* Zone (latest late Oligocene to early Miocene)

7920-8340ft: *Impagidinium velorum* Zone (early Oligocene)

8430-12,150ft: *Trinovantedinium boreale* Zone (early Oligocene)

12,150-12,450ft: *Areosphaeridium dikyooplos* Zone (late Eocene)

NORTON SOUND COST NO. 1 WELL: DINOFLAGELLATE CYST ZONATION

1230-1410ft: *Filisphaera filifera* Zone (Pleistocene)

Remarks: The marine dinoflagellate *F. filifera* occurs rarely in this zone. The *F. filifera* Zone correlates with the lower part of the *Denticulopsis seminae - Actinocyclus occulatus* diatom Zone which occurs from 180-1320ft according to Turner (1983). This indicates an early Pleistocene age based on the diatom zonal scheme of Koizumi (1985). The *F. filifera* Zone is therefore assigned an undifferentiated Pleistocene age.

1410-2850ft: *Filisphaera pilosa* Zone (Pliocene)

Remarks: The upper part of the zone (1410-1860ft) is characterized by several algal species which have a brackish or freshwater habitat, but some marine dinoflagellate cysts such as *Brigantedinium* spp. also rarely occur. This indicates that the depositional environment was marine with some brackish water influence. This interval correlates with the upper part of the *Denticulopsis seminae* var. *fossilis - Denticulopsis kamtschatica* diatom Zone according to Turner (1983). This indicates a late Pliocene age based on the diatom zonal scheme of Koizumi (1985).
Protoperidiniacean dinoflagellate cysts such as *Brigantedinium* spp., *Selenopemphix* spp. and *Xandarodinium variabile* characterize the dinoflagellate cyst assemblages of the middle part of the *F. pilosa* Zone (1860-2400ft), but several species of the freshwater to brackish water also occur. This indicates that the depositional environment may have been a coastal area influenced by river discharge. *Xandarodinium variabile* has been recorded from the late Miocene to early Pleistocene by Bujak (1984a). This interval correlates with the lower part of the *Denticulopsis seminae var. fossilis - Denticulopsis kamtschatica* diatom Zone according to Turner (1983). This indicates a late Pliocene age based on the diatom zonal scheme of Koizumi (1985).

The lower part of the *F. filifera* Zone (2400-2850ft) correlates with the *Rouxia californica* diatom Zone below 2637ft according to Turner (1983). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

2850-5012.2ft: *Hystrichosphaeropsis variabile* Zone (late Miocene)

Remarks: The dinoflagellate cyst assemblages in the upper part of the *H. variabile* Zone (2850-3210ft) have low species diversity and only four species were found, all of which are considered to be marine. *Filisphaera filifera* is the most common. This interval correlates with the middle to upper part of the *Rouxia californica* diatom Zone which occurs from 2637-3464ft according to Turner (1983). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

Several marine dinoflagellate cyst species occur abundantly in the *H. variabile* Zone between 3210-3390ft and reflect an inner to middle shelf environment. This interval correlates with the lower and middle part of the *Rouxia californica* diatom Zone which occurs from 2637-3464ft according to Turner (1983), indicating a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

Marine dinoflagellate cysts have high species diversity in the interval 3390-4410ft with *Filisphaera filifera* being the most common and consistently present. Species belonging to the genera *Spiniferites*, *Impagidinium* and *Hystrichosphaeropsis* have a thin, non-pigmented and fragile cyst wall, a
characteristic of many colder-water gonyaulacacean taxa. These species include *Spiniferites frigidus*, *Impagidinium cornutum* and *Hystrochospaeropsis variabile*. This interval correlates with the upper part of the *Thalassionema schraderi - Actinocyclus ingens* diatom Zone which occurs from 3464-4493ft according to Turner (1983).

The dinoflagellate species diversity is high in the interval 4110-4470ft, and several species of *Operculodinium* and *Spiniferites* such as *O. alsium*, *O. wallii*, *S. reductus*, and *S. ellipsoideus* occur. This interval correlates with the lower part of the *Thalassionema schraderi - Actinocyclus ingens* diatom Zone which occurs from 3464-4493ft according to Turner (1983). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

*Achomosphaera spongiosa* is present in the interval 4470-5012.2ft and also occurs in Miocene sediments of Japan where it was recorded as *Achomosphaera sp. A* by Matsuoka (1983).

**5012.2-7920ft : Heteraulacacysta campanula Zone (latest late Oligocene to early Miocene)**

Remarks: The dinoflagellate cyst assemblages in the upper part of this zone (5012.2-6720ft) have the highest species diversity observed in the Norton COST No. 1 well. The species that occur this zone include *Operculodinium echigoense*, *Heteraulacacysta campanula*, *Operculodinium cf. centrocarpum*, *Lingulodinium machaerophorum*, *Lingulodinium brevispinosum*, *Cribroperidinium giuseppi*, *Tuberculodinium vanampaec*, *Tuberculodinium rossignolae*, *Systematophora ancyrea* and *Reticulatosphaera actinocoronata*. Several species which characterize this zone such as *O. echigoense*, *C. giuseppi*, *S. ancyrea*, and *R. actinocoronata* are known from the early to middle Miocene of Japan (Matsuoka, 1983). The stratigraphic ranges of these species are discussed in the section of this paper on composite zonation.

The marine dinoflagellate cyst assemblages in the lower part of the *H. campanula* Zone (6720-7920ft) have low species diversity, with *Operculodinium cf. centrocarpum* and *Systematophora ancyrea* being the most conspicuous components. The assemblage suggests a nearshore marine to brackish water depositional environment.
7920-8340 ft: *Impagidinium velorum* Zone (early Oligocene)

Remarks: *Impagidinium velorum* occurs in this zone and is also present in the early-middle Eocene to Pliocene of the Bering Sea and the northern North Pacific (Bujak 1984a).

8340-12,150 ft: *Trinovantedinium boreale* Zone (early Oligocene)

Remarks: This zone is characterized by the association of *Trinovantedinium boreale* and *Phthanoperidinium* sp. *T. boreale* has previously been recorded from upper Eocene strata of the Bering Sea by Bujak (1984a), but this species was subsequently found in the early Oligocene of Japan (Bujak and Matsuoka 1986a). The stratigraphic range of the species therefore appears to be late Eocene to early Oligocene in the western and northern North Pacific.

The association of *T. boreale* and *Phthanoperidinium* sp. indicates either alternating nearshore marine and brackish water deposition, or the input of brackish water material to a nearshore marine depositional site.

12,150-12,450 ft: *Areosphaeridium diktyoplokus* Zone (late Eocene)

Remarks: The palynomorph assemblages in this zone contain many caved specimens, rare reworked species and few palynomorphs considered to be in place. The preservation of dinoflagellate cysts is extremely poor, making taxonomic identifications difficult. The age of this zone is indicated as late Eocene and possibly older Eocene by the occurrence of *Hystrichokolpoma salacium* which is known mainly from middle to upper Eocene strata of the Atlantic - European region.

It is difficult to estimate the depositional environment of this zone, because the palynomorph assemblages have low species diversity and the specimens are poorly preserved so that they often could not be identified. However the presence of occasional marine dinoflagellates considered to be in place indicates some marine influence.
3 St. GEORGE BASIN COST NO. 2 WELL: BIOSTRATIGRAPHIC SUMMARY

1460-4340ft : Filisphaera pilosa Zone (Pliocene)
4340-7970ft : Hystrichosphaeropsis variabile Zone (late Miocene)
7970-12,330ft : Heteraulacacysta campanula Zone (latest late Oligocene and early Miocene)
12,330-12,560ft : early Eocene
12,560-13,290ft : late Paleocene
13,290-14,619ft : Early Cretaceous; probably Valanginian

ST. GEORGE BASIN COST NO. 2 WELL: DINOFLAGELLATE CYST ZONATION

1460-4340ft : Filisphaera pilosa Zone (Pliocene)

Remarks: Several marine dinoflagellate cysts including Filisphaera filifera, Impagidinium japonicum, I. velorum and Lejeunecysta sp. indet. are present in the upper part of this zone, plus a few reworked specimens of Systematophora ancyrea and Gonyaulacacysta sp. indet. Specimens of Leiosphaeridia spp., which may represent green algal cysts, also occur. The presence of Impagidinium japonicum and I. velorum indicates that the upper part of this zone is late Pliocene rather than Pleistocene in age, because these dinoflagellate cysts occur in the Pliocene of the southern Bering Sea (Bujak, 1984a) based on calibration against Koizumi’s (1973, 1975) and Barron’s (1980) diatom zones and Ling’s (1980) silicoflagellate-ebridian zones. The upper part of the interval from 1460-2090ft correlates with the upper part of the Denticulopsis seminae var. fossilis diatom Zone which occurs from 1460-2720ft. This indicates a late Pliocene age based on the diatom zonal scheme of Koizumi (1985).

Marine dinoflagellate cysts are rare in the lower part of the F. pilosa Zone from 2090-4340ft and have low species diversity, indicating a nearshore and probably cold-water depositional environment. The lower part of the F. pilosa Zone correlates with the Thalassiosira oestri, Denticulopsis seminae var. fossilis - Denticulopsis kamtschatica and lower part of the D. seminae var. fossilis diatom Zones according to Turner (1984a). This indicates an early to late Pliocene age based on the diatom zonal scheme of

4340-7970ft : *Hystrichosphaeropsis variabile* Zone (late Miocene)

Remarks: The marine dinoflagellate cysts, *Filisphaera filifera* and *Opeculodinium* cf. *centrocarpum* occur rarely in the upper part of this zone (4340-5690ft), indicating a nearshore marine environment. The *H. variabile* Zone between 5240-6050ft may correlate with part of the *Actinoptycus heliopelta* diatom Zone which was tentatively indicated in Turner (1984a). This indicates a late Miocene age based on the diatom zonal scheme of Koizumi (1985).

Several marine dinoflagellate cysts occur in the middle part of the *H. variabile* Zone (5690-6770ft), but they are all long-ranging. The overall assemblage in this section suggests an inner to middle shelf, possibly influenced by freshwater body, because the freshwater green alga *Pediastrum boryanum* is also present.

The dinoflagellates *Spiniferites hexatypicus* and *Impagidinium manumii* occur in the section 6770-7970ft and indicate a late Miocene age. *Impagidinium manumii* has been recorded from Miocene sediments of the Norwegian-Greenland Sea as *Leptodinium* sp. cf. IV by Manum (1976), and *Spiniferites hexatypicus* which is a senior synonym of *S. ovatus* of Bujak (1984a) has also been reported from the late Miocene of Japan (Matsuoka, 1983), the Bering Sea and northern North Pacific area (Bujak, 1984a; Bujak and Matsuoka, 1986a).

The overall assemblage in the interval 4340-7970ft suggests inner to middle shelf deposition with some brackish water influence.

7970-12,330ft : *Heteraulacacysta campanula* Zone (latest late Oligocene to early Miocene)

Remarks : Marine dinoflagellate cysts are common in this zone but these mostly do not include age-diagnostic species, although a few species are useful for estimating the age. *Heteraulacacysta campanula* occurs and is also present in the Norton Sound COST No. 1 well, and has a stratigraphic range extending into the middle Miocene in Italian Miocene stratotypes
(Powell 1986a,b) and this appears to be its youngest worldwide occurrence recorded to date. *Lejeunecysta convexa* also occurs in the *H. campanula* Zone and is known from the latest early Oligocene to earliest middle Miocene of Japan (Matsuoka unpublished data).

The high species diversity of marine dinoflagellate cysts indicates a dipositional environment that was probably warm water and middle to outer shelf.

12,330-12,560ft : Early Eocene (no zonal assignment)

Remarks: This interval is devoid of marine dinoflagellates and the age-assignment is based on the pollen *Erdtmanipollis egelenensis* which has been recorded from the lower Eocene of Germany by Krutzsch (1966) and *Paraalnippollenites alterniporus* which is known from the lower Eocene Reindeer Formation of the Canadian Beaufort-Mackenzie area (McIntyre 1984).

A brackish-water depositional environment is suggested by the absence of typical marine dinoflagellate cysts and the presence of the brackish water genus *Geiselodinium*.

12,560-13,290ft : late Paleocene (unnamed zone)

Remarks: Marine dinoflagellates are mostly absent from this interval and the age-assignment is based on the occurrence of the pollen *Paraalnippollenites confusus* which indicates a Paleocene age for this zone, even though this pollen has been recorded from strata assigned to the middle Eocene in Nevada (Wingate, 1983). Pollen of the *Momipites tenuipolis* group and *Triatriopollenites subtriangularis* also occur and have been previously recorded from the Paleocene of the eastern U.S.A. by Frederiksen (1979), and Frederiksen and Christopher (1978).

The marine dinoflagellate cyst species *Batiacasphaera criosa* occurs rarely. This species has been recorded from middle to upper Eocene strata of DSDP Leg 19, Site 183 by Bujak (1984a), but the earliest occurrence of this species is unknown. An inner shelf environment is tentatively suggested based on the presence of occasional marine dinoflagellate cysts.
Some probable Early Cretaceous reworked specimens of *Taurocusporidae reductus* and *Staplinispora* sp. also occur in this zone.

**13,290-14,619ft : Early Cretaceous : probably Valanginian (unnamedzone)**

Remarks: Dinoflagellate cysts occur abundantly in the zone. *Sirmiodinium grossii* predominates in the middle to lower part of the zone, *Heslertonia heslertonensis* occurs at 13,290ft, *Tanyosphaeridium isocalamus* and *T. magneticum* were observed at 13,600ft, and *Cassiculospaheridium magna* at 14,600ft. The association of these species indicates an Early Cretaceous, probable Valanginian, age for this zone and reflects a fully marine environment. There is no evidence based on the present palynological study to indicate the penetration of Jurassic or older sediments.

**IV Composite Dinoflagellate Zonation**

Three Bering Sea COST wells, the St. George Basin COST NO. 2, Norton Sound COST No. 1 and Navarin Basin COST No. 1, were examined and the following seven zones were erected based on dinoflagellate cysts and associated pollen and spores.

- *Filisphaera filifera* Zone (late Pliocene to early Pleistocene)
- *Filisphaera pilosa* Zone (early to late Pliocene)
- *Hystrophospheraeopsis variabile* Zone (late Miocene)
- *Heteraulacacysta campanula* Zone (latest late Oligocene to early Miocene)
- *Impagidinium velorum* Zone (early Oligocene)
- *Trinovantedinium boreale* Zone (early Oligocene)
- *Areosphaeridium dikyoplokus* Zone (late Eocene)

Correlation of these zones with the following Neogene palynological zonations are discussed in the following section of this paper.

3. The north Japan zonation of Matsuoka et al. (1987).
5. The Bay of Biscay zonation of Harland (1979).
Text-figure 4 Composite ranges of selected dinoflagellate cysts in the Navarin Basin COST No. 1, Norton Sound COST No. 1 and St. George Basin COST No. 2 wells in the Bering Sea.
Text-figure 5 Composite dinoflagellate cyst zonation in the Bering Sea COST wells.

The zonal scheme presented in this paper corresponds with those provisionally proposed by Bujak and Matsuoka (1986a) as follows: Heteraulacacysta campanula Zone = Heterauracacysta campanula Oppel-Zone, Hystrichosphaeropsis variabile Zone = Hystrichosphaeropsis sp. B. Oppel-Zone, Filisphaera pilosa Zone = Filisphaera sp. A Oppel-Zone, and Filisphaera filifera Oppel-Zone = Filisphaera filifera Zone.
FILISPHAERA FILIFERA ZONE

Age: late Pliocene to early Pleistocene.

Observed Section: Norton Sound COST No. 1 well, 1230-1410ft.

Taxa extending upwards into this zone: Filishphaera filifera, Impagidinium japonicum, Impagidinium velorum, Brigantedinium spp.

Taxa with the earliest appearances in the zone: None.

Equivalent palynozones: Laevigatosporites Zone in the Beaufort-Mackenzie area; Spiniferites frigidus Zone and Nematosphaeropsis lemniscata Zone in the northern North Pacific and the southern Bering Sea; Operculodinium centrocarpum Zone and the upper part of the Achomosphaera callosa Zone in the west coast of North Japan.

Discussion: The base of the F. filifera Zone is defined by the latest occurrence of Filisphaera pilosa. The Pleistocene age assigned to this zone is indicated primarily by the associated pollen-spore assemblages which lack Pinuspollenites and Tsugaepollenites and which are typical of the late Pleistocene to Holocene in Alaska (Heusser 1977, 1985). The F. filifera Zone in the Norton Sound COST No. 1 well also contains the silicoflagellate Distephanus octangulatus and Distephanus octaparius whose association indicates assignment spanning the Pleistocene Mesocena quadrangula Zone to the Pleistocene Dictyocha aculata aculata Zone (Turner in Turner (ed.), 1983).

The Laevigatosporites Zone of the Beaufort-Mackenzie area is correlated with the F. filifera Zone based on the abundance of Laevigatosporites, Stereisporites and commonly occurring Piceaepollenites and Polyvestibulopollenites. Based on the diatom-silicoflagellate microfossil assemblage associated with the palynomorphs of the F. filifera Zone, this zone is approximately equivalent to the Spiniferites frigidus and the Nematosphaeropsis lemniscata Zones of the northern North Pacific and the southern Bering Sea (Bujak, 1984a; Bujak and Matsuoka, 1986a), and also to the Operculodinium centrocarpum Zone and the upper part of the Achomosphaera callosa Zone in North Japan (Matsuoka et al., 1987).
Dinoflagellate cysts from the Bering Sea

FILISPHAERA PILOSA ZONE

Age: Pliocene.

Observed sections: Norton Sound COST No. 1 well, 1410-2850ft; Navarin Basin COST No. 1 well, 1536-2730ft; St. George Basin COST No. 2 well, 1460-4340ft.

Taxa with the latest occurrences in the zone: Brigantedinium spp., Filisphaera pilosa, Impagidinium japonicum, Impagidinium velorum, Hystrichokolpoma rigaudiae, Operculodinium cf. centrocarpum, Selenopemphix crenata, Selenopemphix nephroides, Selenopemphix quanta, Xandarodinium variabile.

Taxa with the earliest occurrences in the zone: Selenopemphix crenata, Selenopemphix quanta.

Equivalent palynozones: Chonopodipollis Zone in the Beaufort-Mackenzie area; Impagidinium japonicum Zone in the northern North Pacific and the southern Bering Sea; lower part of the Achomosphaera callosa Zone and the upper part of the Capillicysta fusca Zone in the west coast of North Japan.

Discussion: The top of the F. pilosa Zone is characterized by the highest occurrences of several marine dinoflagellates including F. pilosa. The base is characterized by the latest abundance of Hystrichosphaeropsis variabile and Spiniferites aquilonius.

Several marine to brackish water dinoflagellate cysts occur in this zone including the protoperidinacean taxa, Brigantedinium spp., Selenopemphix nephroides, Seleno. quanta and Xandarodinium variabile. Gonyaulacacean cysts that occur include Filisphaera filifera, Filisphaera pilosa, Impagidinium japonicum, Impagidinium velorum and Hystrichokolpoma rigaudiae.

The association of Xandarodinium variabile, Impagidinium japonicum and Impagidinium velorum characterizes the Pliocene Impagidinium japonicum Zone of the northern North Pacific and the southern Bering Sea (Bujak, 1984a; Bujak and Matsuoka, 1986a).
HYSTRICHOSPHEAROPSIS VARIABILE ZONE

Age: late Miocene.

Observed sections: Norton Sound COST No. 1 well, 2850-5012.2 ft; Navarin Basin COST No. 1 well, 2730-5370 ft; St. George COST No. 2 well, 4340-7970 ft.


Equivalent palynozones: *Tsugaepollenites* Zone in the Beaufort-Mackenzie area. *Spiniferites hexatypicus* Zone in the northern North Pacific and southern Bering Sea; *Capillicysta fusca* Zone and the upper part of the *Ooperculodinium echigoense* Zone in the west coast of North Japan.

Discussion: The top of this zone is characterized by the latest occurrences of several species including *H. variabile*, and the base by the latest occurrences of several taxa including *Heteraulacacysta campanula*, *Systematophora ancyrea*, *Systematophora placacantha* and *Dapsilidinium pastielsii*.

Based on the associated pollen, including an abundance of *Tsugaepollenites igniculus*, the *H. variabile* Zone is correlated with the Miocene *Tsugaepollenites* Zone in the Beaufort-Mackenzie area. The highest persistent occurrence of *Tsugaepollenites* takes place in younger strata in the St. George Basin COST No. 2 well than in the other two examined wells, suggesting that *Tsugaepollenites* persisted into younger strata in this area.
Text-figure 6 Correlation of the composite dinoflagellate cyst zones in the Bering Sea COST wells with Neogene dinoflagellate cyst zones from other areas.
than at the two other, more northern COST locations.

The marine dinoflagellate cyst assemblages in this zone comprise gonyaulacacean species, and in particular the genera *Spiniferites*, *Impagidinium* and *Hystrichosphaeropsis*. Most of these species occur in the Norton Sound COST No. 1 well, but are rare or scarce in the other two wells.

*Reticulatosphaera actinocoronata*, *Spiniferites hexatypicus*, and *Xandarodinium variabile* are common in several other high-latitude Miocene sections drilled in the southern Bering Sea, northern North Pacific and Norwegian-Greenland Sea by the Deep Sea Drilling Project, and the first two species are locally common in the Miocene of the Beaufort-Mackenzie area (Bujak, personal observation). *Impagidinium japonicum*, which is a senior synonym of *Impagidinium pacificum* Bujak, has only previously been recorded from the Pliocene of the southern Bering Sea and northern North Pacific (Bujak, 1984a; Bujak and Matsuoka, 1986a), and North Japan (Matsuoka, 1983).

**HETERAULACACYSTA CAMPANULA ZONE**

**Age**: latest late Oligocene to early Miocene.

**Observed sections**: Norton Sound COST No. 1 well, 5012.2-7920ft; Navarin Basin COST No. 1 well, 5370-11,000ft; St. George Basin COST No. 2 well, 7970-12,330ft.

**Taxa with latest appearances in the zone**: *Distatodinium paradoxum*, *Systematophora ancyrea*, *Systematophora placacantha*, *Heteraulacacysta campanula*, *Lingulodinium machaerophorum*, *Lingulodinium brevispinosum*, *Rottnestia ovata*, *Spiniferites pseudofurcatus*, *Tuberculodinium vancampoae*, *Dapsilidinium pastielsii*, *Pentadinium laticinctum granulatum*, *Lejeunecysta convexa*, *Diphyes* sp. cf. *colligerum*.

**Taxa with earliest appearances in the zone**: *Brigantedinium* spp., *Algidasphaeridium capillatum*, *Impagidinium manumii*, *Spiniferites ellipsoideus*, *Tuberculodinium rossignolaiæ*, *Opeculodinium alsium*, *Opeculodinium wallii*, *Spiniferites nortonensis*, *Achomosphaera spongiosa*, *Spiniferites hexatypicus*, *Heteraulacacysta campanula*, *Lingulodinium machaerophorum*, *Lingulodinium*
brevispinosum, Rottnestia ovata, Spiniferites pseudofurcatus, Tuberculodinium vancampoae, Dapsilidinium pastielsii, Pentadinium laticinctum granulatum, Lejeunecysta convexa, Hystrichokolpoma rigaudiae, Diphyes sp. cf. colligerum.

Equivalent palynozones: The upper part of Ericipites sp. A Zone in the Beaufort-Mackenzie area. The upper part of the Gelatia inflata Zone in the northern North Pacific.

Discussion: The dinoflagellate cyst assemblages of the Heteraulacacysta campanula Zone have the highest species diversity in the three examined COST wells. This assemblage mainly comprises three groups, the first consisting of Spiniferites adnatus, Spiniferites nortonensis and Lingulodinium brevispinosum. The second comprises Achomosphaera spongiosa, Spiniferites ellipsoideus, Operculodinium echigoense, Operculodinium wallii and Lejeunecysta convexa. The third includes Heteraulacacysta campanula, Polysphaeridium subtile, Reticulatosphaera actinocoronata, Selenopemphix nephroides, Systematophora ancyrea, Cribroperidinium giuseppei, Lingulodinium machaerophorum, Tuberculodinium rossignolii and Tuberculodinium vancampoae.

Dinoflagellate cysts of the first and second groups cannot be used to determine the age of the Heteraulacacysta campanula Zone, because the stratigraphic ranges of species of these groups are not fully known. The species of the first group were newly recorded in the Bering Sea during this study, and those of the second group have been described only in the latest early to late Miocene of North Japan, so that these species may extend into older strata.

Within the third group, Distatodinium paradoxum, Heteraulacacysta campanula, Cribroperidinium giuseppei, Systematophora ancyrea, Tuberculodinium rossignolii and Tuberculodinium vancampoae are important species for establishing the age of the Heteraulacacysta campanula zone.

The oldest age of the Heteraulacacysta campanula zone is given by the earliest appearance of Tuberculodinium vancampoae and T. rossignolii. The earliest appearance of these species are from the latest Late Oligocene of the Rockall Plateau (Costa and Downie, 1979), offshore eastern Canada (Williams and Bujak, 1977), and the Piedmont Basin in Italy (Powell, 1986a).
Stover (1977) recorded the earliest appearance of *Tuberculodinium vancampoae* in the Blake Plateau (western North Atlantic) in the *Globorotalia kugleri* Foraminiferal Zone which he assigned to the Early Miocene. However, Bolli and Saunders (1985, p. 159) subsequently placed this zone in the latest part of the Late Oligocene (24.6-25.5 Ma). Williams (1978, p. 788) recorded the earliest occurrence of *T. vancampoae* in core 5, section 1 of DSDP Site 370, Leg 41, offshore Morocco, in sediments assigned to the late Oligocene based on nannoplankton and radiolaria (*Sphenolithus distentus* and *Dorcadospyris ateuchus* Zones respectively). Foraminifera in this core suggest an age possibly extending into the middle Oligocene *Globorotalia opima opima* Zone (P 21).

Ioannides and Colin (1977) recorded *T. vancampoae* in core 5, section 3 of DSDP Site 358, Leg 39, in the southwestern Atlantic Ocean. The occurrence of *Deflandrea phosphoritica* in the core 5, section 1 indicates an age no younger than Oligocene, providing *D. phosphoritica* is in place.

The youngest age of this zone is indicated by the latest occurrences of *Cribroperidinium giuseppei*, *H. campanula* and *Distatodinium paradoxum*. *Cribroperidinium giuseppei* was first described from the early Eocene of northwest Europe by Morgenroth (1966) and was recorded from the early Eocene of the Rockall Plateau (Costa and Downie 1979), the middle Oligocene of Germany (Gocht, 1969 and Benedek, 1972), and the early Miocene of Japan (Matsuoka, 1983).

*H. campanula* was originally described from the Gulf Coast middle Eocene by Drugg and Loeblich (1967). The youngest age of this species is uncertain, although Williams and Bujak (1985) indicated its latest occurrence as being in Planktonic Foraminiferal Zone N8 and Calcareous Nannoplankton Zone NN5, near the base of the Middle Miocene. This is supported by data from the Lemme section of the Italian Piedmont Basin (Powell, 1986a).

*Distatodinium paradoxum* was first described by Brosius (1963) from the late Oligocene of Germany. Its latest described occurrence is in the early Miocene of offshore eastern Canada (Williams and Bujak, 1977). Piasecki (1980) listed this species from the possible middle Miocene Hodde Formation of Denmark, but the age of this formation was mainly based on the molluscan faunas and is uncertain. Therefore, the youngest definite
The age of the *Heteraulacacysta campanula* Zone is early Miocene.

This age is also supported by the occurrence of *Systematophora ancyrea*. The range of this species is middle Eocene to late Miocene in offshore eastern Canada (Williams and Bujak 1977; Williams and Brideaux 1975). However, in Japan this species which was described as *Areoligera senonensis* sensu Gocht by Matsuoka (1983) has its latest occurrence in the early Miocene (Matsuoka 1983; Matsuoka et al. 1987). Consequently based on the concurrent ranges of dinoflagellate cysts, the age of the *Heteraulacacysta campanula* Zone is probably latest late Oligocene to early Miocene.

The dinoflagellate cyst assemblages in this zone are characterized by the presence of warm-water species such as *Tuberculodinium vancampoae*, *Tuberculodinium rossignoliae* and *Lingulodinium machaerophorum*. According to Wall et al. (1977) and Harland (1982), *Tuberculodinium vancampoae* is a subtropical to warm-temperate species in the North Atlantic. Matsuoka (1985a) also concluded that this species and *Lingulodinium machaerophorum* characterize the warm (subtropical to warm-temperate) dinoflagellate cyst assemblages of the western Pacific. The dinoflagellate cyst assemblage of the *Heteraulacacysta campanula* Zone with the highest dinoflagellate species diversity seen in the examined sections from the Bering Sea suggests the warm oceanographic environment, because the species diversity of modern dinoflagellate cyst assemblages increase southwards in the western Pacific and the North Atlantic (Matsuoka, 1985a).

Sancetta (1978, 1979) discussed the paleoceanography in the Pacific during the Cenozoic based on successive assemblages of planktonic microfossils such as planktonic Foraminifera, calcareous nannofossils, radiolaria and diatoms, all of which were recovered from Deep Sea Drilling Project sites. Sancetta (1978) showed four paleo-biogeographic maps in the early Miocene (18-20 Ma), middle Miocene (10-12 Ma), latest Miocene (5-7 Ma) and latest Pleistocene to Holocene (0-0.1 Ma), and in 1979 also illustrated six maps in the Paleocene, early Eocene, late Eocene, early Oligocene and late Oligocene.

According to Sancetta (1978, 1979), two plankton provinces (Tropical and Transitional) were recognized in the late Oligocene of the North Pacific.
A Transitional Province occupied the area from 20°N to 40°N, but no data were available in the northern North Pacific. During the early Miocene, the Subarctic Province developed in offshore western Canada and the Gulf of Alaska. Sancetta (1978) estimated that the Subarctic Province extended westwards across the northern North Pacific and Bering Sea to the western margin, although there is no direct evidence available yet to substantiate this extension, the sites not being drilled to prove this.

Based on the general interpretations of Sancetta, the age of the *Heteraulacacysta campanula* Zone would tend to be late Oligocene, although there is a possibility that it may extend into the early Miocene (but earlier than 18-20 Ma).

**IMPAGIDINUM VELORUM ZONE**

Age: probably early Oligocene.

Observed sections: Norton Sound COST No. 1 well, 7920-8340ft; Navarin Basin COST No. 1 well, 11,000-12,680ft.

Taxa with latest occurrences in the zone: *Lejeunecysta fallax*, *Lejeunecysta granosa*, *Chiropteridium mespilatum*.

Taxa with earliest appearances in the zone: *Impagidinium velorum*, *Lejeunecysta fallax*, *Lejeunecysta granosa*, *Chiropteridinium mespilatum*.

Equivalent palynozones: *Boisduvalia clavatites* Zone in the Beaufort-Mackenzie area. Lower part of the *Spiniferites sp. cf. membranaceus* Zone and possibly also the upper part of the *Trinovantedinium boreale* Zone in the northern North Pacific.

Discussion: This zone was recognized in the Navarin Basin COST No. 1 and Norton Sound COST No. 1 wells, and includes occasional dinoflagellate markers including *Lejeunecysta granosa*. In the Norton Sound COST No. 1 well it is possible that early Oligocene species are reworked into the *Heteraulacacysta campanula* Zone. This interpretation would indicate that the *H. campanula* Zone directly overlies the early Oligocene *Trinovantedinium boreale* Zone, and that the *Impagidinium velorum* Zone is absent from the Norton Sound COST No. 1 well.
Dinoflagellate cysts from the Bering Sea

TRINOVANTEDINIUM BOREALE ZONE

Age: early Oligocene.

Observed sections: Norton Sound COST No. 1 well, 8340-12,150ft: Navarim Basin COST No. 1 well, 12,680-12,770ft.

Taxa with latest occurrences in the zone: *Hystrichosphaeropsis complanata*, *Phthanoperidinium bennettii*, *Lejeunecysta hyalina*, *Trinovantedinium boreale*.

Taxa with earliest appearances in the zone: *Reticulatosphaera actinocoronata*, *Tectatodinium minutum*, *Selenopemphix nephroides*, *Hystrichosphaeropsis complanata*, *Lejeunecysta hyalina*.

Equivalent palyzones: *Boisduvalia clavatites* Zone in the Beaufort-Mackenzie area. Upper part of *Trinovantedinium boreale* zone in the northern North Pacific.

Discussion: The occurrence of *Reticulatosphaera actinocoronata* indicates that the *Trinovantedinium boreale* Zone is no older than early Oligocene. This is supported by the presence of *Hystrichosphaeropsis complanata* which has been described from the early Oligocene of Germany (Eisenack 1954).

*Trinovantedinium boreale* was first described from the northern North Pacific by Bujak (1984a), who suggested that the species is restricted to the late Eocene. Bujak and Matsuoka (unpublished data) subsequently showed that the range extends into the early Oligocene based on its range in southwest Japan.

In the northern North Pacific, the early Oligocene dinoflagellate cyst assemblages described by Bujak (1984a) include *Operculodinium centrocarpum*, *Spiniferites ramosus*, *Spiniferites* sp. cf. *S. membranaceus*, *Impagidinium velorum*, *Impagidinium pallidum*, *Gelatia inflata*, *Hystrichokolpoma* sp. cf. *H. cinctum* and *Hystrichostegylon membraniphorum*. Most of these species were not observed in this study and in the *Ericipites* sp. A Zone of the Beaufort-Mackenzie area by Bujak (1984b).
AREOSPHAERIDUM DIKTYOPLOKUS ZONE

Age: late Eocene.

Observed sections: Navarin Basin COST No. 1 well, 12,770-12,920ft; Norton Sound COST No. 1 well, 12,150-12,450ft.

Taxa with latest occurrences in the zone: Areosphaeridium diktyoplokus, Hystrichokolpoma salacium.

Taxa with the earliest appearances in the zone: Systematosphaera ancyrea, Systematophora placacantha, Trinovantedinium boreale, Hystrichokolpoma salacium, Areosphaeridium diktyoplokus, Phthanoperidinium bennettii.

Equivalent palynozones: Upper part of Tiliaepollenites vescipites Zone in the Canadian Beaufort-Mackenzie area. Lower part of Trinovantedinium boreale Zone in the northern North Pacific.

Discussion: The top of this zone is defined primarily by the latest occurrences of Areosphaeridium diktyoplokus and Hystrichokolpoma salacium, and the base by the earliest appearance of Areosphaeridium diktyoplokus.

Areosphaeridium diktyoplokus, which is a cosmopolitan middle to late Eocene species, has been recorded locally from the Alaska Peninsula, Aleutian Islands (Evitt 1973), the northern North Pacific and the Bering Sea (Bujak 1984a), but this species does not apparently occur in the Canadian Beaufort-Mackenzie area. Areosphaeridium diktyoplokus sensu stricto does not range above the late Eocene.

Trinovantedinium boreale is abundant in this zone in the St. George Basin No. 2 COST well and shows morphological variations in spine length through the section. Older specimens have relative longer spines that those originally illustrated by Bujak (1984a) from lower Oligocene strata of northern North Pacific DSDP sites. Younger specimens from the lower Oligocene sections have shorter species that are of comparable length to those observed by Bujak. This may reflect ecological variation of popula-
tions that coexisted, or alternatively an evolutionary trend from populations with shorter spines to populations with longer spines. Examination of 10ft spaced cuttings samples through this section indicates the latter to be more likely, suggesting that the upper Eocene section in the St. George Basin No. 2 COST well is a condensed sequence.

Relatively low dinoflagellate cyst species diversity is one of the characteristics of the *Areosphaeridium diktyoplokus* Zone, with a high dominance of the species *Areosphaeridium diktyoplokus*, *Trinovantedinium boreale* and *Phthanoperidinium bennettii*. This is also a characteristic of the dinoflagellate cyst assemblages recovered from DSDP Site 183 (Bujak 1984a), but without the observed occurrence of *P. bennettii*.

V List of dinoflagellate and acritarch species

The following species of dinoflagellate cysts and acritarchs are recorded from the Navarin Basin COST No. 1 well, Norton Sound COST No. 1 well and St. George Basin COST No. 2 well.

**Dinoflagellata**

**Gymnodiniales?**

Genus *Algidasphaeridium* gen. nov.

*Algidasphaeridium capillatum* gen. et sp. nov. (Pl. 2, figs. 4-6)

**Peridiniales**

Genus *Achomosphaera* Evitt, 1963

*Achomosphaera spongiosa* sp. nov. (Pl. 1, figs. 5-7; Pl. 2, figs. 1-3)

Genus *Areosphaeridium* Eaton, 1971

*Areosphaeridium diktyoplokus* (Klumpp) Eaton, 1976 (Pl. 1, figs. 1-3)

Genus *Batiacasphaera* Drugg, 1970

*Batiacasphaera criosa* (Bujak) Jan du Chêne, Stover and De Coninck 1984 (Pl. 17, figs. 6-7)

Genus *Brigantedinium* Reid, 1977

*Brigantedinium* spp. (Pl. 17, figs. 6-7)

Genus *Chiropteridium* Gocht, 1960

*Chiropteridium mespilatum* (Maier) Lentin and Williams, 1973
Genus *Cribroperidinium* Neale and Sarjeant, 1962
*Cribroperidinium giuseppei* (Morgenroth) Helenes, 1984 (Pl. 8, figs. 5-6)

Genus *Dapsilidinium* Bujak, Downie, Eaton and Williams, 1980
*Dapsilidinium pastieiisii* (Davey and Williams) Bujak, Downie, Eaton and Williams, 1980 (Pl. 2, figs. 8-9)

Genus *Diphyes* Cookson, 1965
*Diphyes sp. cf. D. colligerum* (Deflandre and Cookson) Cookson, 1965 (Pl. 2, figs. 11-12)

Genus *Distatodinium* Eaton, 1976
*Distatodinium fusiforme* (Matsuoka) Bujak and Matsuoka, 1986 (Pl. 3, fig. 1)
*Distatodinium paradoxum* (Brosius) Eaton, 1976

Genus *Evittosphaerula* Manum, 1979
*Evittosphaerula sp. A* (Pl. 3, fig. 2)

Genus *Filisphaera* Bujak, 1984
*Filisphaera filifera* Bujak, 1984 (Pl. 3, figs. 3-4)
*Filisphaera pilosa* sp. nov. (Pl. 3, figs. 5-9)

Genus *Heteraulacacysta* Drugg and Loeblich, 1967
*Heteraulacacysta campanula* Drugg and Loeblich, 1967 (Pl. 4, figs. 1-2)

Genus *Hystrichokolpoma* Klumpp, 1953
*Hystrichokolpoma rigaudiae* Deflandre and Cookson, 1955 (Pl. 4, fig. 3)
*Hystrichokolpoma salacium* Eaton, 1976 (Pl. 4, fig. 4)
? *Hystrichokolpoma* sp. (Pl. 4, fig. 5)

Genus *Hystrichosphaeropsis* Deflandre, 1935
*Hystrichosphaeropsis arctica* sp. nov. (Pl. 5, figs. 1-4)
*Hystrichosphaeropsis complanata* Eisenack, 1965 (Pl. 4, fig. 6)
*Hystrichosphaeropsis variabile* sp. nov. (Pl. 5, figs. 5-8)
*Hystrichosphaeropsis* sp. cf. *H. obscula* Habib, 1971 (Pl. 4, fig. 7)

Genus *Hystrichostrogylon* Agelopoulos, 1964
*Hystrichostrogylon membraniphorum* Agelopoulos, 1964 (Pl. 5, fig. 9)

Genus *Impagidinium* Stover and Evitt, 1978
Impagidinium cornutum sp. nov. (Pl. 5, fig. 10; Pl. 6 figs. 1-2)
Impagidinium japonicum Matsuoka, 1983 (Pl. 6, figs. 3-4)
Impagidinium manumii sp. nov. (Pl. 6, figs. 5-7)
Impagidinium patulum (Wall) Stover and Evitt, 1978
Impagidinium velorum Bujak, 1984 (Pl. 6, fig. 8)

Genus Kallospaeridium De Coninck, 1969
Kallospaeridium sp. (Pl. 7, fig. 1)

Genus Lejeunecysta Artzner and Dörhöfer, 1978
Lejeunecysta convexa sp. nov. (Pl. 7, fig. 2)
Lejeunecysta fallax (Morgenroth) Artzner and Dörhöfer, 1978 (Pl. 7, fig. 4)
Lejeunecysta granosa Biffi and Grignai, 1983 (Pl. 7, fig. 5)
Lejeunecysta hyalina (Gerlach) Artzner and Dörhöfer, 1978

Genus Lingulodinium Wall, 1967
Lingulodinium brevispinosum sp. nov. (Pl. 7 figs. 8-9; Pl. 8, fig. 1)
Lingulodinium machaerophorum (Deflandre and Cookson) Wall, 1967 (Pl. 7, fig. 7)

? Litosphaeridium parvum sp. nov. (Pl. 8, figs. 2-4)

Genus Operculodinium Wall, 1967
Operculodinium alsium sp. nov. (Pl. 8, figs. 7-9)
Operculodinium echigoense Matsuoka, 1983 (Pl. 9, fig. 1)
Operculodinium wallii Matsuoka, 1983 (Pl. 9, fig. 2)
Operculodinium sp. cf. O. centrocarpum (Deflandre and Cookson) Wall, 1967

Genus Phthanoperidinium Drugg and Leblich, 1967
Phthanoperidinium bennettii sp. nov. (Pl. 9, figs. 4-9)

Genus Pentadinium Gerlach, 1961
Pentadinium laticinctum granulatum Gocht, 1969 (Pl. 9, fig. 3)

Genus Polysphaeridium Davey and Williams, 1966 emend. Bujak, Downie, Eaton and Williams, 1980
Polysphaeridium subtile Davey and Williams, 1966

Genus Reticulatosphaera Matsuoka, 1983
Reticulatosphaera actinocoronata (Bencde) Bujak and Matsuoka, 1986 (Pl. 9, figs. 10-12).

Genus Rottnestia Cookson and Eisenack, 1961
Rottnestia ovata sp. nov. (Pl. 10, figs. 1-2)
Genus *Selenopemphix* Benedek, 1972

*Selenopemphix crenata* sp. nov. (Pl. 10, figs. 6-7)
*Selenopemphix nephroides* Benedek, 1972 (Pl. 10, figs. 3-5)
*Selenopemphix quanta* (Bradford) Matsuoka, 1985

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

*Spiniferites adonatus* sp. nov. (Pl. 10, figs. 8-9; Pl. 11, figs. 1-3)
*Spiniferites aquilonius* sp. nov. (Pl. 11, fig. 6; Pl. 12, fig. 1)
*Spiniferites choanus* sp. nov. (Pl. 13, fig. 7; Pl. 14, figs. 2-3)
*Spiniferites ellipsoideus* Matsuoka, 1983 (Pl. 12, figs. 2-3)
*Spiniferites frigidus* Harland and Reid, 1980 (Pl. 12, figs. 4-5)
*Spiniferites hexatypicus* Matsuoka, 1983 (Pl. 12, figs. 6-7)
*Spiniferites nortonensis* sp. nov. (Pl. 13, figs. 1-2)
*Spiniferites pseudofurcatus* (Klumpp) Sarjenat, 1970 (Pl. 14, fig. 1)
*Spiniferites ramosus ramosus* (Ehrenberg) Loeblich and Loeblich, 1966 (Pl. 13, fig. 3)
*Spiniferites ramosus gracilis* (Davey and Williams) Lentin and Williams, 1973 (Pl. 13, fig. 4)
*Spiniferites reductus* sp. nov. (Pl. 14, figs. 4-5)
*Spiniferites varmae* Lentin and Williams, 1973
*Spiniferites* sp. cf. *S. membranaceus* (Rossignol) Sarjeant, 1970 (Pl. 13, fig. 5)

Genus *Systematophora* Klement, 1960

*Systematophora ancyrea* Cookson and Eosenack, 1965 (Pl. 15, fig. 1-5)
*Systematophora curta* sp. nov. (Pl. 15, figs. 8-11)
*Systematophora placacantha* (Deflandre and Cookson) Devey, Downie, Sarjeant and Williams, 1966 (Pl. 15, figs. 6-7)

Genus *Tectatodinium* Wall, 1967

*Tectatodinium minutum* Matsuoka, 1983 (Pl. 18, fig. 10)

Genus *Tuberculodinium* Wall, 1967

*Tuberculodinium rossignoliae* Drugg, 1970 (Pl. 16, fig. 7)
*Tuberculodinium vancampoa* (Rossignol) Wall, 1970 (Pl. 16, figs. 8-9; Pl. 17, figs. 1-4)

Genus *Xandarodinium* Reid, 1977

*Xandarodinium variabile* Bujak, 1984 (Pl. 17, fig. 15)
Order Uncertain
   Genus *Paralecaniella* Cookson and Eisenack, 1970
   *Paralecaniella identata* (Deflandre and Cookson) Cookson and
   Eisenack, 1970 (Pl. 18, fig. 2)

Acritarcha
   Genus *Cyclopsiella* Drugg and Loeblich, 1967
   *Cyclopsiella* sp. (Pl. 18, fig. 4)
   Genus *Halodinium* Bujak, 1984
   *Halodinium minor* Bujak, 1984 (Pl. 18, fig. 1)
   Genus *Joviella* nov.
   *Joviella magnifica* gen. et sp. nov. (Pl. 18, figs. 5-8)

VI Systematic Description

1 Terminology
   Descriptive terms used in the systematic description are outlined in
   Evitt et al. (1977) for wall structure, paraplates and paratabulation; Stover
   and Evitt (1978) for general cyst shape and size; Sarjeant (1982a) for
   process and other ornament morphology; and Evitt (1985) and Matsuoka
   (1985b) for archeopyle and operculum morphology.

2 Dinoflagellata
   Phylum Pyrrhophya Pascher, 1914
   Class Dinophyceae Fritsch, 1929
   Order Gymnodiniales Lemmermann, 1910
   Genus *Algidasphaeridium* nov.

   *Derivation of name*: Latin algidus + sphaera, cold + ball; with reference to its
   present geographical distribution.

   *Type species*: *Algidasphaeridium capillatum* n. sp., Late Miocene, Nava-
   rin Basin COST No. 1 Well, Bering Sea.

   *Diagnosis*: Spherical skolochorate cysts consisting of a granular pe-
   riphragm and endophragm, covered with numerous solid spines with closed
   distal tips. Apical and antapical horns absent. No ornament representing
   paratabulation. Archopyle chasmic (slit like).

   *Discussion*: *Algidasphaeridium* resembles an acritarchous genus *My-*
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**crhystridium**, but differs from the latter in possessing a chasmic archeopyle and a cyst wall consisting of two layers.

Matsuoka (1985d) reattributed *Multispinula quanta*, the type species of *Multispinula*, to the genus *Selenopemphix* and made a new combination, *Selenopemphix quanta* (Bradford, 1977). As a result, the species *Multispinula? minuta*, which was tentatively assigned to *Multispinula* by Harland and Reid (in Harland et al., 1980), is transferred below to *Algidasphaeridium*, although the archeopyle of this species is presently unknown.

*Algidasphaeridium? minutum* (Harland and Reid, 1980) comb. nov.

**Synonym:** *Multispinula? minuta* Harland and Reid 1980, p. 216-218, fig. 2 M-0.

**Derivation of name:** Latin *capillatus*, hairy; with reference to the hair-like processes.

**Diagnosis:** Small spherical cysts composed of two layers closely adpressed except at the spines. Cyst wall non-pigmented; periphragm thin and granular. Numerous nontabular spines short, solid, flexuous and sometimes distally capitae and closed. No features reflecting paratabulation. Archeopyle chasmic and approximately one-fifth of the cyst diameter.

**Holotype:** Navarin Basin COST No. 1 well, 4530-4620ft, Ring 4 (Plate 2, fig. 5).

**Paratypes:** Navarin Basin COST No. 1 well, 4530-4620ft, Ring 5 (Plate 2, fig. 4); Ring 8 (Plate 2, fig. 6).

**Type locality and horizon:** Navarin Basin COST No. 1 well, 4530-4560ft, central Bering Sea; *Hystrichosphaeropsis variabile* Zone, late Miocene.

**Description:** The small proximate cyst is spherical and covered with numerous hair-like processes. These process are nontabular, flexuous, closed at the proximal and distal ends, and simple or sometimes capitae distally. Paratabular features are absent. The archeopyle is chasmic and formed by a split of about one-fifth of the cyst diameter.

**Dimensions:** Holotype; cyst diameter 32 µm, length of processes 3 µm. Range; Cyst diameter 27-34 µm, length of processes 3-4 µm. Number of specimen measured; 5.

**Discussion:** Several spherical cysts with numerous hair-like processes have been reported to date from surface sediments. These cysts include
Dinoflagellate cysts from the Bering Sea


Algidasphaeridium capillatum is similar to A.? minutum and to Dinoflagellate cyst D of Reid and Harland 1977 in having numerous, solid and flexuous processes. It differs from A.? minutum in its smaller cyst diameter and chasmic archeopyle, and from Dinoflagellate cyst D in not having capitate process terminations.

Thecal affinities: Probably Gymnodiniaceae. The chasmic archeopyle has been observed in modern cysts of Pheopolykrikos hartmannii (Matsuoka and Fukuyo, 1986), Cochlodinium sp. (Matsuoka, 1985b) and Gymnodinium catenatum.

Order Peridiniales Haeckel, 1894

Genus Achomosphaera Evitt, 1963

Type species: Achomosphaera ramulifera (Deflandre, 1937) Evitt, 1963 = Hystrichosphaeridium ramuliferum Deflandre, 1937

Achomosphaera spongiosa sp. nov.
Plate 1, figs. 5-7; Plate 2, figs. 1-3

Achomosphaera sp. A, Matsuoka, 1983, p. 130, pl. 11, fig. 1-5, text-fig. 16
Spiniferites sp./ Achomosphaera sp., Wiggins, 1986, pl. 1, fig. 3.
Achomosphaera sp., Wiggins, 1986, pl. 1, fig. 4.

Derivation of name: Latin, spongion, spongy; with reference to the spongy wall.

Diagnosis: Ellipsoidal to ovoidal proximochorate cyst comprising two layers which are mostly in contact; periphragm thick, spongy and granular; endophragm relatively thin and smooth. Apical and antapical borns absent. Parasutures occasionally visible. Gonal processes with bi- or trifurcate distal extremities. Sutural processes absent. Archeopyle precingular, formed by the loss of plate 3".

Holotype: Navarin Basin COST No. 1 well, 5370-5460ft, Ring 10 (Plate 2, fig. 2).
Paratypes: Navarin Basin COST No. 1 well, 5370-5460ft, Ring 5 (Plate 1, fig. 7); St. George Basin COST No. 2 well, 11,740-11,830ft, Ring 2 (Plate 1, fig. 5).

Type locality and horizon: Navarin Basin COST No. 1 well, 5370-5400ft, Navarin Basin, Bering Sea. *Heteraulacacysta campanula* Zone; late Oligocene to early Miocene.

Description: The cyst is intermediate to small in size, mostly ovoidal to ellipsoidal but rarely subspherical, without apical or antapical horns. The periphragm is spongy, but corroded specimens (shown by Matsuoka 1983, pl. 11, fig. 1-2, 4-5) have a coarsely reticulate appearance. The processes are gonal and solid with trifurcate and rarely bifurcate endings. Stalks of processes are sometimes ornamented with grana and in poorly preserved specimens are perforated due to corrosion. The parasutures are strongly reduced and occasionally faintly visible. The paratabulation is 4', ?a, 6", 6c, 6", 1p, 1"", xs. The archeopyle is precingular, formed by loss of the 3" paraplate. The operculum is free.

Dimensions: Holotype; length of cyst 52µm, width 45µm, length of processes up to 12µm. Range; length of cyst 41-58µm, width of cyst 33-48µm, length of processes 8-13µm. Number of specimens measured 10.

Remarks: The species described as *Achomosphaera* sp. A by Matsuoka is identical with *Achomosphaera spongiosa*. Many of Matsuoka’s specimens are corroded and their periphragm appeared to be reticulate, but relatively well-preserved specimens (Matsuoka, 1983, pl. 11, fig. 3) show the spongy wall structure and absence of reticulation.

Wiggins (1986) recorded the presence of forms intermediate between *Spiniferites* sp. (Wiggins, 1986, pl. 1, figs. 1,2) and *Achomosphaera* sp. (Wiggins, 1986, pl. 1, fig. 4) in the upper Miocene of the Bering Sea which are considered to be synonymous with *A. spongiosa*.

*Achomosphaera spongiosa* resembles *A. sagena* Davey and Williams, *A. callosa* Matsuoka, and *A. crassipellis* (Deflandre and Cookson) in possessing a relatively thick wall and occasionally faint parasutures. It differs from *A. sagena* in having a thinner endophragm and relatively elongate cyst body, and from *A. callosa* and *A. crassipellis* in having a spongy and thinner periphragm.

Previously known range: Early to late Miocene of the west coast of North Japan (Matsuoka, 1983; Matsuoka et al., 1987); late Miocene of the Bering Sea (Wiggins, 1986).

Thecal affinity: Probably Gonyaulacaceae based on its paratabulation.
Genus *Areosphaeridium* Eaton, 1971  

*Areosphaeridium diktyoplokus* (Klumpp, 1953) Eaton, 1971  
Plate 1, figs. 1-3

*Hystrichosphaeridium diktyoplokus* Klumpp, 1953, p. 392, pi. 18, fig. 3-7.  
*Areosphaeridium diktyoplokus* (Klumpp) Eaton, p. 358-359, pl. 1, fig. 3-8; pl. 2, fig. 1-6.

**Previous records**: *Areosphaeridium diktyoplokus* has a worldwide distribution in the middle to late Eocene. It has also been recorded from Oligocene and younger sediments in north Germany (Maier, 1959), Chile (Archangelsky and Fasola, 1971) and Romania (Baltes, 1967), but may be reworked. In the northern North Pacific and the Aleutian Islands, *Areosphaeridium diktyoplokus* was also recorded from upper Eocene sediments by Scholl *et al.*, (1970), Evitt (1976) and Bujak (1984a).

**Thecal affinity**: Possibly Gonyaulacaceae based on its paratabulation.

Genus *Batiacasphaera* Drugg, 1970  
Type species: *Batiacasphaera compta* Drugg, 1970

*Batiacasphaera criosa* (Bujak, 1984) Jan du Chene, Stover and De Coninck, 1984  
Plate 18, fig. 9

*Kallosphaeridium criosum* Bujak, 1984, p. 188, pl. 2, figs. 17-20.  
*Batiacasphaera criosa* (Bujak) Jan du Chene, Stover and De Coninck, 1984, p. 15.

**Remarks**: This species is transferred from *Kallosphaeridium* to *Batiacasphaera* based on possessing four apical paraplates and poorly developed lobes.

**Previous record**: Middle to Late Eocene in the Bering Sea (Bujak 1984a).  
**Thecal affinities**: Unknown.

Genus *Chiropteridium* Gocht, 1960  
Type species: *Chiropteridium lobospinosum* (Gocht in Weiler, 1956)
Gocht, 1060 = *Hysterichosphaeridium lobospinum* Gocht, 1956.

*Chiropteridium mespilatum* (Maier, 1959) Lentin and Williams, 1973
Plate 2, fig. 7

*Galea galea* Maier, 1959, p. 306, pl. 29, fig. 4, text-fig. 2.
*Galea mesnilana* Maier, 1959, p. 306-307, pl. 29, fig. 5-6.
*Galea levis* Maier, 1959, p. 308, pl. 30, fig. 1-2.
*Chiropteridium dispersum* Gocht, 1960, p. 227, pl. 18, fig. 1-16, text-fig. 16-27.
*Membranophoridium partispinosum* Gerlach, 1961, p. 201, pl. 29, fig. 6.
*Chiropteridium galea* (Maier) Sarjeant, 1983, p. 108-111, pl. 1, fig. 1, 5, pl. 2, fig. 1-3, pl. 3, fig. 3, pl. 5, fig. 1.

**Discussion:** According to Sarjeant (1983), the three species which were originally attributed to the genus *Galea* by Maier (1959) are conspecific because the morphological variations of these species lie within the range of *Chiropteridium dispersum* observed by Gocht (1960). Sarjeant (1983) proposed a new combination and selected *Chiropteridium galea* (Maier) for this species. *Galea galea*, however, is a tautonym and illegitimate (Lentin and Williams, 1985), so that *Chiropteridium mespilatum* (Maier, 1959) Lentin and Williams, 1973, is the valid name for this species.

During this study, only a single free operculum of this species was observed. The processes on the operculum bear irregularly furcate distal extremities.

**Previous records:** Most records of this species are restricted to the late Oligocene and earliest early Miocene (Williams and Bujak, 1985). Powell (1986a) recorded this species from upper Oligocene to lower Miocene of the Lemme section of Italy.

**Genus Cribroperidinium** Neale and Sarjeant, 1962 emend.
Davey, 1969; emend Sarjeant, 1982; emend Helenes, 1984

**Type species:** *Cribroperidinium sepimentum* Neale and Sarjeant, 1962.

*Cribroperidinium giuseppei* (Morgenroth, 1966) Helenes, 1984
Plate 7, figs. 5-6

*Gonyaulax giuseppei* Morgenroth, 1966, p. 5, pl. 2, fig. 3-6.
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*Cribroperidinium giuseppei* (Morgenroth) Helenes, 1984, p. 121-122, p. 2, fig. 6-11, pl. 4, fig. 8-13, text-fig. 6G-I.

**Discussion**: This species is characterized by its subspherical to ovoidal shape, the epi- and hypocyst being similar in size. Stover and Evitt (1978) provisionally reattributed *Gonyaulax giuseppei* to *Millioudodinium* because the species has some accessory ridges. Helenes (1984) who revised the genus *Cribroperidinium*, concluded that the development of accessory ridges is not diagnostic for distinguishing *Millioudodinium* from *Cribroperidinium*, and proposed the combination *Cribroperidinium giuseppei*.

**Previously known range**: Eocene to Oligocene (Helenes, 1984). Matsuoka (1983) recorded this species from the middle to late Miocene of North Japan.

**Thecal affinities**: *Cribroperidinium giuseppei* is a species which is probably related to the modern genus *Gonyaulax* based on its paratabulation, archeopyle and the presence of a ventral pore on the epicyst.

Genus *Dapsilidinium* Bujak et al., 1980

Type species: *Dapsilidinium pastielsii* (Davey and Williams, 1966) Bujak, et al., 1980 = *Polysphaeridium pastielsii* Davey and Williams.

*Dapsilidinium pastielsii* (Davey and Williams, 1966) Bujak et al., 1980

Plate 2, figs. 8-9

*Polysphaeridium pastielsii* Davey and Williams, 1966, p. 92-93, pl. 4, fig. 10.

*Dapsilidinium pastielsii* (Davey and Williams, 1966) Bujak et al., 1980, p. 28.

**Discussion**: *Dapsilidinium pastielsii* is similar to *Diphyes colligerum* (Deflandre and Cookson) in having long conical processes with capitate tips, but differs in lacking a large antapical process. *D. pastielsii* is distinguished from *Polysphaeridium zoharyi* (Rossignol) in having an apical archeopyle, and from *D. pseudocolligerum* (Stover) in having shorter and wider processes.

**Previous record**: Early to late Eocene of England (Bujak et al., 1980) and late Oligocene to middle Miocene of northwest Italy (Powell, 1986a, b).


Type species: *Diphyes colligerum* (Deflandre and Cookson, 1955)
Cookson, 1965 = *Hystrichosphaeridium colligerum* Deflandre and Cookson, 1955

*Diphyes sp. cf. colligerum* (Deflandre and Cookson, 1955) Cookson, 1965  
Plate 2, figs. 11-12; Text-fig. 7

*Hystrichosphaeridium colligerum* Deflandre and Cookson, 1955, p. 278-279, pi. 7, fig. 3.  
*Diphyes colligerum* (Deflandre and Cookson) Cookson, 1965, p. 86-87, pi. 9, fig. 1-12.  
*Diphyes colligerum* (Deflandre and Cookson) Cookson emend. Davey and Williams, 1966, p. 96-97, pl. 4, fig. 2-3.

Text-figure 7 *Diphyes sp. cf. colligerum* (Deflandre and Cookson) Cookson, 1965.  
a: Morphological variation in the process shape, b: Lateral view. Scale bar; 10 μm.

**Description** : Chorate cysts intermediate in size, with a wall consisting of a granular periphragm and smooth endophragm adpressed except at the processes. Two types of processes are present. The large antapical process is open distally and is cylindro-conical, whereas the other smaller processes are slender, tapering, vary in length, and may or may not be open distally. Adjacent processes occasionally fuse at the base. The archeopyle is apical tetratabular with a free operculum.

**Dimensions** : Range; cyst diameter 42-45 μm × 56-68 μm, length of antapical process 15-27 μm, length of slender processes up to 20 μm. Number of specimens measured: 5.

**Discussion** : The present specimens of *Diphyes sp. cf. colligerum* are characterized by having slender processes of varying length. These speci-
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Mens are also distinctive because of their large cyst diameter (58-70μm). *Diphyes colligerum* from the Eocene London clay is 30-33μm (Davey and Williams, 1966), in Popes Creek, Maryland, is 35-44μm (Goodman and Witner, 1985), in Hanover, Virginia, is 28-45μm (Goodman and Witner, 1985), in Oak Grove, Virginia is 32-42μm (Goodman and Witner, 1985).

*Thecal affinites*: Probably related to the Gonyaulacaceae.

Genus *Distatodinium* Eaton, 1976
Type species: *Distatodinium craterum* Eaton, 1976

*Distatodinium fusiforme* (Matsuoka, 1974) Bujak and Matsuoka, 1986
Plate 3, fig. 1

*Tanyosphaeridium fusiform* Matsuoka, 1974, p. 332-333, pi. 46, fig. 4, 9-10.
*Distatodinium fusiforme* (Matsuoka) Bujak and Matsuoka, 1986, p. 236

*Discussion*: *Tanyosphaeridium fusiform* was described by Matsuoka (1974) and was reattributed to the genus *Distatodinium* by Bujak and Matsuoka (1986b) because of its distally branched processes. This species differs from *D. craterum* Eaton in lacking trabeculae and from *D. paradoxum* (Brosius) in possessing a more elongate cyst body. *D. fusiforme* differs from *D. ellipticum* (Cookson) in having fewer processes.

*Previously known range*: Early to middle Miocene of central Japan (Matsuoka, 1974).

*Thecal affinity*: Unknown; possibly related to the *Gonyaulax* lineage based on its tabulation.

Genus *Evittosphaerula* Manum, 1979
Type species: *Evittosphaerula paratabulata* Manum, 1979

*Evittosphaerula*? sp. A.
Plate 3, fig. 2

*Description*: The intermediate proximate cyst consists of a central body and ectophragmal network. Processes may be absent between the central body and the ectophragm. The central body is spherical and has a smooth surface. The outer ectophragmal network indicates an incomplete gonyaulacacean paratabulation, but it is difficult to determine this in detail.
owing to poor preservation and folding. Trabeculae are mostly slender and without ornament, and are wider and membranous gonally. The archeopyle has not been determined.

**Dimensions**: Range; diameter of central body 28-31 μm, diameter of overall cyst 48-56 μm. Number of specimens measured: 2.

**Discussion**: The present species is similar to *Evittosphaerula paratabulata* in its ectophragmal network, but differs in having a central body. *Evittosphaerula?* sp. A differs from *Nematosphaeropsis labyrinthea* in lacking processes and paired trabeculae.

**Thecal affinities**: Unknown, but based on its paratabulation this species may be attributable to the *Gonyaulax* lineage

Genus *Filisphaera* Bujak, 1984

Type species: *Filisphaera filifera* Bujak, 1984

*Filisphaera filifera* Bujak, 1984

Plate 3, figs. 3-4

*Tectatodinium pellitum* Wall, Matsuoka 1983, p. 128, pl. 5, fig. 1-2.

*Filisphaera filifera* Bujak 1984, p. 185, pl. 1, fig. 7-12.

**Remarks**: The morphological differences between *Filisphaera filifera* and *F. pilosa* are discussed below.

**Previously known range**: Late Miocene to early Pleistocene of Japan (Matsuoka et al. 1987), the northern North Pacific and the eastern Bering Sea (Bujak 1984a).

**Thecal affinity**: Unknown. Possibly a member of the *Gonyaulax* lineage based on its precingular archeopyle.

*Filisphaera pilosa* sp. nov.

Plate 3, figs. 5-9

**Derivation of name**: Latin, *pilus*, hair; with reference to the small spines scattered on the cyst surface.

**Diagnosis**: Spherical to subspherical proximate cyst with two distinct ornament types on the surface and with neither apical nor antapical horns; short spines densely distributed and relatively large granules scattered randomly. No ornament reflects the paratabulation except the archeopyle.
No features delimit either the paracingulum or parasulus. Archeopyle precingular, formed by the loss of paraplate 3°.

**Holotype**: St. George Basin COST No. 2 well, 1910-2000ft, Ring 2, (Plate 3, fig. 7).

**Paratypes**: Slide St. George Basin COST No. 2 well, 1460-1550ft, Ring 6, (Plate 3, fig. 9); Norton Sound COST No. 1 well, 2490-2520ft, Ring 2 (Plate 3, fig. 5).

**Type horizon**: St. George Basin COST No. 2 well, 3710-3800ft, *Filisphaera pilosa* Zone, St. George Basin, Southern Bering Sea; early to late Pliocene.

**Description**: The proximate cyst is spherical to subspherical without apical or antapical projections. The cyst wall consists of a thin endophragm and thicker periphragm composed of radiating fibers. Small dark granules are sparsely and randomly distributed on the cyst surface. The remainder of the periphragm bears densely spaced short slender spines. Processes and other features reflecting the paratabulation are lacking except for the archeopyle. The paracingulum and parasulcus are also absent. The archeopyle is trapezoidal and precingular, formed by the loss of paraplate 3°.

**Dimensions**: Holotype; cyst diameter 52 μm, length of radial spines ca. 0.8 μm, diameter of grains ca. 0.8 μm. Range: cyst diameter 41-53 μm.

**Number of specimens measured**: 10.

**Remarks**: *Filisphaera pilosa* differs from *F. filifera* in having solid granules that are sparsely distributed on the cyst surface. *F. pilosa* differs from species of *Tectatodinium* and *Operculodinium* in possessing short fibrous spines.

**Thecal affinities**: Unknown, but possibly related to the *Gonyaulax* lineage based on its precingular archeopyle.

**Genus Heteraulacacysta** Drugg and Loeblich, 1967; emend, Bujak in Bujak et al., 1980

**Type species**: *Heteraulacacysta campanula* Drugg and Loeblich, 1967

*Heteraulacacysta campanula* Drugg and Loeblich, 1967
Plate 4, figs. 1-2

*Heteraulacacysta campanula* Drugg and Loeblich, 1967, p. 183-184, pl. 1, fig. 6-8c, text-fig. 2.
Discussion: Heteraulacacysta campanula is characterized by its smooth to granular periphragm due to its lenticular body which is compressed antero-posteriorly and epicystal archeopyle. This species is most commonly seen in polar view.

Previously known range: Early Oligocene to early Miocene (Williams and Bujak, 1985). Powell (1986 a,b) also recorded specimens similar to H. campanula from the late Oligocene to middle Miocene of the Piedmont Basin of northeastern Italy.

Thecal affinities: This species may be closely related to the modern genus Triadinium (= Goniodoma Stein, 1883, or Heteraulacus Diesing, 1850). Drugg and Loeblich (1967) observed that the paratabulation of Heteraulacacysta campanula is similar to that of modern thecate species Triadinium polyedricus (= Heteraulacus polyedricus), particularly with respect to the presence of an apical pore paraplate and three antapical paraplates. Stover and Evitt (1978) subsequently considered that this cyst species is more closely related to the genus Pyrodinium than to the Triadinium, but did not clarify their opinion.

Pyrodinium and Triadinium both have the same plate formula of 3', 7", 6c, 6"', 1"", 1p, 5s, but the distinction between them is based on the distribution of plates. In the genus Triadinium the first precingular plate is separated from the second apical plate, whereas in the genus Pyrodinium plate 1" contacts plate 2'.

According to the present observations and the paratypes illustrated by Drugg and Loeblich (1967; pl. 1, fig. 6), Heteraulacacysta campanula does not possess a first precingular paraplate which contacts the second apical paraplate. H. campanula may therefore be more closely related to the modern genus Triadinium.

Genus Hystrichokolpoma Klumpp, 1953; emend. Williams and Downie, 1966

Type species: Hystrichokolpoma cinctum Klumpp, 1953

Hystrichokolpoma rigaudiae Deflandre and Cookson, 1955
Plate 4, fig. 3

Hystrichokolpoma rigaudiae Deflandre and Cookson, 1955, p. 279-281, pl. 6, fig. 6, 10, text-fig. 42.
Previous known range: The oldest known occurrence of *Hystrichokolpoma rigaudiae* is from the middle Eocene of England (Williams and Downie, in Davey et al., 1966), and the youngest occurrence is in the early Pleistocene of Japan (Matsuoka, 1976, 1979, 1983) and the Pleistocene of Israel (Rossignol, 1962).

Thecal affinities: Based on the paratabulation represented by the processes and archeopyle, *Hystrichokolpoma rigaudiae* may have affinities with the Gonyaulacaceae. However, no modern genus of this family possesses 1" and 2" paraplates which are strongly reduced, and a 4' paraplate which contacts the anterior sulcal paraplate, all features characteristic of *Hystrichokolpoma*.

*Hystrichokolpoma salacium* Eaton, 1976
Plate 3, fig. 4

*Hystrichokolpoma salacium* Eaton 1976, p. 271-272, pl. 11, figs. 1-3, text-fig. 16.

Discussion: *Hystrichokolpoma salacium* differ from *H. rigaudiae* in having the majority of processes without distal tubules and frequently with longitudinal folding at the distal extremities.

Previously known range: early Eocene to early Oligocene (Williams and Bujak, 1985).

Thecal affinities: Unknown. This species may be related to the modern Gonyaulacaceae based on its paratabulation.

Type species: *Hystrichosphaeropsis ovum* Deflandre, 1935

*Hystrichosphaeropsis arctica* sp. nov.
Plate 5, figs. 1-4

Derivation of name: Greek, arctoios, northern; with reference to the geographical distribution of this species.

Diagnosis: Bicavate intermediate cyst, ellipsoidal to ovoidal, consisting of a thin, smooth transparent periphragm and endophragm adpressed around the paracingulum. Epicyst subspherical with a well-developed pericoel and without an antapical horn. Apical pericoel sometimes reduced;
antapical pericoel variable and with coarsely reticulate distal extremity. Parasutural septa strongly reduced and periphragm highly folded, so that the paratabulation is not represented except for the paracingulum and archeopyle sutures. Parasulcus and paracingulum weakly delimited by a shallow indentation of the cyst wall. Archeopyle precingular, formed by the loss of paraplate 3°.

**Holotype**: Norton Sound COST No. 1 Well, 3030-3060ft, Ring 5 (Plate 5, fig. 4).

**Paratype**: Norton Sound COST No. 1 Well, 4470-4500ft, Ring 6 (Plate 5, fig. 2).

**Type location and horizon**: Norton Sound COST No. 1 Well, 3030-3060ft, Norton Sound, Bering Sea; *Hystrichosphaeropsis variabile* Zone, late Mio-cene.

**Description**: The ellipsoidal to ovoidal cyst sometimes possesses a small apical boss which may be rarely absent. The endocyst is also ellipsoidal. The cyst wall comprises a smooth, thin and unornamented periphragm, and an endophragm adpressed to the periphragm along the paracingulum. The parasutural septa are faintly developed except for a well-developed paracingulum and parasulcus. An antapical pericoel is sometimes present.

**Discussion**: *Hystrichosphaeropsis arctica* sp. nov. is similar to *H. obscura* Habib and *H. variabile* sp. nov., but differs from the former in possessing a smooth thin endophragm and in lacking a well-developed apical pericoel. *H. arctica* is distinguished from *H. variabile* in lacking a conspicuous apical horn and sometimes an antapical pericoel, although intermediate forms between *H. arctica* and *H. variabile* occur with a variably developed apical horn and parasutural septa. This intergradation suggests that *H. arctica* and *H. variabile* may be related.

**Dimension**: Holotype; over all length 51 µm, width 33 µm, length of endocyst 41 µm, length of apical horn 4 µm. Range: over all length 51-62 µm, width 33-38 µm, length of endocyst 40-41 µm, length of apical horn 0-4 µm, Number of specimens measured: 6.

**Thecal affinities**: Unknown, although *H. arctica* is probably a member of the Gonyaulacaceae based on its precingular archeopyle.

*Hystrichosphaeropsis complanata* Eisenack, 1965

Plate 4, fig. 6
Hystrichosphaeropsis complanata Eisenack, 1965, p. 153, pl. 14, fig. 5-7, pl. 15, fig. 5, text-fig. 2-3.

Discussion: Hystrichosphaeropsis complanata is similar to H. ovum Deflandre and H. obscura Habib in having well-developed apical and antapical pericoels, but differs from both in having a lateral pericoel around the paracingulum. This periceol is shown in the specimen illustrated by Eisenack (1965, pl. 14, fig. 6 and text-fig. 3).

Previous record: late Eocene to early Oligocene of West Germany (Eisenack, 1965).

Thecal affinities: Unknown, although this species may be related to the modern Gonyaulacaceae.

Hystrichosphaeropsis variabile sp. nov.
Plate 5, figs. 5-8; Text-fig. 8.

Derivation of name: Latin, variabilis, changeable; with reference to the variable cyst body and ornament.

Text-figure 8  Hystrichosphaeropsis variabile sp. nov. Oblique lateral view of the holotype. Scale bar; 10 μm.

Diagnosis: Ovoidal to ellipsoidal, intermediate cavate cyst. Epicyst broadly conical with a short apical horn; hypocyst subspherical with a conspicuous pericoel and without horns. Cyst wall comprising thin, smooth to chagrinate periphragm and a thin endophragm, both phragma adpressed at the paracingulum and over most of the epicyst. Parasutural septa high and smooth, without distal ornament. No furcate processes occur gonally.
Paratabulation incompletely reflected by parasutural septa as 4’ (?) , 6”, 6c, 6””, 1p (?), 1””, xs. Paracingulum indicated by six rectangular paraplates which are transversely expanded. Parasulcus delimited by parasutural ridges, but number of parasulcal plates unknown. Archeopyle precingular, sometimes reduced and formed by the loss of paraplate 3”.

**Holotype**: Norton Sound COST No. 1 well, 3930-3960ft, Ring 3 (Plate 5, fig. 5).

**Paratype**: Norton Sound COST No. 1 well, 3840-3870ft, Ring 5 (Plate 5, fig. 6).

**Type horizon and Locality**: Norton Sound COST No. 1 well, 3930-3960ft, Norton Sound, Bering Sea; *Hystrichosphaeropsis variabile* Zone; late Miocene.

**Description**: The overall cyst shape varies from elongate ovoidal to polygonal. A smooth to chagrinate periphragm and endophragm are mostly in contact on the epicyst, the epicystal pericoel being relatively small and cornucavate. An apical horn is usually present and is short and distally closed. The hypocystal pericoel is variably developed and is distally open with a hypocystal flange that is sometimes irregularly reticulate to roughly denticulate. The parasutural crests are smooth, high and membranous, without processes and easily deformed. The paracingulum is well-developed and almost circular, and the parasulcus is represented by a shallow indentation of the periphragm. Owing to the thin and smooth parasutural septa, the parasuture between the 1’ and 4’ is often reduced. The paratabulation is often incompletely indicated. The archeopyle is trapezoidal and precingular (3”).

**Dimensions**: Holotype; overall length 71μm, width 40μm, length of endocyst 48μm, length of apical horn 8μm, width of paracingulum ca. 6μm. Range: overall length 48-71μm, width 35-40μm, length of endocyst 35-48μm, length of apical horn 5-8μm. Number of specimens measured: 6.

**Discussion**: *Hystrichosphaeropsis variabile* is similar to *Spiniferites frigidus* Harland and Reid, which was first described as *Rottnestia amphicavata* by Dobell and Norris (in Harland et al., 1980), in possessing a well-developed antapical pericoel, but differs in lacking processes. *H. variabile* also resembles *H. obscura*, but differs in having a smooth surface of the inner capsule, and a more strongly developed antapical pericoel with roughly reticulate to denticulate distal extremity.

**Thecal affinities**: Unknown, but possibly related to the Gonyaulacaceae.

Hystrichosphaeropsis? rectangularis Bujak in Bujak et al., 1980, p. 66, pl. 16, fig. 10-12, text-fig. 15.

Discussion: H.? sp. cf. H. rectangularis is characterized by its hypocystal pericoel and the absence of parasutural processes and an apical horn. These features also characterize Hystrichosphaeropsis? rectangularis, but the specimens from the Bering Sea differ from H.? rectangularis in lacking an apical pericoel and a well-defined paracingulum.

This species differs from Hystrichosphaeropsis variabile in possessing a more spherical body and in lacking a distinctive apical horn.

Thecal affinities: Unknown, but possibly related to the Gonyaulacaceae.

Genus Hystrichostrogylon Agelopoulos, 1964; emend.

Stover and Evitt, 1978

Type Species: Hystrichostrogylon membraniphorum Agelopoulos, 1964

Hystrichostrogylon membraniphorum Agelopoulos, 1964

Plate 5, fig. 9

Hystrichostrogylon membraniphorum Agelopoulos, 1964, p. 674, text-fig. 1-2.


Previously known range: Early to middle Eocene according to Williams and Bujak (1985), with additional records from the early to middle Miocene of North Japan (Matsuoka, 1983), the early Oligocene of the northern North Pacific (Bujak, 1984a), and the upper Oligocene to the middle Miocene of Italy (Powell, 1986a,b).

Thecal affinities: This species is similar to species of Spiniferites, some of which are the cyst stage of the modern genus Gonyaulax.

Genus Impagidinium Stover and Evitt, 1978

Type species: Impagidinium dispertitum (Cookson and Eisenack, 1965)

Stover and Evitt, 1978 = Leptodinium dispertitum Cookson and Eisenack, 1965

Impagidinium cornutum sp. nov.
Impagidinium sp. of Wiggins, 1986, pl. 4, figs. 1-6.

Text-figure 9 Impagidinium cornutum sp. nov.  
Ventral surface of the holotype.  
Scale bar ; 10 μm.

Derivation of name: Latin, cornutus, bearing horns ; with reference to the apical horn.

Diagnosis: Small to intermediate proximate cyst with an ovoidal to roundly hexagonal shape. Epicyst roundly triangular in dorso-ventral view, slightly larger than hypocyst and bearing a distinctive small apical horn; hypocyst trapezoidal in dorso-ventral view and lacking an antapical horn. Cyst wall comprising a smooth periphragm and endophragm. Parasutures membranous, sometimes perforated, mostly low but distinct and representing the paratabulation as 4', 6", 6c, 6"", 1p, 1"" and xs. Paraplate 4' similar to the 1' in shape and size; 6" narrowly triangular; 1"" longitudinally narrow. Paracingulum displaced by twice of its width; slightly helicoidal; anterior and posterior sulcal paraplates present, but others obscure. Archeopyle precingular (3") ; operculum detached.

Holotype: Norton Sound COST Well No. 1, 3570-3600ft, Ring 1, (Plate 6 fig. 1).

Paratype: Norton Sound COST No. 1 Well, 3570-3600ft, Ring 5 (Plate 6, fig. 2); Norton Sound COST No. 1 Well, 4380-4410ft, Ring 6 (Plate 5, fig. 10).

Type horizon and locality: Norton Sound COST No. 1 Well, 3570-3600ft, Norton Sound, Bering Sea; Hystrichophaeropsis variabile Zone; late Miocene.

Description: The cyst body varies from ovoidal to roundly polygonal with a hypocyst that is usually trapezoidal in dorso-ventral view. The epicyst varies from trapezoidal to roundly triangular in dorso-ventral view and forms a short, conical, hollow horn that is distally closed and sometimes truncated. The distinct parasutures are membranous and sometimes
perforated. The paratabulation indicated by the parasutural septa is 4', 6', 6c, 6", 1p, 1", xc, although the boundary between the first and fourth apical paraplates is usually strongly reduced. The 3' paraplate does not contact the 6" paraplate which is smaller and typically triangular. All of the precingular paraplates except for the sixth have distinct parasutures. All six cingular paraplates are developed and are transversely rectangular, and the paracingulum is laevorotary and displaced by approximately one to two paracingular width. Paraplate 1" is reduced and the 1p paraplate is located below the 2" paraplate. The parasulcus is slightly curved and extends onto the epicyst but does not reach the centre of the hypocyst. The precingular archeopyle is slightly reduced and is formed by the loss of paraplate 3'.

**Dimensions**: Holotype; length of cyst 52μm, width 44μm, length of apical horn 6μm, height of parasutures ca. 3μm. Range: length of cyst 45-52μm, width 39-44μm, length of apical horn 5-7μm, height of parasutures 3-4μm. Number of specimens measured: 6.

**Remarks**: *Impagidinium cornutum* sp. nov. is similar to *I. japonicum* Matsuoka in having distinctive parasutures and a complete set of precingular plates. However, the characteristic apical horn and perforated parasutural septa distinguish *I. cornutum* from this species and other species of *Impagidinium*.

*I. cornutum* resembles *Psaligonyaulax cf. simplicia* (Cookson and Eisenack) recorded from the middle to late Eocene of the Norwegian-Greenland Sea by Manum (1976, pl. 2, fig. 5, 6), but differs in possessing a shorter and more spherical cyst body and a less well-developed hypocystal pericoel. Wiggins (1986) recorded the *Impagidinium* sp. which is probably conspecific with *I. cornutum* from core material of the Navarin Basin in the Bering Sea.

**Thecal affinities**: *Impagidinium cornutum* may be related to the modern Gonyaulacaceae based on its paratabulation and archeopyle type.

*Impagidinium japonicum* Matsuoka, 1983
Plate 6, figs. 3-4

*Impagidinium japonicum* Matsuoka, 1983, p. 120-121, pl. 6, fig. 3-5, text-fig. 13.

**Discussion**: The ovoidal to subspherical cyst shape distinguishes *Im-
**Impagidinium japonicum** from *I. strialatum* (Wall) which has a more elongate cyst body. *I. japonicum* also has an almost complete paratabulation except at the parasulcus, whereas *I. strialatum* always possesses reduced parasutures in several areas, as discussed by Bujak (1984).

**Previous record:** Early Pliocene to early Pleistocene of North Japan (Matsuoka, 1983) and the early and late Pliocene of the northern North Pacific and the Bering Sea (Bujak 1984).

**Thecal affinities:** Based on its paratabulation, *Impagidinium japonicum* is probably a member of the modern Family Gonyaulacaceae.

*Impagidinium manumii* sp. nov.
Plate 6, figs. 5-7; Text-fig. 10

*Leptodinium* sp. IV Manum 1976, pl. 1, fig. 18

**Derivation of name:** Named after Dr. Svein Manum for his work on Tertiary dinoflagellate cysts of the Norwegian-Greenland Sea.

**Diagnosis:** Intermediate proximate cyst with an ovoidal to ellipsoidal shape. Epicyst broadly triangular in dorso-ventral view, approximately equal to the hypocyst in size, and without an apical projection; hypocyst hemispherical without antapical horns. Cyst wall composed of a thick spongy periphragm and a thin smooth endophragm, adpressed except at the parasutural septa. Septa roughly undulate, somewhat membranous, low and granular, and clearly representing the paratabulation, 4', 6", 6c, 6", 1p, 1"", xs. The 4' paraplate is rectangular, similar to paraplate 1' in shape and size; paraplate 6" narrowly triangular; paraplate 1"" small, usually strongly reduced and narrowly rectangular. Paracingulum distinct
and displaced laevorotary; parasulcus delimited by parasutural septa, and straight to slightly sigmoidal. Archeopyle precingular, formed by the loss of paraplate 3°.

**Holotype**: Norton Sound COST No. 1 Well, 3840-3870ft, Ring 2 (Plate 6, fig. 5).

**Paratype**: Norton Sound COST No. 1 Well, 3930-3960ft, Ring 8 (Plate 6, fig. 6).

**Type horizon and locality**: Norton Sound COST No. 1 Well, depth 3840-3870ft, Norton Sound, Bering Sea; *Hystrichophaeropsis variabile* Zone; late Miocene.

**Description**: The central body is generally longer than broad, although specimens with a spherical endocyst rarely occur. The periphragm is spongy, 1.5 to 2 µm thick and forms parasutural septa which are undulate and well-developed over the entire cyst. Paraplate 6° is typically triangular and has parasutural crests that are lower in height than the other precingular paraplates. The 1° paraplate is much reduced. The paracingulum is well-defined by parasutural septa and almost complete, laevorotary and displaced by half its own width. The parasulcus extends onto the epicyst, widens toward the antapex, and comprises paraplates as, ps, ls, rs. The archeopyle is trapezoidal, precingular and formed by the loss of paraplate 3°.

**Dimensions**: Holotype; length of central body 54 µm, width 54 µm, height of parasutural septa ca, 4 µm, thickness of cyst wall ca, 2 µm. Range; length of cyst 54-56 µm, width 48-54 µm, height of parasutural septa 5-6 µm. Number of specimens measured; 5.

**Remarks**: *Impagidinium manumii* resembles *I. sphaericum* (Wall), but differs in having a thicker spongy periphragm and in lacking an apical boss. *I. manumii* is also similar to *I. multiplexum* (Wall and Dale) in possessing a granular periphragm, but differs in having lower parasutural septa (about one-third of the cyst diameter) and well-developed paracingular plates. *Leptodinium* sp. IV of Manum (1976, pl. 1, fig. 18) and *Impagidinium* sp. of Wiggins (1986, pl. 2, fig. 1-2) may be conspecific with *Impagidinium manumii*.

Wiggins (1986) noted that *Impagidinium* sp. has five precingular paraplates, because the paraplate which is equivalent to the 6° paraplate in Kofoidian terms appears to be missing. Based on observation of this species in the Bering Sea, the 6° paraplate is variable in shape, is sometimes not strongly reduced, and therefore the presence of this paraplate can be recognized from the topological relations in the parasulcus, paracingulum,
the 5" and 4' paraplate.

Previous record: Leptodinium sp. IV of Manum was recorded from the early Miocene of the Norwegian-Greenland Sea (Manum 1976), and Impagidinium spp. of Wiggins (1986) was also recorded from the late Miocene of the Bering Sea.

Thecal affinities: Based on its paratabulation, this species is probably related to the modern genus Gonyaulax.

Impagidinium velorum Bujak, 1984
Plate 6, fig. 8

Impagidinium velorum Bujak, 1984, p. 187-188, pl. 2, fig. 13-16.

Discussion: Impagidinium velorum is characterized by its small spherical central body with very high membranous parasutural septa. It is difficult to determine a paratabulation owing to the high septa. Some specimens observed during this study are slightly different from the holotype and paratype shown by Bujak (1984, pl. 2, fig. 13-16) in having septa with irregularly denticulate to serrate margins.

Previous record: Middle-late Eocene to late Pliocene of DSDP Sites 183, 186, 189 and 192 in the northern North Pacific and the Bering Sea (Bujak, 1984a), and late Miocene to late Pliocene of North Japan (Matsuoka, unpublished data).

Thecal affinities: This species may be related to the modern Family Gonyaulacaceae.

Genus Lejeunecysta Artzner and Dörhöfer, 1978; emend. Bujak in Bujak et al., 1980

Type species: Lejeunia hyalina Gerlach, 1961 = Lejeunecysta hyalina (Gerlach, 1961) Artzner and Dörhöfer, 1978

Lejeunecysta convexa sp. nov.
Plate 7, fig. 2; Plate 19, figs. 1-2; Text-fig. 11

Lejeunecysta sp. A of Powell, 1986b, pl. 3, fig. 2.

Derivation of name: Latin, convex; with reference to the convex outline of the hypocyst in dorso-ventral view.
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Text-figure 11  *Lejeunecysta convexa* sp. nov. A : Dorsal surface of the holotype B ; Ventral surface of the paratype C ; Dorsal surface of another specimen. Scale bar ; 10 μm.

*Diagnosis*: Intermediate to small proximate pentagonal cyst compressed dorso-ventrally. Epicyst longer than hypocyst, conical with concave to straight sides in dorso-ventral view with two small acuminate antapical horns. Cyst wall comprising an autophragm which is brownish-pigmented and smooth without ornament. Paracingulum well-developed; parasulcus shallow. Paratubulation absent except for archeopyle and paracingulum. Archeopyle simple intercalary, formed by the loss of paraplate 2a.

*Holotype*: St. George Basin COST No. 2 Well, 9830-9920ft, Ring 4 (Plate 6, fig. 2).

*Paratype*: Slide no. SZ 561219 K2 (Plate 19, fig. 1, Text-fig. 11B), Nishikurosawa Formation. Oga Peninsula, Akita, Japan. Early to early Middle Miocene.

*Type horizon and locality*: St. George Basin COST No. 2 Well, 9830-9920ft, St. George Basin, Bering Sea. *Heteraulacacysta campanula* Zone; late Oligocene to early Miocene.

*Description*: The sides of the epicyst vary in dorso-ventral view from straight to convex and those of the hypocyst from straight to concave. The cyst wall is pigmented brown, non-fluorescent and consists of an autophragm with a smooth surface. Two conspicuous antapical horns diverge slightly. The paracingulum is continuous but weakly marked by folds. The parasulcus is represented by a shallow indentation. The intercalary archeopyle is trapezoidal and is formed by the loss of paraplate 2a.

*Dimensions*: Holotype; length of cyst 59 μm, width 55 μm length of antapical horns 8 μm. Range; length of cyst 46-59 μm width 32-55 μm. Number of specimens measured: 5.
Discussion: *Lejeunecysta convexa* is similar to *L. pulchra* Biffi and Grignani and *Lejeunea* sp. B of Bradford, 1977, in its elongate pentagonal cyst body. The new species differs from *L. pulchra* in lacking a conspicuous apical horn and weak indentation between the two antapical horns, and in possessing a clearly marked paracingulum. It differs from *Lejeunecysta* sp. B of Bradford, 1977, in possessing two well-developed antapical horns.

Previous record: Early Oligocene Ashiya Group of West Japan, middle Miocene Onnagawa Formation of North Japan (Matsuoka, unpublished data) and the middle Miocene (Serravalliam) of the Piedmont Basin, Italy (Powell, 1986b).

Thecal affinities: Unknown; possibly a cyst of the subgenus *Protoperidinium* based on its brownish single cyst wall and simple intercalary archeopyle formed by the loss of paraplate 2a.


Plate 7, fig. 4

*Lejeunea fallax* Morgenroth 1966, p. 2-3, pl. 1, fig. 6-7.

Discussion: Specimens assigned to *Lejeunecysta fallax* in this study differ from the specimens of *L. fallax* recorded from the late Miocene to late Pliocene of the northern North Pacific and the Bering Sea by Bujak (1984a) in lacking an apical projection, and are more similar to the holotype of Morgenroth (1966; pl. 1, fig. 6). Morphological variation in this species also includes the degree of antapical horn development.

Previous records: Middle Oligocene of Germany (Morgenroth, 1966, Benedek, 1972); middle Eocene to Oligocene of DSDP Site 370 (Williams, 1978); late Oligocene to early Miocene of DSDP Site 338, Norwegian-Greenland Sea (Manum, 1976); Oligocene of Nigeria (Biffi and Grignani, 1983); late Miocene to late Pliocene of DSDP Sites 185, 187, 188, 189 and 190, northern North Pacific and Bering Sea (Bujak, 1984a).

Thecal affinities: Unknown; possibly a cyst of the subgenus *Protoperidinium* based on its brownish pigmented single cyst wall and intercalary archeopyle formed by the loss of paraplate 2a.

*Lejeunecysta granosa* Biffi and Grignani, 1983
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Plate 7, fig. 5


Discussion: Lejeunecysta granosa is characterized by an autophragm bearing small granules and a paracingulum delineated by two rows of granules. The parasulcus widens towards the antapex. The specimens from the Bering Sea different slightly from the holotype illustrated by Biffi and Grignani (1983; pl. 4, fig. 2) in having a more elongate cyst body and two small antapical horns. These differences are considered to fall within the morphological variation of the species.

Previous record: Oligocene of Nigeria (Biffi and Grignani, 1983).

Thecal affinities: Unknown; possibly related to the modern subgenus Protoperidinium.

Lejeunecysta hyalina (Gerlach, 1961; emend. Kjellstrom, 1972)
Artzner and Dörhöfer, 1978
Plate 7, fig. 6


Discussion: Lejeunecysta hyalina differs from L. fallax in having an epicyst which is similar in length to the hypocyst, and in having two well-developed antapical horns. Intermediate forms between these two species were occasionally observed during the present study.

Previously known range: Middle Eocene to early Miocene (Williams and Bujak, 1985).

Thecal affinities: Unknown; possibly related to the modern thecate subgenus Protoperidinium based on its brownish pigmented wall and intercalary archeopyle formed by the loss of paraplate 2a.

Genus Lingulodinium Wall, 1967; emend. Wall and Dale in Wall et al., 1973
Type species: Lingulodinium machaerophorum (Deflandre and Cookson, 1955) Wall, 1967 = Hystrichosphaeridinium machaerophorum Deflandre and
Cookson, 1955

*Lingulodinium brevispinosum* sp. nov.
Plate 7, figs. 8-9; Plate 8, fig. 1

*Lingulodinium* sp. B, Williams and Brideaux, 1975, pl. 18, figs. 3-4.

*Derivation of name*: Latin, *brevis* + *spinōsus*, short + thorny; with reference to the short processes.

*Diagnosis*: Intermediate subspherical proximochorate cyst. Cyst wall consisting of granulate periphragm and thin endophragm closely adpressed except at processes. No features except for archeopyle sutures representing paratabulation. Processes apparently nontabular, hollow, short, roundly conical to bulbose, and closed distally. Archeopyle compound precingular (from 2" (?) to 5" paraplates) or sometimes a combination of the precingular and apical paraplates (all apical paraplates + 2" (?) to 5" paraplates). Archeopyle sutures complete, but operculum sometimes remaining attached.

*Holotype*: Navarin Basin COST No. 1 Well, 7020-7110ft, Ring 5 (Plate 7, fig. 8).

*Paratype*: Navarin Basin COST No. 1 Well, 6930-7020ft, Ring 1 (Plate 7, fig. 9).

*Type horizon and locality*: Navarin Basin COST No. 1 Well, 6930-6960ft, Navarin Basin, Bering Sea. *Heteraulacacysta campanula* Zone; late Oligocene to early Miocene.

*Description*: The proximochorate cyst is spherical to subspherical when complete. The periphragm is thick and granular, and forms many nontabular processes which are short, bulbose to roundly conical approximately 0.15 of the cyst diameter and lacks spinose ornament. Paratabulation is not indicated by any features except for the archeopyle.

*Dimensions*: Holotype; cyst diameter 50 x 52 μm, length of processes 6-8 μm. Range: cyst diameter 40-54 μm, length of process 6-8 μm. Number of specimens measured: 5.

*Remarks*: *Lingulodinium brevispinosum* is characterized by its short processes. This species is similar to the specimens assigned to *Lingulodinium machaerophorum* (Deflandre and Cookson) from upper Pleistocene to Holocene sediments of the Black Sea illustrated by Wall and Dale (in Wall et al., 1973) in having short processes. However, the latter differs from *Lingulodinium brevispinosum* in possessing larger distal nodules on the
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processes.

Previous record: Lingulodinium sp. of Williams and Brideaux, 1975 was recorded from upper Eocene or Oligocene sediments of the Grand Banks offshore Newfoundland (Williams and Brideaux, 1975).

Thecal affinities: Unknown; probably related to the Gonyaulacaceae based on the comparison of the archeopyle of the modern cyst Lingulodinium machaerophorum.

Lingulodinium machaerophorum (Deflandre and Cookson, 1955)
Wall, 1967
Plate 7, fig. 7

Hystrichosphaeridium machaerophorum Deflandre and Cookson, 1955, p. 274, pl. 9, fig. 4, 8.
Baltisphaeridium machaerophorum (Deflandre and Cookson) Gerlach, 1961, p. 191, pl. 28, fig. 11.
Lingulodinium machaerophorum (Deflandre and Cookson) Wall, 1967, p. 109-110, pl. 15, fig. 16-17, text-fig. 6.

Discussion: The morphological variation of this species includes the length and shape of the processes and the number of precingular plates in the archeopyle (Wall et al., 1973). This species occurs in the warm-temperate surface sediments of the western Pacific (Matsuoka, 1985).

Previously known range: The oldest occurrence of Lingulodinium machaerophorum is Paleocene and the youngest occurrence is Recent according to Williams and Bujak (1985).

Thecal affinities: A thecate form of this cyst is known to be Gonyaulax polyedra Stein based on unialgal cyst cultures incubated by Wall and Dale (1968) and Kobayashi et al. (1981). Dodge (1985) suggested that the thecate forms of this cyst should be separated from the genus Gonyaulax based on differences in thecal tabulation from those of Gonyaulax (sensu lato). This is also supported by the difference in archeopyle from that of Spiniferites bulloideus (Deflandre and Cookson) and other cyst species which are equivalent to Gonyaulax spinifera (Claparède and Lachmann), Lingulodinium machaerophorum having a compound or combination archeopyle, whereas Spiniferites possesses a simple precingular archeopyle.

Genus Litospheraeidium Davey and Williams, 1966 emend.
Davey and Verdier, 1973; emend. Lucas-Clark, 1984
Type species: *Litosphaeridium siphonophorum* (Cookson and Eisenack) Davey and Williams, 1966 = *Hystrichosphaeridium siphonophorum* Cookson and Eisenack, 1958

? *Litosphaeridium parvum* sp. nov.
Plate 8, figs. 2-4; Text-fig. 12

*Derivation of name*: Latin, *parvus*, little; with reference to the small central body.

**Diagram**: Small proximate cyst with a spherical to subspherical central body comprising two wall layers. Endophragm thin and smooth; periphragm finely granular. Processes intratabular, hollow, broad, short, cylindrical to tubiferum with mostly entire to slightly recurved and open distal extremities. Processes distributing at the apical, precingular, postcingular, posterior intercalary and antapical regions, with a few processes on the parasulcus. Paracingular processes lacking. Parasutures absent. Paratabulation indicated by processes and archeopyle sutures as 4', 6"; 0c, 6", 1p, 1"" and 0-2 (?) s. Archeopyle apical, possessing several archeopyle sutures, and comprising four paraplates.

**Holotype**: Navarin Basin COST No. 1 Well, 7830-7920ft, Ring 1 (Plate 8, fig. 2).

**Paratypes**: Norton Sound COST No. 1 Well, 4380-4410ft, Ring 5 (Plate 8, fig. 4); Norton Sound Cost No. 1 Well, 5190-5220ft, Ring 4 (Plate 8, fig. 3).

**Type locality and horizon**: Navarin Basin COST No. 1 Well, 7830-7920ft, central Berina Sea; *Heterculacysta campanula* Zone; late Oligocene to early Miocene.

**Description**: The cyst wall consists of a smooth thin periphragm which is adpressed to the endophragm between the processes. The two walls are
Dinoflagellate cysts from the Bering Sea

neither spongy nor fibrous. The processes are smooth and variable in diameter and distal morphology. The four apical and probably the posterior intercalary processes are sometimes smaller than the remaining processes. The distal extremities of the processes vary from entire to slightly recurved, but this feature is constant on a single specimen. The archeopyle is apical and is formed by the loss of four apical paraplates. It is not known whether the operculum is simple or compound.

**Discussion**: This species is provisionally assigned to the genus *Litosphaeridium* because of its apical archeopyle, lack of paracingular processes, and small cyst body.

*Litosphaeridium parvum* differs from species of *Hystrichosphaeridium* in lacking cingular processes and from species of *Cordosphaeridium* in having an apical archeopyle and in lacking a fibrous periphragm and processes.

*L. parvum* is similar to Dinocyst IV of Manum, 1976, which was recorded from middle-upper Oligocene to middle Miocene sediments of the Norwegian-Greenland Sea, in forming an apical archeopyle and in having a small cyst body. *L. parvum* differs from Dinocyst IV of Manum in possessing tubiform processes and a smooth periphragm. It is possible that the two species are conspecific, because the shape of processes is more variable in specimens from the Bering Sea. Dinocyst II of Manum, 1976 also differs from *L. parvum* is possibly forming a precingular archeopyle.

**Dimensions**: Holotype; diameter of central body 19-21 µm, length of processes 8 µm, Range; diameter of central body 18-21 µm-21-22 µm, length of processes 5-8 µm. Number of specimens measured: 5.

**Thecal affinities**: Unknown, possibly a member of the *Gonyaulax* lineage based on its paratabulation.

Genus *Operculodinium* Wall, 1967


**Discussion**: Neogene species of *Operculodinium* include *Operculodinium centrocarpum*, *O. crassum* Harland, *O. echigoense* Matsuoka, *O. israelianum* (Rossignol), *O. logispinigerum* Matsuoka and *O. wallii* Matsuoka. All of these are characterized by having a spherical cyst body with many simple processes. They are distinguished by the following characteristics:
1 Cyst small; less than 40 μm .............................................. 2
1 Cyst intermediate; more than 50 μm .................................. 3
2 Cyst wall reticulate; processes long and cylindrical with capitate
  tips .............................................................................. O. centropcarpum
2 Cyst wall psilate to granulate; processes long and conical with
  acuminate, bifid or fucrate endings .................. O. longispinigerum
3 Cyst wall spongy, fibrous ............................................... 4
3 Cyst wall reticulate ........................................................ 5
4 Cyst wall relatively thick (more than 3 μm); processes long
  conical ................................................................. O. crassum
4 Cyst wall relatively thin (less than 2 μm); processes short
  conical................................................................. O. israelianum
5 Processes conical with small bifid tips ..................... O. echigoense
5 Processes long, slender, flexible ............................ O. wallii

Intermediate forms between O. crassum and O. israelianum have been
observed in the Neogene sequences of North Japan, suggesting a possible
phylogenetic relationship between these two species.

Operculodinium alsium sp. nov.
Plate 8, figs. 7-9

Operculodinium sp. I Manum, 1976, pl. 1, figs. 23, 24

Derivation of name: Latin, alsius, cold; with reference to the cold water occurrence
of this species.

Diagnosis: Intermediate subspherical to ovoidal proximochorate cyst. Cyst wall comprising
a reticulate periphragm and a smooth endophragm
adpressed between processes. Processes numerous, short, hollow, cylindrical
or sometimes conical, apparently nontabular with closed
and sometimes truncated distal extremities. Processes reticulate at the base. No features
except for archeopyle sutures reflect the paratabulation. Archeopyle
precingular, formed by the loss of paraplate 3°.

Holotype: Norton Sound COST No. 1 Well, 4200-4230ft, Ring 5, (Plate 8,
fig. 8).

Paratype: Norton Sound COST No. 1 Well, 5012.2ft, Ring 16, (Plate 8,
fig. 9).

Type horizon and locality: Norton Sound COST No. 1 Well, 4200-4230ft,
Norton Sound, Bering Sea. Hystrichosphaeropsis variabile Zone; late Mio-
Dinoflagellate cysts from the Bering Sea

Description: The subspherical to ovoidal cyst possesses a thick reticulate periphragm and a relatively thin smooth endophragm. Many of the processes are cylindrical with truncated distal endings, but some are short, conical and a few adjacent processes are rarely joined. The archeopyle is trapezoidal, precingular and formed by the loss of paraplate 3°.

Dimensions: Holotype; cyst diameter $55 \times 62 \mu m$, length of processes up to $7 \mu m$, Range; cyst diameter $47-62 \mu m$, length of processes $5-7 \mu m$. Number of specimens measured; 5.

Remarks: The short cylindrical processes with truncated distal extremities and the relatively thick and reticulate periphragm distinguish *Operculodinium alsium* from other species of *Operculodinium*. *Operculodinium* sp. I recorded by Manum (1976, pi. 1, fig. 23-24) from upper Eocene sediments of the Norwegian-Greenland Sea may be conspecific with *O. alsium* because it apparently has a reticulate periphragm and short cylindrical processes.

Thecal affinities: Possibly related to the modern genus *Protoceratium* of the Gonyaulacaceae.

*Operculodinium echigoense* Matsuoka, 1983
Plate 9, fig. 1

*Operculodinium echigoense* Matsuoka, 1983, p. 126, pi. 7, fig. 1-5, 8.

Discussion: *Operculodinium centrocarpum*, *Operculodinium echigoense*, *Operculodinium crassum* and *Operculodinium israelianum* are similar in possessing a spherical cyst body and numerous processes. *O. echigoense* differs from the other species in having a larger cyst body which typically exceeds $80 \mu m$, and in bearing fewer processes which are flexuous. Larger cysts previously attributed to *Operculodinium centrocarpum* were recorded from the Miocene of offshore eastern Canada by Bujak (1984) and the Pleistocene of the Caribbean Sea by Wall (1967). These specimens may be conspecific with *Operculodinium echigoense*.

*Operculodinium wallii* Matsuoka, 1983
Plate 9, fig. 2

*Operculodinium wallii* Matsuoka 1983, p. 127, pl. 9, fig. 9, pl. 9, fig. 1-4.
Discussion: Operculodinium wallii resembles O. israelianum and O. crassum, but differs in possessing longer and more slender processes with small bifid distal terminations.

Previous record: Late Miocene to early Pleistocene of North Japan (Matsuoka, 1983; Matsuoka et al., 1987).

Thecal affinities: Possibly related to the modern Gonyaulacacean genus Protoceratium.

Type species: Phthanoperidinum amoenum Drugg and Loeblich, 1967

Phthanoperidinium bennettii sp. nov.
Plate 9, figs. 4-9; Text-fig. 13

Derivation of name: Named for the palynologist Dr. John Bennett.

Text-figure 13 Phthanoperidinium bennettii sp. nov. a: Ventral surface of the holotype, b: Dorsal surface of the paratype. Scale bar; 10 μm.

Diagnosis: Small to intermediate proximate cyst with an ovoidal to roundly hexagonal shape. Epicyst roundly pentagonal in dorsoventral view, always larger than hypocyst and bearing a small apical horn; hypocyst truncated, possessing two small asymmetrical antapical horns. Cyst wall comprising psilate to granulate periphragm, and thick and smooth endophragm. Paratabulation clearly defined as 4', 3a, 7', 6c (?), 5'', 0p, 2''', xs by low and smooth parasutural crests. Paraplate 2a iso- to lati-theta form, forming the intercalary archeopyle. Paracingulum displaced in half
of its width. Parasulcus wide, shallow and almost straight, extending deeply onto both of epi- and hypocysts.

**Holotype**: Navarin Basin COST No. 1 Well, 12740-12750ft, Ring 4 (Plate 9, fig. 4).

**Paratype**: Navarin Basin COST No. 1 Well, 12,740-12,750ft, Ring 1 (Plate 9, fig. 8), Ring 5 (Plate 9, fig. 5), Ring 8 (Plate 9, fig. 6).

**Type horizon and locality**: Navarin Basin COST No. 1 Well, 12740-12750ft, Navarin Basin, Bering Sea. *Trinovantedinium boreale* Zone; early Oligocene.

**Description**: The proximate cyst comprises a periphragm and endophragm which are mostly adpressed. The periphragm is relatively thin, psilate to granulate, and the endophragm is thick and smooth. The epicyst is convexly conical with a short blunt or rounded apical horn. The hypocyst possesses two very small and asymmetrical antapical horns, the right antapical horn always being reduced. Parasutures are represented by low smooth crests without distal ornament. The paratabulation of 4′, 3a, 7″, 6c(?), 5‴, 2‴‴, and xs is well defined. Paraplate 1′ is pentagonal and contacts paraplates 2′, 4′, 1″, 7‴ and the anterior sulcal paraplates. The 2a paraplate is iso- to lati-thetaform (hexagonal). The paracingulum is laevorotary and the cingular paraplates may be obscure because the paracingulum is narrow and often deformed. The parasulcus is wide and extends deeply onto the epicyst and hypocyst. The parasuture between the sulcus and the first apical paraplate is well developed. An archeopyle is formed by the loss of paraplate 2a.

**Dimensions**: Holotype; length of cyst 56μm, width 49μm, height of antapical horn 2.8μm, width of paracingulum 6μm. Range; length of cyst 44-56μm, width 40-53μm, height of antapical horn 1-3μm, width of paracingulum 5-6μm. Number of specimens measured; 10.

**Remarks**: *Phthanoperidinium benetti* differs from other species of *Phthanoperidinium* in having a broad sulcus and an epicyst which is much larger than the hypocyst.

**Thecal affinity**: *P. benetti* is attributable to the Peridinioid lineage based on its paratabulation.

Genus *Pentadinium* Gerlach, 1961; emend. Benedek et al., 1982
Type species: *Pentadinium laticinctum* Gerlach, 1961

Plate 9, fig. 3
Pentadinium laticinctum Gerlach, 1961 subsp. granulatum Gocht, 1969, p. 29-30, pl. 9, fig. 17-18, text-fig. 20.

Discussion: Pentadinium laticinctum granulatum is characterized by its thick granular endophragm and periphragm.

Previously known range: Middle Oligocene of Germany (Gocht, 1969); early Oligocene of DSDP Site 370 (Williams, 1978); early Oligocene to early Miocene of the Blake Plateau (Stover, 1977); late Oligocene to middle Miocene of Italy (Powell, 1986b).

Thecal affinities: Unknown; although the paratabulation of this species is distinctive (1-3′, 5″, 5″′, 1″") , the species is possibly related to the modern Gonyaulacaceae based on its simple precingular archeopyle formed by the loss of paraplate 3″.

Genus Reticulatosphaera Matsuoka, 1983; emend, Bujak and Matsuoka, 1986

Type species: Reticulatosphaera actinocoronata (Benedek, 1972) Bujak and Matsuoka, 1986 = Cleistosphaeridium actinocoronatum Benedek, 1972

Reticulatosphaera actinocoronata (Benedek, 1972)
Bujak and Matsuoka, 1986
Plate 9, figs. 10-12

Cannosphaeropsis sp. b., Shimakura et al., 1971, pl. 1, fig. 15.
Cleistosphaeridium actinocoronatum Benedek 1972, p. 34, pl. 12, fig. 13; text-fig. 13.
Impletosphaeridium sp. I, Manum 1976, pl. 6, fig. 8-9.
? Areosphaeridium actinocoronatum (Benedek) Stover and Evitt, 1978
Reticulatosphaera stellata Matsuoka 1983, p. 116, pl. 4, fig. 8-11; text-fig. 10.

Discussion: The archeopyle is indistinct in the holotype of this species (originally Cleistosphaeridium actinocoronatum), but a precingular archeopyle formed by the loss of paraplate 3″ is present in well-preserved specimens (Matsuoka, 1983; pl. 4, fig. 8).

Previously known range: This species is cosmopolitan in the Oligocene to Pliocene. The oldest recorded occurrence is the late Oligocene of offshore eastern Canada (Williams and Bujak, 1977) and the youngest occurrence in the late Pliocene of Japan (Matsuoka, 1983).
Thecal affinity: Reticulatosphaera actinocoronata is probably related to the modern Gonyaulacaceae.

Genus Rottnestia Cookson and Eisenack, 1961
Type species: Rottnestia borussica (Eisenack, 1954) Cookson and Eisenack, 1961 = Hystrichosphaera borussica Eisenack, 1954

Rottnestia ovata sp. nov.
Plate 10, figs. 1-2; Text-fig. 14

Derivation of name: Latin, ovatus, egg-shaped; with reference to the ovoidal endocyst.

Text-figure 14 Rottnestia ovata sp. nov. Dorsal surface of the holotype. Scale bar: 10 μm.

Diagnosis: Polygonal to elongate, bicavate intermediate proximochorate cyst. Endocyst ovoidal. Granular periphragm and smooth endophragm separated in the apical and antapical region by pericoels. Epicyst hemispherical and slightly smaller than hypocyst, with a poorly developed apical pericoel beneath the small apical horn which possesses a furcate process; hypocyst elongate hemispherical with moderately well-developed pericoel and two larger gonal processes. Parasutural septa low, slightly membranous near the furcate processes, and reflecting the paratabulation 3′ (?), 6″, 6c, 6″′, 1p, xs. Processes mostly gonal, solid, and short with furcate distal extremities. Paracingulum relatively wide and almost circular; parasulcus poorly delimited by parasutural ridges, and almost straight. Archeopyle precingular, formed by the loss of paraplate 3″.

Holotype: Norton Sound COST No. 1 Well, 6630-6660ft, Ring 7 (Plate 10, fig. 1).

Paratype: Navarin Basin COST No. 1 Well, 6000-6090ft, Ring 3 (Plate 10, fig. 2).
Type horizon and locality: Norton Sound COST No. 1 Well, 6630-6660ft. Norton Sound, Bering Sea. *Heteraulacacysta campanula* Zone; late Oligocene to early Miocene.

*Description*: The endocyst is ovoidal and the outline of the periphragm is elongate polygonal due to the presence of apical and antapical pericoels. The apical pericoel is small and cornucavate, whereas the antapical pericoel is larger and expanded. The apical horn is small, conical and typically branched. Two projections are present on the antapical area, and are formed by longer gonal processes. Most gonal processes have short solid stalks with trifurcate or sometimes bifurcate endings. The paracingulum is circular and moderately wide. The archeopyle is precingular and formed by the loss of paraplate 3°.

*Dimension*: Holotype; length of cyst 53 μm, width 33 μm, length of apical horn 6 μm, height of parasuture 3 μm. Range; length of cyst 38-51 μm, width 33-37 μm, length of apical horn up to 7 μm. Number of specimens measured: 5.

*Discussion*: The presence of gonal processes and bicavation indicates that this species is attributable to the genus *Rottnestia*. *R. ovata* differs from *R. borussica* (Eisenack) in possessing an antapical pericoel and in having a smaller apical horn. *R. ovata* is similar to *Hystrichosphaeropsis arctica*, *H. variabile* and *Spiniferites ellipsoideus* but is distinguished from the two species of *Hystrichosphaeropsis* in possessing gonal processes, and from *S. ellipsoideus* in having more conspicuous apical and antapical pericoels.

*Thecal affinities*: Unknown; probably related to the Gonyaulacaceae based on its paratabulation and precingular archeopyle.

Genus *Selenopemphix* Benedek, 1972; emend. Bujak in Bujak et al., 1980
Type species: *Selenopemphix nephroides* Benedek, 1972

*Selenopemphix crenata* sp. nov.
Plate 10, figs. 6-7; Text-fig. 15

*Derivation of name*: Latin, *cretatus*, roundly serrate; with reference to the serrate paracingular margin.

*Diagnosis*: Small proximate cyst, circular to reniform in polar view, strongly compressed along the polar axis. Cyst wall pigmented brown, comprising a smooth to chagrinate autophragm. A single small apical horn
Dinoflagellate cysts from the Bering Sea

Text-figure 15  *Selenopemphix crenata* sp. nov.
Antapical surface of the holotype. Scale bar: 10 μm.

present; two antapical horns undifferentiated and forming a single broad, truncated projection. Paratabulation unrepresented except for archeopyle sutures. Paracingulum delimited by two finely serrate parallel ridges; parasulcus indicated by shallow indentation of the autophragm. Archeopyle intercalary and offset to the right of the dorsal midline. Operculum comprising paraplate 2a.

*Holotype:* Norton Sound COST No. 1 Well, 4380-4470ft, Ring 9, (Plate 10, fig. 6)

*Paratype:* Norton Sound COST No. 1 Well, 2130-2160ft, Ring 1, (Plate 10, fig. 7)

*Type horizon and locality:* Norton Sound COST No. 1 Well, 4380-4470ft, Norton Sound, Bering Sea. *Hystrichosphaeropsis variabile* Zone, late Miocene

*Dimensions:* Holotype; cyst diameter 34 μm, height of paracingular list ca. 2 μm, Range; cyst diameter 34-74 μm. Number of specimens measured; 3.

*Description:* The small proximate cyst is compressed dorso-ventrally, brownish in color and does not fluoresce. The cyst wall consists of a smooth to slightly granulate autophragm without ornament. The epicyst has a small apical boss and the hypocyst possesses a single broad antapical projection. The paracingulum is characterized by two parallel ridges with vaginate to crenulate margins. The parasulcus is short, distinctive, is represented by a shallow indentation of the autophragm and does not extend onto the epicyst. The archeopyle is hexagonal intercalary, formed by the loss of paraplate 2a and is displaced to the right of the dorsal midline.

*Discussion:* *Selenopemphix crenata* is similar to *S. nephroides*, but differs in having serrate paracingular margins. It also differs from *S. coronata* Bujak in lacking bifurcate spines on the paracingular crests, and from *S. selenoides* Benedek in lacking a perforated autophragm and in
Selenopemphix sp. C of Duffield and Stein (1986, pi. 1, fig. 6) and Selenopemphix sp. E of Duffield and Stein (1986, pl. 1, fig. 9) in possessing a denticulate paracingular margin, but differs from them in possessing serrate paracingular ridge.

*Thecal affinities*: Unknown, but this species is probably related to the modern *Protoperidinium subinerme* based on its cyst shape and archeopyle.

*Selenopemphix nephroides* Benedek, 1972; emend. Bujak, 1980

Plate 10, figs. 3-5

*Selenopemphix nephroides* Benedek, 1972, p. 48, pl. 11, fig. 15; pl. 16, fig. 5-8.  
*Selenopemphix nephroides* Benedek, emend. Bujak et al., 1980, p. 86.

Discussion: Bujak (1984) considered that *Omanodinium alticinctum* Bradford, 1975 (= *Selenopemphix alticinctum* (Bradford) Matsuoka, 1985) may be conspecific with *S. nephroides*, but this species differs from *S. alticinctum* (Bradford) Matsuoka, 1985 in having a larger cyst body (*S. nephroides* is approximately 59 \( \mu \text{m} \) in width, Benedek, 1972) whereas *S. alticinctum* is approximately 33 \( \mu \text{m} \) in width), in lacking a distinctive denticulate paracingular margin and in bearing a finely granulate to longitudinally striations on the cyst wall. Matsuoka (unpublished data) suggested that the geographical distribution of *S. nephroides* is a cool-temperate regions around Japan, whereas *S. alticinctum* is usually found in the warm-temperate regions and was originally described from the surface sediments of the Persian Gulf.

Previously known range: Middle Eocene to late Miocene according to Williams and Bujak (1985). The species has also been recorded as the cyst of *Protoperidinium subinerme* from Recent surface sediments (Wall and Dale, 1968). The species therefore appears to range into the Holocene.

*Thecal affinities*: Cyst form of *Protoperidinium subinerme* based on unialgal cyst cultures carried out by Wall and Dale (1968).

Genus *Spiniferites* Mantell, 1850; emend. Sarjeant, 1970  
Type species: *Spiniferites ramosus* (Ehrenberg, 1838) Loeblich and Loeblich, 1966 = *Xanthidium ramosum* Ehrenberg, 1838.

*Spiniferites adnatus* sp. nov.  
Plate 10, figs. 8-9; Plate 11, figs. 1-3; Text-fig. 16
**Derivation of name:** Latin, *adnatus*, joined to or united with; with reference to the processes which are often connected laterally.

![Text-figure 16 Spiniferites adonatus sp. nov. Dorsal surface.](image)

Scale bar: 10 μm.

**Diagnosis:** Intermediate ovoidal to elongate proximochorate cyst. Epicyst hemi-ellipsoidal and always longer than hypocyst, with or without apical boss. Cyst wall thin; periphragm smooth to chagrinate, endophragm smooth. Processes mostly gonal, membranous or sometimes hollow, short cylindrical to tubiform with irregularly foliate, furcate or rarely secate distal extremities. Parasutural septa distinctive, low, sometimes membranous and representing the paratabulation 4’, 6’, 6c, 6”’, 1p, 1”” and xs. Parasutural septa between paraplates 1””, 3””-4””, and between paraplates 1’ and 2’ often membranous with branched to entire distal ends. Paracingulum clear, almost circular and comprising six equatorially expanded rectangular paraplates; parasulcus delimited by parasutural septa and almost straight. Archeopyle simple precingular formed by the loss of paraplate 3”.

**Holotype:** Norton Sound COST No. 1 Well, 4650-4680ft, Ring 1 (Plate 10, fig. 8).

**Paratype:** Norton Sound COST No. 1 Well, 6810-6840ft, Ring 1 (Plate 10, fig. 9), Norton Sound COST No. 1 Well, 5730-5760ft, Ring 1 (Plate 11, fig. 2).

**Type horizon and locality:** Norton Sound COST No. 1 Well, 4650-4680ft, Norton Sound, Bering Sea. Systematophora ancyrea Zone; late Oligocene.

**Description:** The cyst body varies from ovoidal to ellipsoidal and the epicyst is longer than the hypocyst. The cyst wall comprises a periphragm and endophragm adpressed between the processes. The processes are mostly gonal, membranous, cylindrical to tubiform, with extremities that vary from bifurcate to irregularly foliate. Some of the gonal processes are hollow and distally secate. The parasutures are distinctive and often membranous between the 1”” and 3””-4”” paraplates, and sometimes be-
between the 1' and 2' papaplates. These membranous parasutural septa are hystricate to entire. The paracingulum is approximately circular and the parasulcus is almost straight. The archeopyle is precingular, reduced, and the operculum is monoplacoid (3") and detached.

**Dimension**: Holotype; length of cyst 53µm, width 45µm, length of processes up to 9µm, Range; length of cyst 39-53µm, width 33-46µm, length of processes 8-12µm. Number of specimens measured; 10.

**Discussion**: *Spiniferites adnatus* resembles *S. nortonensis* sp. nov. in possessing membranous gonal processes and parasutural septa, but differs in having a more elongate cyst body and longer processes. *S. adnatus* is also similar to *S. ellipsoideus*, *S. membranaceus* (Rossignol) and *S. mirabilis* (Rossignol), but is distinguished from *S. ellipsoideus* in having a larger cyst body and hollow gonal processes, from *S. membranaceus* in possessing an ovoidal cyst body and hollow processes with foliate distal extremities, and from *S. mirabilis* in possessing only gonal and sometimes hollow processes.

**Thecal affinities**: Unknown; possibly related to the genus *Gonyaulax*.

*Spiniferites aquilonius* sp. nov.
Plate 11, fig. 6; Plate 12, fig. 1; Text-fig. 17

**Derivation of name**: Latin, *aquilonius*, northern; with reference to the northern occurrence of the species.

**Diagnosis**: Intermediate ovoidal to subspherical proximochorate cyst. Epicyst almost equal to hypcyst in size and shape, without apical projec-
tion; hypocyst without antapical projections. Periphragm non-pigmented, smooth to finely granular; endophragm thin and smooth; both adpressed except at processes. Parasutural septa distinctive and membranous without ornament, and clearly representing the paratabulation 4', 9a, 6'', 6c, 6'', 1p, 1''", xc. Processes gonal, long, slender and erect with trifurcate distal extremities which are mostly short, bifid and often irregularly and roughly reticulate. Sutural processes absent. Shaft of processes membranous especially at the base and concave-triangular in transverse cross section. Paracingulum comprising six rectangular paraplates, and relatively narrow and laevorotary. Parasulcus delimited by well-developed parasutural ridges, almost straight, and expanding onto the epicyst. Archeopyle simple, precingular and sometimes reduced; operculum monoplacoid (3") and detached.

**Holotype:** Norton Sound COST No. 1 Well, 3120-3150ft, Ring 6 (Plate 11, fig. 6).

**Paratype:** Norton Sound COST No. 1 Well, 3210-3240ft, Ring 2 (Plate 12, fig. 1).

**Type horizon and locality:** Norton Sound COST No. 1 Well, 3120-3150ft, Norton Sound, Bering Sea. *Hystrichophaeropsis variabile* Zone; late Miocene.

**Description:** The cyst body varies from subspherical or ovoidal to ellipsoidal in shape. The epicyst is similar to the hypocyst in size and lacks an apical horn. An antapical horn is absent. The cyst wall is smooth and relatively thick. The processes are membranous and sometimes perforated near their distal ends. The distal tips are trifurcate with bifid ends, and are usually irregularly perforated. Parasutural septa are also membranous. The paracingulum is approximately one-sixth of the cyst length, laevorotary and displaced by approximately its own width.

**Dimension:** Holotype; length of cyst 55μm, width 45μm, length of processes 15μm, width of paracingulum 7μm, Range; length of cyst 52-55μm, width 43-45μm, length of processes up to 15μm. Number of specimens measured; 5.

**Discussion:** *Spiniferites aquilonius* is similar to *Achomosphaera andalusiensis* Jan du Chene (a senior synonym of *Spiniferites septentrionalis* Harland). Both species possessing gonal processes with reticulate distal extremities, but *S. aquilonius* differs in having parasutural septa plus longer and more membranous processes.

**Thecal affinities:** Unknown; probably related to the modern genus
Gonyaulax based on its paratabulation and archeopyle.

Spiniferites choanus sp. nov.
Plate 14, figs. 2-3; Text-fig. 18

Derivation of name: Greek, choanos, funnel; with reference to the processes which have funnel-shaped distal extremities.

Text-figure 18 Spiniferites choanus sp. nov.
Oblique ventral surface of the holotype. Scale bar; 10 μm

Diagnosis: Intermediate ellipsoidal to ovoidal proximochorate cyst. Epicyst slightly conical with a small apical node; hypocyst subspherical, without antapical projection. Cyst wall composed of a finely granulate periphragm and thin smooth endophragm in contact except at the parasutural septa and processes. Processes mostly gonal and rarely sutural; gonal processes with membranous shafts, buccinate and irregularly secate, or sometimes perforated distal extremities which are often recurved; sutural processes membranous, small and simple, mostly with bifid or trifid distal endings. Parsutural septa low but distinctive, and reflecting the paratabulation 4′(?), 0a, 6″, 6c, 6″′, 1p, 1″″, xs. Paraplate 6″ small and triangular; paraplate 1″″ much reduced. Paracingulum relatively narrow, less than one-tenth of the cyst length, and displaced by approximately twice of its own width in a laevorotary direction. Parasulcus prominent, including at least two paraplates; anterior and posterior sulcal paraplates, almost straight and slightly widening antapically. Archeopyle simple precingular and formed by the loss of paraplate 3″.

Holotype: Navarin Basin COST No. 1 Well, 6210-6300ft, Ring 8 (Plate 14,
Dinoflagellate cysts from the Bering Sea

Paratype: Navarin Basin COST No. 1 Well, 6000-6090 ft, Ring (Plate 14, fig. 2).

Type horizon and locality: Navarin Basin COST No. 1 Well, 6210-6300 ft, Navarin Basin, Bering Sea. Heteraulacacysta campanula Zone; late Oligocene to early Miocene.

Description: The cyst body varies from ovoidal to ellipsoidal, with a chagrinate periphragm and smooth endophragm which are ad pressed except at the processes and parasutural septa. The processes are relatively short (approximately one-fifth of cyst length), mostly gonal, tapering or tubiform, with membranous stalks and roughly secate or rarely entire distal extremities. Sutural processes are rarely present, simple and oblate distally. The operculum is monoplacoid (3") and detached.

Dimensions: Holotype; length of cyst 70 μm, width 54 μm, length of processes 17-18 μm. Range: length of cyst 63-70 μm, width 54-60 μm, length of processes 16-20 μm. Number of specimens measured; 5.

Discussion: Spiniferites choan us differs from S. pseudofurcatus (Klumpp) in having an ellipsoidal to ovoidal rather than subspherical central body and shorter membranous processes with roughly secate distal extremities. S. choan us differs from S. adnatus in possessing longer gonal processes with secate distal tips, and in lacking a membranous parasuture.

Thecal affinities: Unknown; possibly related to the modern genus Gonyaulax based on its paratabulation and precingular archepyle.

Spiniferites ellipsoideus Matsuoka, 1983
Plate 12, figs. 2-3.

Spiniferites ellipsoideus Matsuoka, 1983, p. 132-133, pl. 13, fig. 6-7.

Discussion: Spiniferites ellipsoideus is characterized by its elongate cyst body. The species is similar to S. elongatus but differs in possessing a shorter and wider cyst body. Spiniferites ellipsoideus also resembles S. frigidus in having an elongate cyst body, but is distinguished by its lack of well-developed membranous parasutural septa.

Previously known range: Middle Miocene to early Pliocene of Japan (Matsuoka, 1983; Matsuoka et al., 1987).

Thecal affinity: Unknown; probably related to the modern genus Gonyaulax.
Spiniferites frigidus Harland and Reid, 1980
Plate 12, figs. 4-5

*Spiniferites frigidus* Harland and Reid in Harland et al., 1980, p. 213-216, figs. 2A-J; text-fig. 3
*Rottneista amphicavata* Dobell and Norris in Harland et al., 1980, p. 218-220, fig. 4A-N, text-fig. 5-7.

**Discussion**: The present specimens of *Spiniferites frigidus* have a well-developed antapical pericoel and are similar to those recorded from the western Bering Sea by Bujak (1984a) and to *Rottneista amphicavata* from the Beaufort Sea by Dobell and Norris (in Harland et al., 1980). Bujak (1984a) concluded that *Spiniferites frigidus* and *Rottneista amphicavata* are conspecific because the extension of the periphragm and antapical pericoel are highly variable and therefore not diagnostic for separation of the two species.

*Spiniferites frigidus* is similar to *S. elongatus* Reid and *S. ellipsoideus* in possessing an elongate cyst body. Intermediate forms between *S. elongatus* and *S. frigidus* were observed in Recent sediments of the southern Barents Sea by Harland (1982). *S. frigidus* differs from *S. elongatus* in possessing well-developed parasutural septa and distinctive furcate processes.

**Previously known range**: Recent and sub-Recent sediments of the southern Barents Sea (Harland, 1982); late Pleistocene of the northern North Pacific and the western Bering Sea (Bujak, 1984a); Holocene of Akkeshi Bay, North Japan (Matsuoka, 1987).

**Thecal affinity**: The paratabulation of this cyst suggests that *Spiniferites frigidus* is probably a species of the modern genus *Gonyaulax*.

Spiniferites hexatypicus Matsuoka, 1983
Plate 12, figs. 6-7

*Spiniferites hexatypicus* Matsuoka, 1983, p. 133-134, pl. 13, fig. 1-3; text-fig. 18.
*Spiniferites ovatus* Bujak 1984, p. 192, pl. 3, fig. 15-18.

**Discussion**: *S. hexatypicus* is characterized by its roundly hexagonal to ovoidal cyst body with short, solid gonal processes. *Spiniferites ovatus* Bujak is a junior synonym of *S. hexatypicus* Matsuoka and is a different
species from *S. ovatus* Matsuoka.

*Previously known range*: Early Miocene to early Pliocene of Japan (Matsuoka, 1983; Matsuoka et al., 1987); late Miocene of the northern North Pacific and the Bering Sea (Bujak, 1984a; Bujak and Matsuoka, 1986).

*Thecal affinity*: Probably related to the modern genus *Gonyaulax* based on its paratabulation.

*Spiniferites nortonensis* sp. nov.
Plate 13, figs. 1-2; Text-fig. 19

*Derivation of name*: with reference to its occurrence in the Norton Sound of the Bering Sea.

Text-figure 19  *Spiniferites nortonensis* sp. nov.
Dorsal surface of the holotype.
Scale bar: 10 \( \mu m \).

*Diagnosis*: Intermediate roundly pentagonal to subspherical proximo-chorate cysts. Epicyst similar to hypocyst in size and shape; both lacking polar projections. Periphragm thick and coarsely granular and endophragm thinner and smooth; both phragma in contact except at processes and parasutures. Processes of two types; gonal processes short, relatively wide, cylindrical, sometimes membranous at the base and hollow with irregularly furcate to foliate distal extremities; sutural processes rare simple bifid or non-furcate distally. Parasutural septa membranous moderately high, without ornament and representing the paratabulation 4', 0a, 6", 6c, 6'", 1p, 1''", xs. Paracingulum prominent but narrow, comprising six transversely rectangular paraplates and laevorotary; parasulcus shallow and mostly lacking defined sulcal paraplates. Archeopyle simple precingular and formed by the loss of paraplate 3''.

*Holotype*: Norton Sound COST No. 1 Well, 6630-6720ft, Ring 4 (Plate 13,
Paratype: Norton Sound COST No. 1 Well, 5370-5400ft, Ring 3 (Plate 10, fig. 2).

Type horizon and locality: Norton Sound COST No. 1 Well, 4470-4500ft, Norton Sound, Bering Sea. Hystrichophaeropsis variabile Zone; late Miocene.

Description: The central body varies from subspherical to roundly pentagonal and lacks apical and antapical horns. Gonal and sutural processes are present. The gonal processes are variable in shape and are cylindrical, tapering or buccinate, and sometimes membranous at the base. The distal extremities of the gonal processes vary from minutely denticulate to irregularly furcate. Sutural processes occur rarely and are simple. The paracingulum is relatively narrow (about 4 μm wide) and strongly helicoid. The parasulcus is shallow and mostly without delineated sulcal paraplates.

Dimensions: Holotype; length of cyst 58 μm, width 51 μm, length of processes 12-14 μm, Range; length of cyst 51-58 μm, width 41-51 μm, length of processes 9-12 μm. Number of specimens measured; 5.

Discussion: Spiniferites nortonensis sp. nov. is characterized by its central body shape and short broad gonal processes with irregular distal endings. The species resembles S. bulloideus (Deflandre and Cookson) in possessing a relatively small and subspherical central body, but differs in having short, wide and sometimes membranous gonal processes. S. nortonensis is also similar to S. strictus Matsuoka, described from the Pliocene of North Japan by Matsuoka (1983), but differs in bearing short and sometimes hollow gonal processes.

Thecal affinities: Unknown; probably related to the genus Gonyaulax based on the paratabulation.

Spiniferites pseudofurcatus (Klumpp, 1953) Sarjeant, 1970
Plate 14, fig. 1

Hystrichokibotium pseudofurcatus Klumpp 1953, p. 388, pl. 16, figs. 12-14.
Hystrichosphaera tertiaria Eisenack and Gocht 1960, p. 515; text-fig. 4.
Hystrichosphaera buccina Davey and Williams 1966, p. 42-43, fig. 1; text-figs. 10-11.
Spiniferites pseudofurcatus (Klumpp) Sarjeant 1970, p. 76.
Spiniferites sp. aff. S. buccinus Davey and Williams; Matsuoka 1974, p. 325-326, pl. 45, figs. 1,2.
Discussion: The morphological variation of this species includes the length of processes (the present specimens possess shorter processes than the type specimen) and the cyst shape which is subspherical to ellipsoidal. The specimen shown in Pl. 14, fig. 1 has a typical subspherical cyst body with short hollow processes.

Previously known range: Late Paleocene to middle Miocene according to Williams & Bujak (1985); Powell (1986a,b,c) also recorded this species from the late Oligocene to late Miocene of Italy.

Thecal affinities: Unknown; possibly related to the modern Gonyaulaceae based on its paratabulation.

**Spiniferites ramosus** subsp. *ramosus* (Ehrenberg) Loeblich and Loeblich, 1966

Plate 13, fig. 3

*Xanthidium ramosum* Ehrenberg 1838, pl. 1, figs. 1-2, 5.
*Spiniferites ramosus* (Ehrenberg) Loeblich and Loeblich 1966, p. 56.

Discussion: In the modern West Pacific, *Spiniferites ramosus* is restricted to the warm-water regions.

Previously known range: Cretaceous to Recent according to Williams (1978).

Thecal affinities: A cyst of the *Gonyaulax spinifera* complex based on unialgal incubation carried out by Wall and Dale (1968).

**Spiniferites ramosus** subsp. *gracilis* (Davey and Williams, 1966)

Lentin and Williams, 1973

Plate 13, fig. 4

*Hystrichosphaeridium plicatum* Maier, 1959, p. 318, pl. 33, fig. 1.
*Hystrichosphaera ramosa* var. *gracilis* Davey and Williams, 1966, p. 34-35, pl. 1, fig. 5; pl. 5, fig. 6.
*Spiniferites ramosus* subsp. *gracilis* (Davey and Williams) Lentin and Williams 1973, p. 130.

Discussion: This subspecies of *S. ramosus* is characterized by its long, solid and slender gonial and sutural processes. *Spiniferites ramosus gracilis* is similar to *S. lentzi* Reid and *S. hyperacanthus* (Deflandre and Cookson). It differs from *S. lentzi* in having longer processes and fewer sutural proc-
esses, and from *S. hyperacanthus* in having longer and slender processes.

*Previously known range:* Cenomanian to Miocene according to Davey and Williams (1966).

*Thecal affinities:* Unknown, although *Spiniferites ramosus* is a cyst of the *Gonyaulax spinfera* complex.

*Spiniferites reductus* sp. nov.

Plate 14, figs. 4-5

Derivation of name: Latin; *reductus*, reduced; with reference to the short processes.

Diagnosis: Intermediate to small subspherical to ovoidal proximo-chorate cyst. Epi- and hypocyst hemispherical and without projections. Cyst wall comprising a thin and granular periphragm and smooth endophragm, which are adpressed except at processes and the granular parasutures. Processes gonal and sutural; both types solid, short, conical and membranos at the bases. Gonal processes trifurcate and sutural processes bifurcate distally. Paratabulation reflected by parasutural septa and archeopyle sutures as 4', 0a, 6", 6c, 6"", 1p, 1"", xs. Paracingulum delimited by six rectangular paraplates and displaced in a laevorotary direction by approximately its own width; parasulcus represented by low parasutural septa, extending onto the epicyst and almost straight. Archeopyle simple precingular and formed by the loss of paraplate 3".

Holotype: Navarin Basin COST No. 1 Well, 5850-5940ft, Ring 10 (Plate 14, fig. 4).

Paratype: Norton Sound COST No. 1 Well, 4110-4140ft, Ring 3 (Plate 14, fig. 5).

Type horizon and locality: Navarin Basin COST No. 1 Well, 5850-5880ft, Navarin Basin, Bering Sea. *Heteraulacacysta campanula* Zone; late Oligocene to early Miocene.

Description: The central body varies from subspherical to ovoidal with a trapezoidal hypocyst in dorso-ventral view. Apical and antapical horns are absent. The cyst wall consists of a periphragm and endophragm adpressed between processes. The gonal and sutural processes are short, granular and membranos at the base. One, two or rarely three sutural process occur between the pre- and postcingular gonal processes. The paracingulum is moderately wide and displaced by approximately one cingular width, and the parasulcus is almost straight. The archeopyle is a simple precingular type formed by the loss of paraplate 3".
Dimensions: Holotype; length of cyst body 52 μm, width 43 μm, length of processes up to 10 μm. Range; length of cyst 50–53 μm, width 43–49 μm, length of processes 8–10 μm. Number of specimens measured; 5.

Discussion: Spiniferites reductus sp. nov. is similar to Achomosphaera spongiosa in having a granular periphragm, but differs in having parasutural and sutural processes. S. reductus resembles S. nortonensis and S. hexatypicus in having short processes, but differs from S. nortonensis in lacking hollow gonal processes and in possessing a thinner periphragm, and from S. hexatypicus in having a granular periphragm plus gonal and sutural processes with membranous bases. S. reductus resembles S. lentzii (Reid) in possessing many sutural processes, but is distinguished in having a granular periphragm and shorter processes.

Thecal affinities: Unknown; possibly the cyst of a species of Gonyaulax based on its paratabulation.

Spiniferites varmae Lentin and Williams, 1973 emend. herein
Plate 19, fig. 3; Text-fig. 20

Hystrichosphaera pseudofurcata Varma and Dangwal, 1964, p. 66-67, pl. 2, fig. 7-8.
Spiniferites varmae Lentin and Williams, 1973, p. 131

Text-figure 20 Spiniferites varmae Lentin and Williams, 1973. Oblique dorsal surface (specimen; Navarin 6570-6660 ft RI) Scale bar; 10 μm.

Emended Diagnosis: Spherical to subspherical intermediate proximochorate cyst without horns, comprising a smooth to fairly granular periphragm and a smooth endophragm adpressed between the processes. Parasutural septa distinctive and relatively high. Processes short, sometimes hollow, tapering to cylindrical with foliate to patulate or recurved distal extremities. Paratabulation indicated by parasutural septa as 4' (?), 6", 6c, 6", 1p, 1". Archeopyle precingular, formed by the loss of para-
Dimensions of the figured specimen: length of cyst 70 \(\mu m\), width 65 \(\mu m\), length of processes 15 \(\mu m\).

Discussion: The diagnosis of S. varmae is emended to include reference to its precingular archeopyle and paratabulation. S. varmae was first described as Hystrichosphaera pseudofurcata by Varma and Dangwal (1964) but the name H. pseudofurcata was pre-occupied by Klumpp (1953) for another species. Lentin and Williams (1973) therefore designed the new species name S. varmae for the taxon.

S. varmae is similar to S. pseudofurcatus, but differs in possessing a spherical central body and relatively short gonal processes with patulate to recurved endings.

Previous record: Pre-Miocene (Oligocene or Eocene) of the Cambay Basin, western India (Varma and Dangwal, 1964); late Oligocene (N3) of the Piedmont Basin, Italy (Powell, 1986a).

Thecal affinities: Unknown; possibly related to the modern Gonyaulacaceae based on its paratabulation and archeopyle.

Genus Systematophora Klement, 1960
Type species: Systematophora Cookson and Eisenack, 1965

Systematophora ancyrea Cookson and Eisenack, 1965
Plate 15, figs. 1-5

Systematophora ancyrea Cookson and Eisenack, 1965, p. 126, pl. 14, fig. 1-3.

Discussion: The less completely developed penitabular process complexes distinguish Systematophora ancyrea from S. placacantha (Defflandre and Cookson).

Previous record: Late Eocene of southwestern Victoria, Australia (Cookson and Eisenack 1965); middle Eocene of the Grand Banks off eastern Canada (Williams and Brideaux 1975), late Eocene to middle Miocene of DSDP site 370, offshore northwestern Africa (Williams 1978); early to middle Miocene of Japan (Matsuoka 1974, 1983).

Thecal affinities: Unknown.

Systematophora curta sp. nov.
Plate 15, figs. 8-11; Text-fig. 21
Dinoflagellate cysts from the Bering Sea

Text-figure 21 Systematophora curta sp. nov.
Free operculum of the paratype.
Scale bar; 10 μm.

Derivation of name: Latin, curtus, short; with reference to the short processes.

Diagnosis: Intermediate subspherical proximochorate cyst with slight polar compression. Cyst surface finely granulate. Paratabulation represented by penitabular process complexes as 4°, 6°, 6c, 6"", 1p(?), 1"", Os. Penitabular complexes variable; apical area having incomplete annulate types with two to four small processes on each paraplate; pre- and postcingular areas with six box-like penitabular complexes but the 1"" process complex somewhat reduced and small; antapical area possessing one large annulate complex. Processes short, solid, wide and tubiform to buccinate with simple flat distal extremities. Most of bases of the adjacent processes not connecting and reduced. Paracingulum delineated by six rectilinear complexes and approximately circular; parasulcus with process complexes. Archeopyle tetratabular, apical, formed by the loss of four paraplates.

Holotype: Navarin Basin COST No. 1 Well, 6660-6750ft, Ring 7 (Plate 15, fig. 9).

Paratype: Navarin Basin COST No. 1 Well, 6660-6750ft, Ring 6 (Plate 15, fig. 11) ; 6750-6840ft, Ring 10 (Plate 11, fig. 10).

Type horizon and locality: Navarin Basin COST No. 1 Well, 6660-6750ft, Navarin Basin, Bering Sea. Heteraulacacysta campanula Zone; late Oligocene to early Miocene.

Description: The cyst body is subspherical, without horns at the apex and antapex, but sometimes has processes at the apex that are longer than the other processes. The cyst wall consists of two layers which are strongly adpressed over most of the cyst body. The penitabular complexes are annulate or rectilinear. The processes are usually wide and short, with slightly recurved or simple distal tips. Three apical penitabular complexes are present, but one of these probably includes the 1' and 4' paraplates based on its shape (Text-fig. 21). The first postcingular process complex is very small. The paracingulum is represented by approximately six recti-
linear ridges, and is almost circular. The parasulcus lacks processes. The archeopyle is apical and is formed by the loss of all of the apical para-plates.

*Dimensions:* Holotype; cyst diameter 48 μm, length of processes 6-7 μm. Range; cyst diameter 43-53 μm, length of processes 5-9 μm, diameter of free operculum, 35 × 38 μm-41 × 39 μm. Number of specimens measured; 8.

*Discussion:* *Systematophora curta* is characterized by the possession of well-developed penitabular complexes and processes that are mostly solid, wide, cylindrical to tubiform, with simple or recurved distal extremities. The species differs from other species of *Systematophora* because of its short processes.

*Thecal affinities:* Unknown.


*Hystrichosphaeridium placacanthum* Deflandre and Cookson 1955, p. 276, pl. 9, fig. 1-3.

*Systematophora placacantha* (Deflandre and Cookson) Davey et al., 1969, p. 17.

*Systematophora placacantha* (Deflandre and Cookson) Davey et al., emend. May, 1980, p. 68.

*Discussion:* The present specimens of *Systematophora placacantha* are more similar to those of *S. placacantha* illustrated by Williams and Brideaux (1975, pl. 27, fig. 1) than to the holotype in having slightly shorter and wider processes.

*Previously known range:* Middle Eocene to middle Miocene according to Williams and Bujak (1985).

*Genus Tectatodinium* Wall, 1967

*Type species:* *Tectatodinium pellitum* Wall, 1970

*Tectatodinium minutum* Matsuoka, 1983

*Plate 18, fig. 10

*Tectatodinium minutum* Matsuoka, 1983, p. 127, pl. 5, fig. 6, pl. 6, fig. 7.

*Remarks:* This species is characterized by a granular surface of the periphragm and smaller cyst body.
Previous record: late Early Miocene to Late Miocene or younger in Japan (Matsuoka 1983).

Thecal affinities: Unknown; possibly related to the modern genus Gonyaulax based on its precingular archeopyle.

Thecal affinities: Unknown.


Type species: *Trinovantedinium capitatum* Reid, 1977

*Trinovantedinium boreale* Bujak, 1984
Plate 16, figs. 1-6


Discussion: Morphological variations of this species include the process length, cyst shape and horn development as noted by Bujak (1984a). Late Eocene populations possess longer processes than do those from the lower Oligocene of the Bering Sea.

*Trinovantedinium capitatum* differs from *Apectodinium homomorphum* (Deflandre and Cookson) in not having lateral horns, in usually possessing a paracingulum indicated by two rows of processes and in having shorter processes. The differences between *T. boreale* and *T. capitatum* were discussed by Bujak (1984a).

Previous record: Late Eocene of DSDP site 183 in the northern North Pacific (Bujak, 1984a).

Thecal affinities: Unknown; possibly related to the subgenus *Protoperidinium* of the family Protoperidiniaceae based on the intercalary archeopyle and non-pigmented cyst wall.

Genus *Tuberculodinium* Wall, 1967


*Tuberculodinium rossignoliae* Drugg, 1970 emend. herein
Plate 16, fig. 7

Emended diagnosis: Large to intermediate subspherical to oblate cyst with hollow processes. Cyst wall consisting of two layers which are always separated by processes. Ectophragm very thin and sometimes incomplete between adjacent processes. Processes probably intratabular, spherical to very short, cylindrical. Less than twenty processes present on the precingular and postcingular series, being absent from paracingular, parasulcal, apical and posterior intercalary and antapical regions. Archeopyle hypocystal, formed by the loss of either two or three posterior intercalary paraplates. Operculum sometimes attached to the hypocyst, but generally detached.

Remarks: The diagnosis is emended to include reference to the hypocystal archeopyle and the number of processes. In the original diagnosis, Drugg (1970) indicated a precingular archeopyle usually consisting of two paraplates. Comparison with Tuberculodinium vancampoae (Rossignol) indicate that both species have a hypocystal archeopyle. Matsuoka (1985) reported the number of opercular plates in modern Tuberculodinium vancampoae as varying from two to five, and suggested that the number of opercular papaplates is not diagnostic for Tuberculodinium species.

Previously known range: Late Eocene-Oligocene to Pliocene of the Grand Banks (Williams and Brideaux, 1975); early Miocene in Sumatra (Drugg, 1970); middle Miocene of Denmark (Piasecki, 1980); early to late Oligocene of the Gulf of Mexico (Matsuoka, unpublished data).

Thecal affinity: Probably a species related to the modern genus Pyrophacus. In modern Pyrophacus, two different cysts are known, these being P. steinii (Schiller) and P. holorogium (Stein). Only P. steinii (= Tuberculodinium vancampoae) has processes, whereas P. holorogium does not possess processes. T. rossignoliiæ may be more closely related to Pyrophacus steinii.

Tuberculodinium vancampoae (Rossignol) Wall, 1967
Plate 16, figs. 8-9; Plate 17, figs. 1-4


Discussion: T. vancampoae differs from other species of Tuberculodinium in possessing apical processes and a larger cyst body. The modern geographical distribution of this cyst is restricted to warm-water (subtropical to
warm temperate) regions including the region off Hachinohe, North Japan where it is influenced by the warm-water Tsugaru current.

*Thecal affinity*: *Pyrophacus steinii* (Schiller) Wall and Dale. Matsuoka (1985c) concluded that *Tuberculodinium vancampoae* is also the cyst form of *Pyrophacus steinii* subsp. *vancampoae* based on unialgal cyst cultures.

*Previously known range*: The oldest known occurrences of this extant species are the middle to late Oligocene of DSDP Site 375 off West Africa (Williams, 1978), the late Oligocene of the Rockall Plateau (Costa and Downie, 1979), the middle to late Oligocene offshore of eastern Canada (Williams and Bujak, 1977), and late Oligocene of the Piedmonte Basin, Italy (Powell, 1986a).

**Genus Xandarodinium** Reid, 1977

Type species: *Xandarodinium xanthonium* Reid, 1977

*Xandarodinium variabile* Bujak, 1984

Plate 17, fig. 5

*Xandarodinium variabile* Bujak, 1984, p. 194-195, pl. 4, figs. 7-10; text-fig. 3.

**Discussion**: *Xandarodinium variabile* is characterized by its dorso-ventrally compressed cyst, variable process morphology, and brownish pigmented cyst wall. It differs from *X. xanthonium* (Reid) in having more slender processes.

*Previous record*: Late Miocene to early Pleistocene of DSDP Sites 184, 184B, 186, 187, 188, 189, 190, 191 and 192, northern North Pacific and the Bering Sea (Bujak, 1984); late Miocene to early Pleistocene of North Japan (Matsuoka et al., 1987); late Oligocene to early Miocene of Italy (Powell, 1986a).

*Thecal affinities*: *X. variabile* is morphologically similar the modern cyst *X. xanthonium* whose thecate form is indicated to be *Protoperidinium divaricatum* (Meunier) Parke et Dodge by Matsuoka et al. (1982).

**Order Uncertain**

**Genus Paralecaniella** Cookson and Eisenack, 1970; emend. Elsik, 1977

Type species: *Paralecaniella indentata* (Deflandre and Cookson, 1955) Cookson and Eisenack, 1970 = *Epicephalopyxis indentata* Deflandre and
Cookson 1955.

**Paralecaniella indentata** (Deflandre and Cookson, 1955)
Cookson and Eisenack, 1970; emend. Elsik, 1977
Plate 18, fig. 2

*Epicephalopyxis indentata* Deflandre and Cookson, 1955, p. 292, pl. 9, fig. 5-7, text-fig. 56.


*Paralecaniella indentata* (Deflandre and Cookson) Cookson and Eisenack, emend. Elsik, 1977, p. 96-100, pl. 1, fig. 1-16, pl. 2, fig. 1-12, text-fig. 1.

**Description**: This small subspherical palynomorph consists of a smooth, thin, filmy outer wall, and a relatively thick and smooth inner wall. A shallow indentation is present on the peripheral margin of the outer wall and does not penetrate the inner wall.

**Discussion**: Elsik (1977) reattributed *Paralecaniella indentata* to the Dinophyceae based on the presence of an opening interpreted as an epitractal archeopyle in specimens obtained from the Lower Tertiary of the Gulf of Alaska and the Paleocene and lower Eocene Pebble Point Section, Australia. The specimens from the Bering Sea do not show paratabulation or an archeopyle.

**Previous record**: Paleocene to late Eocene, and Miocene or older of Victoria, Australia (Deflandre and Cookson, 1955; Cookson and Eisenack 1965); Early Tertiary of Tasmania (Cookson and Eisenack, 1967), Late Cretaceous of the Isle of Wight, England (Clark and Verdier, 1967), Early Tertiary of the Gulf of Alaska (Elsik, 1977).

**Botanical affinities**: Cookson and Eisenack (1970) considered that *Paralecaniella* is attributed to the Family Lecaniellaceae Cookson and Eisenack 1970, and was related to extant Volvocales (?) of the Chlorophyceae based on the organism usually splitting into two discoidal bodies. Elsik (1977) subsequently studied the morphology of *Paralecaniella indentata* and suggested affinities with the Dinophyceae because of a supposed paracingulum and archeopyle.
3 *Incerta sedis (Acritarcha)*

Group Acritarcha Evitt, 1963

Genus *Cyclopsiella* Drugg and Loeblich, 1967

Type species: *Cyclopsiella elliptica* Drugg and Loeblich, 1967

*Cyclopsiella* sp.

Plate 18, fig. 4

Discussion: The present species differs from *C. elliptica* in possessing a well developed periphragm and *C. vieta* Drugg and Loeblich in bearing no fold on an equatorial zone.

Botanical affinities: A cyst of some forms of marine phytoplankton (Drugg and Loeblich 1967).

Genus *Halodinium* Bujak, 1984

Type species: *Halodinium major* Bujak, 1984

*Halodinium minor* Bujak, 1984

Plate 18, fig. 1

*Halodinium minor* Bujak, 1984, p. 196, pl. 4, figs. 18-20

Discussion: According to Bujak (1984a), *H. minor* differs from *H. major* in possessing a smaller body. The central pylome of the figured specimen is not thickened on the margin.

Previous record: Early to late Pleistocene in the Bering Sea (Bujak, 1984a).

Botanical affinities: Unknown.

Genus *Joviella* gen. nov.

Derivation of name: Latin, Jovis, Jupiter; with reference to the circular outline and reddish brown color.

Type species: *Joviella magnifica* sp. nov.; late Miocene; Navarin Basin No. 1 COST Well, Navarin Basin, central Bering Sea.

Diagnosis: Spherical to subspherical reddish brown microfossil. Organic wall consisting of a thick outer wall covered with roughly reticulate
ornament and an adpressed inner wall. No opening is present. Radial pores are absent.

Discussion: Several spherical palynomorphs that are not attributable to the fossil dinoflagellates are known, and include *Leiosphaeridia* (Acri-tarcha), and *Tasmanites* and *Tytthodiscus* (Prasinophyceae). *Joviella* differs from *Leiosphaera* in possessing ornament on its surface and in lacking a cyclopyle, and from *Tasmanites* and *Tytthodiscus* in lacking radial pores.

Botanical affinities: Unknown; possibly the resting spores or systs of algae.

***Joviella magnifica*** sp. nov.
Plate 18, figs. 5-8

Derivation of name: Latin, *magnus*, large, great; with reference to the relatively large spherical morphology.

Diagnosis: Subspherical reddish brown palynomorph, consisting of a thick, corrugate outer wall and a relatively thin smooth inner wall which are adpressed. Roughly corrugate structures on the outer wall are derived from numerous laevigate muri. No opening occurs.

Holotype: St. George Basin COST No. 2 Well, 7310-7400ft, Ring 3 (Plate 18, fig. 6).

Paratype: St. George Basin COST No. 2 Well, 7310-7400ft, Ring 1 (Plate 18, fig. 8), Ring 4 (Plate 18, fig. 7).

Type horizon and locality: St. George Basin COST No. 2 Well, 7310-7400ft, St. George Basin, Bering Sea. *Hystrichosphaeropsis variabile* Zone; late Miocene.

Description: The specimens recovered from the Bering Sea are usually folded and rarely have two small bosses on opposite sides of the body. A large slit may occur, but this is neither constant nor regular in the position.

Dimensions: Holotype: diameter of central body 68 μm, height of muri ca. 1 μm. Range; diameter of central body 60-71 μm. Number of specimens measured; 10.

Botanical affinities: Unknown
Text-figure 22 Occurrence chart of the selected species of dinoflagellate cysts in the Navarin Basin COST No. 1 well.
<table>
<thead>
<tr>
<th>Sample Depth</th>
<th>Species</th>
</tr>
</thead>
</table>

Text-figure 23 Occurrence chart of the selected species of dinoflagellate cysts in the Norton Sound COST No. 1 well.
## Text-figure 24 Occurrence Chart of the selected species of dinoflagellate cysts in the St. George Basin COST No. 2 well.

<table>
<thead>
<tr>
<th>Sample Depth</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>00 - 05</td>
<td><em>Heterolauracysta campanula</em></td>
</tr>
<tr>
<td>05 - 10</td>
<td><em>Zone Hypstrichosphaera variabilis</em></td>
</tr>
<tr>
<td>10 - 15</td>
<td><em>Zone Filiisphaera pilosa</em></td>
</tr>
<tr>
<td>15 - 20</td>
<td><em>Zone Impagidinium velorum</em></td>
</tr>
<tr>
<td>20 - 25</td>
<td><em>Zone Impagidinium steveni</em></td>
</tr>
<tr>
<td>25 - 30</td>
<td><em>Zone Impagidinium truncatum</em></td>
</tr>
<tr>
<td>30 - 35</td>
<td><em>Zone Impagidinium vernalis</em></td>
</tr>
<tr>
<td>35 - 40</td>
<td><em>Zone Impagidinium antarcticum</em></td>
</tr>
<tr>
<td>40 - 45</td>
<td><em>Zone Impagidinium hudsonicum</em></td>
</tr>
<tr>
<td>45 - 50</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>50 - 55</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>55 - 60</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>60 - 65</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>65 - 70</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>70 - 75</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>75 - 80</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>80 - 85</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>85 - 90</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>90 - 95</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
<tr>
<td>95 - 100</td>
<td><em>Zone Impagidinium sp.</em></td>
</tr>
</tbody>
</table>

### Rocked-Out Zones

- **Zone Heterolauracysta campanula**
  - Sample depths: 00 - 05
- **Zone Hypstrichosphaera variabilis**
  - Sample depths: 05 - 10
- **Zone Filiisphaera pilosa**
  - Sample depths: 10 - 15
- **Zone Impagidinium velorum**
  - Sample depths: 15 - 20
- **Zone Impagidinium steveni**
  - Sample depths: 20 - 25
- **Zone Impagidinium truncatum**
  - Sample depths: 25 - 30
- **Zone Impagidinium vernalis**
  - Sample depths: 30 - 35
- **Zone Impagidinium antarcticum**
  - Sample depths: 35 - 40
- **Zone Impagidinium hudsonicum**
  - Sample depths: 40 - 45
- **Zone Impagidinium sp.**
  - Sample depths: 45 - 50, 50 - 55, 55 - 60, 60 - 65, 65 - 70, 70 - 75, 75 - 80, 80 - 85, 85 - 90, 90 - 95, 95 - 100
VII ACKNOWLEDGEMENTS

We wish to thank Ron Turner and John Larson of the Mineras Management Service in Anchorage, U.S.A., and Mike Clark, Ed Davies and Javier Helenes of the Bujak Davies Group in Calgary, Canada, for their constructive criticism and advance regarding the manuscript. We also thank Barbara Williams for patiently typing the many drafts of the text and Yuriko Masuda for her kind assistance in preparing of some text-figures.

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Explanation of Plates 1-19
Explanation of Plate 1

Figs. 1-3  *Areosphaeridium diktyoplokus* (Klumpp) Eaton, 1976
1 : Slide no. Navarin 12770-12780ft B1, optical cross section in lateral view.
3 : Slide no. Navarin 12770-12780ft R2, optical cross section in apical-antapical view.

Fig. 4  *Achosphaera remulifera* (Deflandre) Evitt, 1963
Slide no. Navarin 11000-11090ft R3.

Figs. 5-7  *Achosphaera spongiosa* sp. nov.
5 : Paratype, slide no. St. George 11740-11830ft R2, optical cross section of dorso-ventral view.
6 : Slide no. Norton 5730-5760ft R6, lateral view showing a precingular archeopyle (arrow).
7 : Paratype, slide no. Navarin 5370-5460ft R5, showing parasutures strongly reduced.

Scale bar : 20 μm.
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Plate 1
Figs. 1-3 *Achosphaera spongiosa* sp. nov.
1: Slide no. Navarin 6480-6570ft R3, specimen broken.
2: Holotype, slide no. Navarin 5370-5460ft R10, optical cross section in dorso-ventral view, showing reduced parasutural septa.
3: Paratype, slide no. Norton 4110-4140ft R3, showing a free operculum in the body cavity (arrow).

Figs. 4-6 *Algidasphaeridium capillatum* gen. et sp. nov.
4: Paratype, slide no. Navarin 4530-4620ft R5, showing a chasmic archeopyle (a) and showing hair-like spines (b).
5: Holotype, slide no. Navarin 4530-4620ft R4, showing a chasmic archeopyle.

Fig. 7 *Chiropteridium mespilatum* (Maier) Lentin and Williams, 1973
Slide no. Navarin 11360-11430ft R5, free operculum corresponding to an apical part.

Figs. 8-9 *Dapsilidinium pastielsii* (Davey and Williams) Bujak, Downie Eaton and Williams, 1980
8: Slide no. Navarin 6660-6750ft R1, lateral view.
9: Slide no. Norton 6450-6480ft R1, lateral view.

Fig.10 *Cordosphaeridia sp.*
Slide no. Norton 4290-4380ft R2.

Figs. 11-12 *Diphyes* sp. cf. *colligerum* (Deflandre and Cookson) Cookson, 1965.
11: Slide no. Navarin 6840-6930ft R4, optical cross section in lateral view.
12: Slide no. Navarin 6750-6840ft R12, optical cross section, showing a large apical archeopyle.

Scale bar: 20 μm.
Explanation of Plate 3

Fig. 1  *Distatodinium fusiforme* (Matsuoka) Bujak and Matsuoka, 1986
Slide no. Norton 6241.6 R5, lateral view.

Fig. 2  ?*Evittosphaerula* sp. A
Slide no. Norton 3330-3360ft R7, lateral view, showing an endophragm with reticulate periphragm (a) and part of a periphragm (b).

Figs. 3-4  *Filisphaera filifera* Bujak, 1984
4 : Slide no. St. George 4430-4520ft R1, showing an attached operculum (arrow).

Figs. 5-9  *Filisphaera pilosa* sp. nov.
5 : Paratype, slide no. Norton 2490-2520ft R2, specimen folded.
6 : Slide no. Norton 3030-3060ft R7, showing an attached operculum (arrow).
7 : Holotype, slide no. St. George 1910-2000ft R2, part of the cyst surface with granules or very short processes (b).
8 : Paratype, slide no. St. Geroge 2900-2990ft R1, showing a precingular archeopyle.
9 : Paratype, slide no. St. George 1460-1550ft R6, free operculum probably corresponding to the trapezoidal 3” paraplate.

Scale bar : 20 µm.
Explanation of Plate 4

Figs. 1-2  *Heteraulacysta campanula* Drugg and Loeblich, 1967
1: Slide no. Norton 6221.5 R3, antapical view (?).
2: Slide no. Norton 5190-5220ft R2, apical view (?).

Fig. 3  *Hystrichokolpoma rigaudiae* Deflandre and Cookson, 1955
Slide no. Navarine 7290-7380 R4, showing small tubulet ornaments on the large processes (a; arrow).

Fig. 4  *Hystrichokolpoma salacium* Eaton, 1976
Slide no. Norton 12150-12180ft R4, lateral view.

Fig. 5  ? *Hystrichokolpoma* sp.
Slide no. St. George 2990-3080ft R2.

Fig. 6  *Hystrichosphaeropsis complanata* Eisenack, 1965
Slide no. Norton 10350-10380ft R2.

Fig. 7  *Hystrichosphaeropsis* sp. cf. *obscura* Habib, 1972
Slide no. Norton 4290-4320ft R1, specimen corroded.

Scale bar: 20 μm.
Explanation of Plate 5

Figs. 1-4  *Hystrichosphaeropsis arctica* sp. nov.
1: Holotype, slide no. Norton 3030-3060ft R9, optical cross section in dorso-ventral view (a) and showing a list of paracingulum (b; arrow).
2: Paratype, slide no. Norton 4470-4500ft R6, optical cross section in dorso-ventral view (a) and ventral surface (b).
3: Slide no. Navarin 5640-5730ft R4, optical cross section in dorso-ventral view.
4: Paratype, slide no. Norton 4110-4140ft R5, specimen without apical horn, showing a pericoel well developed in the hypocyst (a).

Figs. 5-8  *Hystrichosphaeropsis variabile* sp. nov.
5: Holotype, slide no. Norton 3930-3960ft R3, optical cross section in dorso-ventral view, showing a conspicuous antapical pericoel in the hypocyst (a).
6: Paratype, slide no. Norton 3840-3870ft R5, optical cross section in dorso-ventral view, showing a well developed antapical pericoel.
8: Paratype, slide no. Norton 3930-3960ft R8.

Fig. 9  *Hystrichostrogylon membraniphorum* Agelopoulus, 1964
Slide no. Norton 12150-12180ft R3, optical cross section in dorso-ventral view.

Fig. 10  *Impagidinium cornutum* sp. nov.
Paratype, Slide no. Norton 4380-4410ft R6, dorso-ventral view, showing a large apical horn.

Scale bar: 20 μm.
Explanation of Plate 6

Figs. 1-2  *Impagidinium cornutum* sp. nov.
1: Holotype, slide no. Norton 3570-3600ft R1, optical cross section in oblique dorso-ventral view, showing an apical horn (a; arrow), ventral surface showing the triangular 6° paraplate (b) and dorsal surface showing a precingular archeopyle (c).
2: Paratype, slide no. Norton 3570-3600ft R5, dorso-ventral view.

Figs. 3-4  *Impagidinium japonicum* Matsuoka, 1983

Figs. 5-7  *Impagidinium manumii* sp. nov.
5: Holotype, slide no. Norton 3840-3870ft R2, oblique dorsal view, showing a precingular archeopyle (a; interference contrast) and optical cross section in dorso-ventral view (b).
6: Paratype, slide no. Norton 3930-3960ft R8, lateral view, specimen deformed (interference contrast).
7: Paratype, slide no. Norton 3840-3870ft R1, apical view showing a precingular archeopyle (interference contrast).

Fig. 8  *Impagidinium velorum* Bujak, 1984

Fig. 9  *Spiniferites adnatus* sp. nov.
Paratype, slide no. Norton 7830-7860ft R2, apical-antapical view.

Scale bar: 20 µm.
Explanation of Plate 7

Fig. 1 *Kallosphaeridium* sp.
Slide no. Norton 6450-6480ft R4, lateral view showing an apical archeopyle (?).

Fig. 2 *Lejeunecysta convexa* sp. nov.
Holotype, slide no. St. George 9830-9920ft R4, optical cross section in dorso-ventral view.

Fig. 3 *Lejeunecysta* sp.
Slide no. Norton 5012.2 R5, dorso-ventral view.

Fig. 4 *Lejeunecysta fallax* (Morgenroth) Artzner and Dörhöer, 1978
Slide no. Norton 8010-8040ft R4, dorso-ventral view.

Fig. 5 *Lejeunecysta granosa* Biffi and Gringnani, 1981
Slide no. Navarin 11240-11330ft R1, dorso-ventral view, showing an intercalary archeopyle (a), and the paracingulum (b).

Fig. 6 *Lejeunecysta hyalina* (Gerlach) Artzner and Dörhöer, 1978
Slide no. Navarin 12740-12830ft R6, dorso-ventral view.

Fig. 7 *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall, 1967

Fig. 8-9 *Lingulodinium brevispinosum* sp. nov.
8: Holotype, slide no. Navarin 7020-7110ft R5, probably ventral view, showing an archeopyle suture (a; arrow) and optical cross section (b).
9: Paratype, slide no. Navarin 6930-7020ft R1, optical cross section.

Scale bar: 20 \( \mu \)m.
Dinoflagellate cysts from the Bering Sea

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Plate 7
Explanation of Plate 8

Fig. 1  *Lingulodinium brevispinosum* sp. nov.
Paratype, slide no. Navarin 6930-7020ft R1, optical cross section.

Figs. 2-4  *Litosphaeridium parvum* sp. nov.
2: Holotype, slide no. Navarin 7830-7920ft R1, probably dorso-ventral view, showing an apical archeopyle (?) (b; interference contrast).
4: Paratype, slide no. Norton 4380-4410ft R5, orientation unclear.

Figs. 5-6  *Cribroperidinium giusepeii* (Morgenroth) Helenes, 1984
5: Slide no. Norton 6540-6570ft R9, ventral surface.

Figs. 7-9  *Operculodinium alcium* sp. nov.
7: Paratype, slide no. Norton 5012.2ft R16, lateral view, showing a precingular archeopyle.
8: Holotype, slide no. Norton 4200-4230ft R5, oblique lateral view, showing an operculum attached (a; arrow, interference contrast).
9: Paratype, slide no. Norton 5012.2ft R19, dorsal surface, showing a precingular archeopyle.

Scale bar: 20 μm.
Explanation of Plate 9

Fig. 1 Operculodinium echigoense Matsuoka, 1983
Slide no. Navarin 7650-7740ft R6, optical cross section in dorso-ventral view.

Fig. 2 Operculodinium wallii Matsuoka, 1983
Slide no. Navarin 7470-7560ft R5, apical surface, showing an operculum attached (arrow).

Fig. 3 Pentadinium laticinctum subsp. granulatum Gocht, 1969

Figs. 4-9 Phthanoperidinium bennetti sp. nov.
4: Holotype, slide no. Navarin 12740-12750ft R4, ventral surface.
5: Paratype, slide no. Navarin 12710-12720ft R5, optical cross section in dorso-ventral view.
6: Paratype, slide no. Navarin 12740-12750ft R8, dorsal surface, showing an intercalary archeopyle (arrow).
7: Paratype, slide no. Navarin 12740-12750ft R3, ventral surface.
8: Paratype, slide no. Navarin 12740-12750ft R1, dorsal surface.
9: Slide no. 12740-12750ft R3, dorsal surface (?).

Figs. 10-12 Reticulatosphaera actinocoronata (Benedek) Bujak and Matsuoka, 1986

Scale bar: 20 µm.
Explanation of Plate 10

Figs. 1-2 *Rottnestia ovata* sp. nov.
1: Holotype, slide no. Norton 6630-6660ft R7, optical cross section in dorso-ventral view (a).
2: Paratype, slide no. Navarin 6000-6090ft R3, lateral view, showing short processes with small furcate distal tips.

Figs. 3-5 *Selenopemphix nephroides* Benedek, 1972
3: Slide no. Norton 4200-4230ft R9, apical surface, showing an apical horn.
4: Slide no. Norton 5012.2ft R12, optical cross section in polar view, showing a margin of paracingular lists.
5: Slide no. Norton 2130-2160ft R1, apical surface.

Figs. 6-7 *Selenopemphix crenata* sp. nov.
6: Holotype, slide no. Norton 4380-4410ft R1, antapical view, showing a parasulcus and an antapical horn (a) and optical cross section in polar view, showing a parasulcus and shallow denticulate margins of the paracingulum (b).
7: Paratype, Norton 2130-2160ft R2, optical cross section in polar view.

Figs. 8-9 *Spiniferites adnatus* sp. nov.
8: Holotype, slide no. Norton 4650-4680ft R1, dorsal surface (a; interference contrast, b; phase contrast)
9: Paratype, slide no. Norton 6810-6840ftA R1, lateral view, showing an adnate processes on the hypocyst (arrow).

Scale bar: 20 μm.
Explanation of Plate 11

Figs. 1-3  *Spiniferites adnatus* sp. nov.
1: Slide no. Norton 6270-6300ft R2, lateral view.
2: Paratype, slide no. Norton 5730-5760ft R1, lateral view.
3: Slide no. Norton 6221.5ft R1, lateral view (?).

Fig. 4  *Spiniferites* sp. aff. *membranaceus* (Rossignol) Sarjeant, 1970
Slide no. Norton 6630-6720 R1, lateral view (?).

Fig. 5  *Spiniferites* sp. aff. *adnatus* sp. nov.

Fig. 6  *Spiniferites aquilonius* sp. nov.
Holotype, slide no. Norton 3120-3150ft R6, optical cross section in dorso-ventral view (a), oblique dorsal view, showing a precingular archeopyle (b) and distal part of processes, showing diagnostically reticulate extremities (c, d).

Scale bar : 20 μm.
Explanation of Plate 12

Fig. 1  *Spiniferites aquilonius* sp. nov.
Paratype, slide no. Norton 3210-3240ft R2, oblique lateral view (a) and optical cross section in oblique lateral view (b).

Figs. 2-3  *Spiniferites ellipoideus* Matsuoka, 1983
2: Slide no. Norton 3750-3780ft R2, optical cross section in dorso-ventral view.
3: Slide no. Navarin 6840-6930ft R2, optical cross section in dorso-ventral view.

Figs. 4-5  *Spiniferites frigidus* Harland and Reid, 1980
4: Slide no. Norton 3480-3510ft R2, lateral view.

Figs. 6-7  *Spiniferites hexatypicus* Matsuoka, 1983
6: Slide no. St. Geroge 6770-6860ft R2, optical cross section in dorso-ventral view.
7: Slide no. Navarin 6300-6380ft R8, lateral view (?).

Scale bar: 20 μm.
Explanation of Plate 13

Figs. 1-2  *Spiniferites nortonensis* sp. nov.

1: Holotype, slide no. Norton 6630-6660ft R4, dorsal view, showing a precingular archeopyle (a) and optical cross section in dorso-ventral view (b).


Fig. 3  *Spiniferites ramosus* subsp. *ramosus* (Ehrenberg) Loeblich and Loeblich, 1966

   Slide no. Norton 6360-6390ft R6, optical cross section in apical-antapical view.

Fig. 4  *Spiniferites ramosus* subsp. *gracilis* (Davey and Williams) Lentin and Williams, 1973

   Slide no. Norton 5012.2ft R1, optical cross section in lateral view.

Fig. 5  *Spiniferites* sp. cf. *adnatus*.

   Slide no. Norton 6540-6560ft R6, optical cross section in dorso-ventral view.

Fig. 6  *Spiniferites* sp.

   Slide no. Norton 4200-4230ft R4, oblique dorsal surface, showing a precingular archeopyle.

Fig. 7  *Spiniferites choanus* sp. nov.

   Slide no. Norton 5280-5310ft R4, optical cross section in dorso-ventral view.

Fig. 8  *Spiniferites* sp.

   Slide no. Norton 4470-4500ft R1, optical cross section in lateral view.

Scale bar: 20 μm.
Explanation of Plate 14

Fig. 1 *Spiniferites pseudofurcatus* (Klumpp) Sarjeant, 1970
Slide no. Navarin 7470-7560ft R4, dorsal surface, showing a precingular archeopyle.

Figs. 2-3 *Spiniferites choanus* sp. nov.
2: Paratype, slide no. Navarin 6000-6090ft R8, lateral view.
3: Holotype, slide no. Navarin 6210-6300ft R8, optical cross section in dorso-ventral view, showing well-developed processes (a; arrow) and oblique dorsal view (b).

Figs. 4-5 *Spiniferites reductus* sp. nov.
4: Holotype, slide no. Navarin 5850-5940ft R10, ventral view (a) and dorsal surface, showing a precingular archepyle (b).
5: Paratype, slide no. Norton 4110-4140ft R3, dorsal view, showing a precingular archepyle.

Scale bar: 20 μm.
Explanation of Plate 15

Figs. 1-5 *Systematophora ancyrea* Cookson and Eisenack, 1965
1: Slide no. Navarin 6480-6570ft R2, oblique lateral view, showing an apical archopyle.
2: Slide no. Navarin 11000-11090ft R2, apical-antapical view.
3: Slide no. Norton 6450-6480ft R11, lateral view, showing an apical archeopyle.
4: Slide no. Norton 6360-6390ft R5, optical cross section in apical-antapical view.
5: Slide no. Norton 6450-6480ft R4, free operculum consisting of three paraplates.

Figs. 6-7 *Systematophora placacantha* (Deflandre and Cookson) Davey, Downie, Sarjeant and Williams, 1966
7: Slide no. Norton 5820-5850ft R5, free operculum consisting of three paraplates.

Figs. 8-11 *Systematophora curta* sp. nov.
8: Paratype, slide no. Navarin 6750-6840ft R7, free operculum consisting of three apical paraplates.
9: Holotype, slide no. Navarin 6660-6750ft R7, oblique antapical view, showing post-cingular and antapical paraplates.
11: Paratype, slide no. Navarin 6660-6750ft R6, free operculum consisting of three apical paraplates.

Scale bar: 20 µm.
Dinoflagellate cysts from the Bering Sea

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Plate 15

Images of various dinoflagellate cysts.
Figs. 1-6  *Trinovantedinium boreale* Bujak, 1984
2 : Slide no. Navarin 12740-12750ft R10, specimen possessing round cyst body.
3 : Slide no. Navarin 12740-12750ft R6, specimen possessing an apical horn.
5 : Slide no. Norton 6810-6900ftB R1, specimen providing a conspicuous apical and two antapical horns.
6 : Slide no. Navarin 12680-12690ft R2, lateral view, showing a cyst body depressed dorso-ventrally.

Fig. 7  *Tuberculodinium rossignoliae* Drugg, 1970
Slide no. Norton 4110-4140ft R4, optical cross section in apical-antapical view, specimen having fewer number of processes.

Figs. 8-9  *Tuberculodinium vancampoae* (Rossignol) Wall, 1967
8 : Slide no. Norton 5640-5670ft R7, apical-antapical view.
9 : Slide no. Norton 6221.5ft R14, antapical surface, showing enlarged hypocystal archepyle.

Scale bar : 20 μm.
Explanation of Plate 17

Figs. 1-4  *Tuberculodinium vancampoae* (Rossignol) Wall, 1967

1: Slide no. Norton 6221ft R11, antapical surface, showing three posterior intercalary paraplates and archeopyle sutures.

2: Slide no. Norton 6221.6ft R5, antapical surface, showing two posterior intercalary paraplates.

3: Slide no. Navarin 7650-7740ft R2, antapical surface, showing an enlarged hypocystal archeopyle.

4: Slide no. Navarin 7200-7290ft R7, corroded specimen without a distal part of processes.

Fig. 5  *Xandarodinium variabile* Bujak, 1984

Slide no. Navarin 3120-3290ft R1, lateral view.

Figs. 6-7  *Brigantedinium* spp.

6: Slide no. Norton 1770-1800ft R1, showing a smooth cyst wall.

7: Slide no. Norton 2130-2170ft R4, showing an archeopyle deformed (arrow).

Scale bar: 20 μm.
Dinoflagellate cysts from the Bering Sea

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Plate 17
Explanation of Plate 18

Fig. 1  *Halodinium minor* Bujak, 1984  

Figs. 2  *Paralecaniella identata* (Deflandre and Cookson) Cookson and Eisenack, 1970  
2: Slide no. Navarin 12680-12770ft R1, specimen corroded.

Fig. 3  *Impletosphaeridium* sp.  
Slide no. Norton 7380-7410ft R5, specimen broken.

Fig. 4  *Cyclopsiella* sp.  
Slide no. Norton 6360-6450ft R9, specimen having a circular opening (arrow).

Figs. 5-8  *Joviella magnifica* gen. et sp. nov.  
5: Paratype, slide no. St. George 7310-7400ft R1.  
6: Holotype, slide no. St. George 7310-7400ft R1a.  
7: Paratype, slide no. St. George 7310-7400ft R4.  
8: Paratype, slide no. St. George 7310-7400ft R1.

Fig. 9  *Batiacasphaera criosa* (Bujak) Jan du Chene, Stover and De Coninck, 1984  
Slide no. Norton 9540-9570ft R5.

Fig. 10  *Tectatodinium minutum* Matsuoka, 1983  
Slide no. St. George 5780-5870ft R1, lateral view, showing a precingular archeopyle and free operculum within the cyst (arrow).

Scale bar : 20 μm.
Figs. 1-2  *Lejeunecysta convexa* sp. nov.
1 : Paratype, slide no. SZ561208 R-K2, ventral surface, showing a convex outline of the epicyst (specimen corroded).
2 : Slide no. SZ561208 R-K3, optical cross section in dorso-ventral view, showing a straight outline of the epicyst (specimen corroded).

Fig. 3  *Spiniferites varmae* Lentin and Williams, 1973
Slide no. Navarin 6570-6660ft R1, optical cross section in dorso-ventral view, showing a circular outline.

Fig. 4  *Spiniferites aquilonius* sp. nov.
Slide no. Norton 3210-3240ft Rr-1. Microphotographs taken with different optics of the Olympus BH 2 Microscope, a : normal optics, b ; phase contrast optics, c ; fluorescence optics with blue excitation.

Fig. 5  *Filisphaera pilosa* sp. nov.

Fig. 6  *Filisphaera filifera* Bujak, 1984
Slide no. Norton 3330-3360ft R2, fluorescence microphotograph with blue excitation; age of specimen, late Miocene.

Fig. 7  *Spiniferites aquilonius* sp. nov.
Slide no. Norton 3210-3240ft Rr-1, fluorescence microphotograph with blue excitation; age of specimen, late Miocene.

Fig. 8  *Spiniferites adonatus* sp. nov.
Slide no. Norton 6221.5ft R1, fluorescence microphotograph with blue excitation; age of specimen late Oligocene to early Miocene.

Scale bar : 20 μm