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Organic-walled dinoflagellate cysts from surface sediments of Akkeshi Bay and Lake Saroma, North Japan

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Contents

Abstract

Modern dinoflagellate cysts recovered from surface sediments of Akkeshi Bay and Lake Saroma in Hokkaido, North Japan are described under the cyst-based classification. They contain ten genera and twenty-five species which include six new species of the Protoperidiniaceae (*Brigantedinium grande, B. asymmetricum, B. irregulare, Lejeunecysta psuchra L.? epidoma,* and *Trinovantedinium pallidifulvum*) and five indeterminate species. The dinoflagellate cyst assemblages in both Lake Saroma and Akkeshi Bay are characterized by the dominance of the protoperidiniacean cysts especially brown spherical *Brigantedinium* species and the scarcity of species of *Spiniferites, Lingulodinium* and *Tuberculodinium*. Comparison with the previous studies around the Japanese Islands, the assemblage is considered to represent a typical cold water one.

Based on modern biological and physical oceanographic data in the world, the protoperidiniacean-dominated cyst assemblage suggests the high primary production in both upwelling and other eutrophy regions.

Introduction

Around the Japanese Islands, two major different currents are present; the cold Oyashio current and the warm Kuroshio current, from which another warm Tsushima current brabches. Many marine organisms are sensitive for environmental conditions such as temperature, salinity and nutrient. Therefore, most of plankton associations, especially phytoplankton such as diatoms, coccolithophorids and dinoflagellates are considerably different between the areas influenced by the Kuroshio and Oyashio currents respectively (Aikawa 1936).

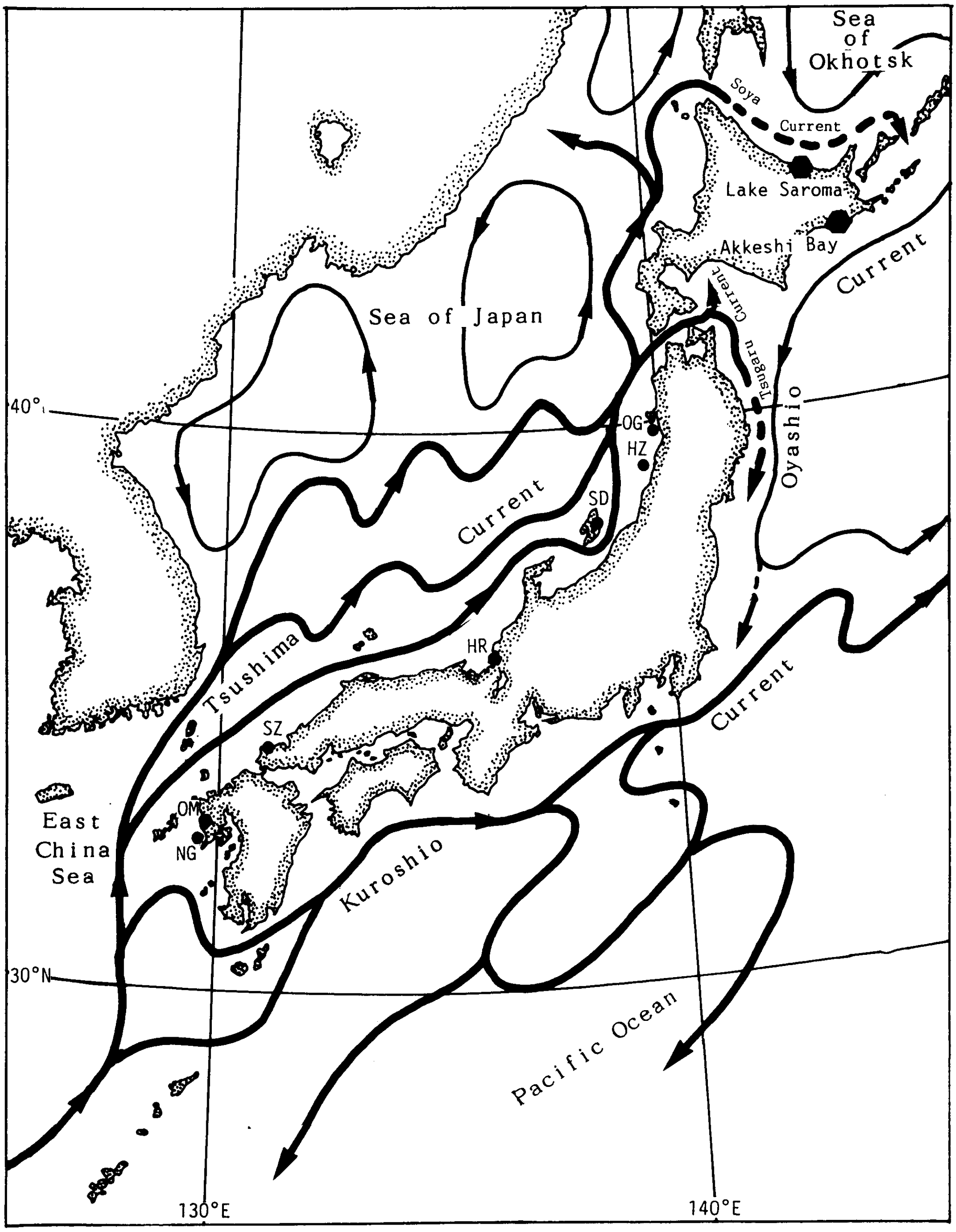
Harland et al. (1980) studied the cold sub-Recent dinoflagellate cyst assemblage of the Beaufort Sea and described diagnostic species such as *Spiniferites frigidus* Harland and Reid which is also a senior synonym of *Rottnestia amphicavata* Dobell and Norris and *Algidasphaeridium* ? *minutum* (Reid) for a cold water assemblage. Harland (1982) and Harland and Sharp (1986) also recorded the modern dinoflagellate cyst assemblage in the southern Barents Sea, which is characterized by abundance of *Spiniferites elongatus-S. frigidus* complex.

Around Japan, Matsuoka (1985b) described the modern warm water dinoflagellate cysts from the region which are wholly influenced by the Tsushima current.

Matsuoka (1976a) also reported the modern dinoflagellte cyst assemblage of off-Hachinohe in North Japan, which is mainly influenced by the Oyashio current. This area, however, is also considerably effected by the warm Tsugaru current which is one of branches of the Tsushima warm current. According to this, the dinoflagellate cyst assemblage of off-Hachinohe probably represents the mixed environment of the warm and cold currents.

Two areas presently studied are located in Hokkaido, North Japan. Akkeshi Bay is a typical inner bay and is wholly influenced by the Oyashio current. Since Lake Saroma is situated near the terminal of the warm Soya current which is a branch of the Tsushima current, this lake is slightly effected only from late spring to early autumn by this current and in winter is freezed over. Therefore, the dinoflagellate cyst assemblage in those two areas represent the cold water assemblage in the West Pacific Ocean.

The purpose of the present paper is to describe dinoflagellate cysts from Akkeshi Bay and Lake Saroma, and then clarify the modern cold water dinoflagellate cysts around North Japan.



Text-fig. 1 Index map showing locations of Akkeshi Bay and Lake Saroma, the areas previously studied by Matsuoka (1985 a,b), and the current system around the Japanese Islands. NG, OM, SZ, HR, SD, HZ, and OG appeared in Matsuoka (1986b).

Environmental Condition

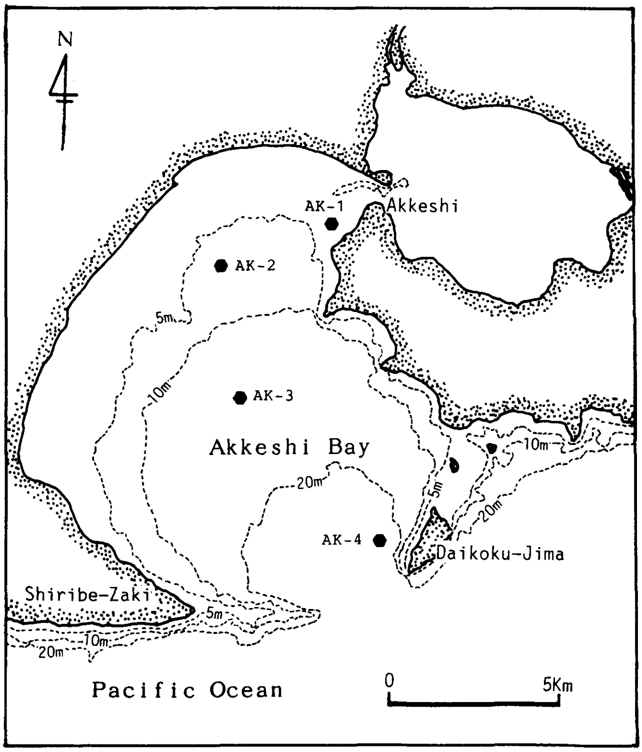
Akkeshi Bay (Text-figs. 1 & 2)

Akkeshi Bay is located at the southeast coast of Hokkaido (approximately Lat. 43°05′ N, Long. 144°55′ E) and faces the Pacific Ocean. This bay is separated from the Pacific Ocean by a narrow straight (approximately 6km in maximum width), and at the bay mouth, there is the deepest (−30m), but most parts of this bay are shollower than −20m in depth.

The bottom sediments of this bay are fine sand to mud, but around the Senpoushi-sho (bank) and the Nakase, the basement rocks are exposed (Watanabe, 1969).

Akkeshi Bay is one of bays which directly influenced by the cold Oyashio current. In summer the water temperature rises around 14°C, but in winter it drops around 1.5°C at the surface, and the salinity is 32.6 to 33.0‰ (Japan Oceanographic Data Centre (ed.) 1975). This bay is also influenced by a freshwater carried by the Bekanbetsu River through Lake Akkeshi.

Lake Saroma (Text-figs. 1 & 3)



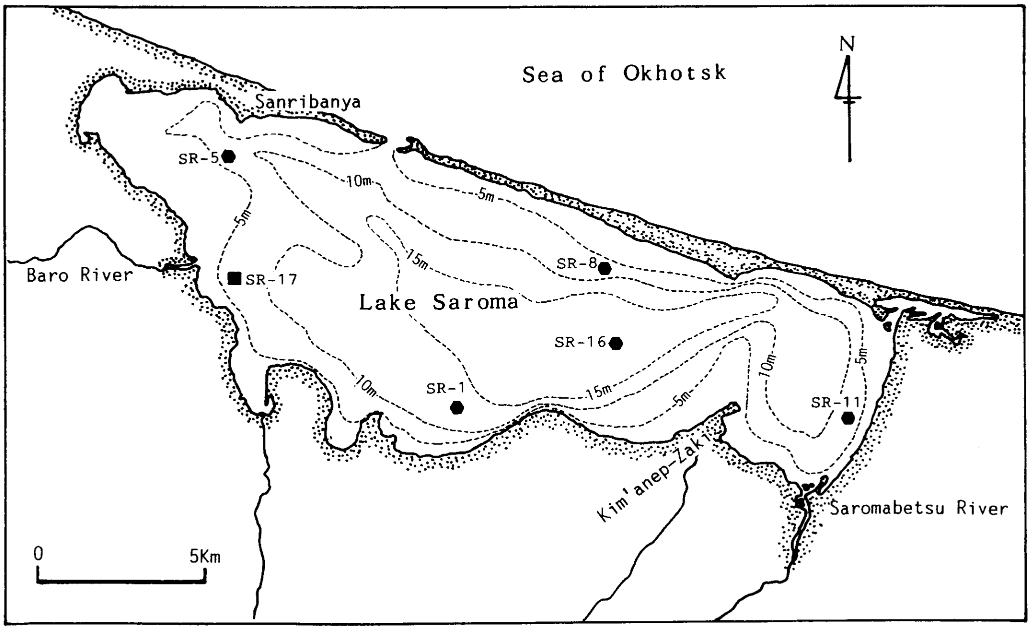
Text-fig. 2 Location map showing the sampling stations in Akkeshi Bay.

Lake Saroma is situated at the northeastern part of Hokkaido (approximately Lat. 44°15′ N, Long. 143°30′ E) and looks toward the Sea of Okhotsk. This lake is a lagoon, and is separated from the Sea of Okhotsk by a slender and long sand bar, and artificialy connected with the sea by a very narrow straight at 2.5 km east of Sanri-Banya on 1929. According to this, the salinity in Lake Saroma is similar to that of the Sea of Okhotsk (33.0 to 33.2‰, Japan Oceanographic Data Centre (ed.) 1979)

Lake Saroma is approximately 25.7 km in longitude and approximately 9.5 km in latitude, and is devided into two sub-basins by a small bank running from Cape Kim'anep to Fukushima. The eastern sub-basin is smaller and shallower than the western sub-basin, and is −12m in maximum depth. The western sub-basin has approximately −20m depth in maximum. There are several small rivers running into this lake, and two rivers, Baro and Saromabetsu are larger.

According to Satake (1967), bottom sediments of the lake are mostly composed of silt and clay except for the small bank and sand bar near the Sea of Okhotsk where sandy sediments are exposed.

Lake Saroma is frozen over from January to March, and the temperature under ice is between 1°C and 0°C. From spring through summer to autumn, this lake is influenced by the warm Soya current, a branch of the Tsushima



Text-fig. 3 Location map showing the sampling stations in Lake Saroma.

current, but the region around this lake is nearly terminal end of the Soya current. The surface temperature is approximately 15°C in summer.

Sampling location and method

Totally nine samples, four from Akkeshi Bay and five from Lake Saroma, were provided for the present study. All samples were collected with a simple gravity corer ; TFO Gravity Corer in July 1980 (Text-figs. 2, 3). These samples were kept in a refrigirator before the analysis.

Preparation method

The method of preparation of samples after collecting and palynological procedure were followed by the same way previously used in Matsuoka (1985a).

Terminology

Descriptive terms used in this study are mainly outlined in Evitt et al. (1977), Stover and Evitt (1978), Sarjeant (1982), Evitt (1985) and Matsuoka (1985e). The perifex 'para' in description for the cyst morphology is also adopted here.

Systematic description

The following cyst species are described in this paper ;

Order Gonyaulacales Taylor, 1980
  Family Gonyaulacaceae Lindemann, 1928
    Genus *Spiniferites* Mantell, 1850
      Spiniferites sp.
        cf. *S. bulloideus* (Deflandre and Cookson) Sarjeant, 1970
      Spiniferites sp. cf. *S. delicatus* Reid, 1974
      Spiniferites elongatus Reid, 1974
      Spiniferites frigidus Harland and Reid, 1980
      Spiniferites ramosus (Ehrenberg) Loeblich and Loeblich, 1966
    Genus *Operculodinium* Wall, 1967
      Operculodinium centrocarpum (Deflandre and Cookson) Wall, 1967

Family Pyrophacaceae Lindemann, 1928
Genus *Tuberculodinium* Wall, 1967
Tuberculodinium vancampoae (Rossignol) Wall, 1967
Order Peridiniales Taylor, 1980
Family Protoperidiniaceae Bujak and Davies, 1983
Subfamily Diplopsaloideae Bujak and Davies, 1983
Genus *Dubridinium* Reid, 1977
Dubridinium caperatum Reid, 1977
Dinoflagellate cyst type D
Subfamily Protoperidinioideae Bujak and Davies, 1983
Genus *Brigantedinium* Reid, 1977
Brigantedinium cariacoense (Wall) Reid, 1977
Brigantedinium majusculum Reid, 1977
Brigantedinium simplex (Wall) Reid, 1977
Brigantedinium grande sp. nov.
Brigantedinium asymmetricum sp. nov.
Brigantedinium irregulare sp. nov.
Genus *Lejeunecysta* Artzener and Dörhöfer, 1978
Lejeunecysta concreta (Reid) comb. nov.
Lejeunecysta psuchra sp. nov.
Lejeunecysta ? epidoma sp. nov.
Genus *Selenopemphix* Benedeck, 1972
Selenopemphix nephroides Benedeck, 1972
Selenopemphix quanta (Bradford) Matsuoka, 1985
Genus *Trinovantedinium* Reid, 1977
Trinovantedinium capitatum Reid, 1977
Trinovantedinium pallidifulvum sp. nov.
Genus *Votadinium* Reid, 1977
Votadinium carvum Reid, 1977
Votadinium spinosum Reid, 1977
Genus Uncertain
Dinoflagellate cyst type A
Order Gymnodiniales Lemmermann, 1910
Family Polykrikaceae Lindemann, 1928
Genus *Polykrikos* Bütschli, 1873
Polykrikos schwartzii Bütschli, 1873
Polykrikos sp. cf. *P. kofoidii* Chatton, 1914
Order Uncertain

Dinoflagellate cyst type B
Dinoflagellate cyst type C
Dinoflagellate cyst type E

A few other cysts are also recorded from Lake Saroma and Akkeshi Bay. They include *Nematosphaeropsis labyrinthea* (Ostenfeld), *Lingulodinium machaerophorum* (Deflandre and Cookson), *Protogonyaulax affinis* Inoue and Fukuyo, and *Peridinium ponticum* Wall and Dale.

In the synonym list for each species, the previous records only from the Quaternary sediments with microphotographs except for the holotype are listed up in this paper.

Class Dinophyceae Pascher, 1914
Order Gonyanlacales Taylor, 1980
Family Gonyanlacaceae Lindemann, 1928

Genus *Spiniferites* Mantell 1854 emend. Sarjeant 1970
Type species : *Spiniferites ramosus* (Ehrenberg 1837) Loeblich and Loeblich 1966

Spiniferites sp. cf. *S. bulloideus* (Deflandre and Cookson 1955) Sarjeant 1970
Plate 2, figures 5–6

1955 *Hystrichosphaera bulloidea* Deflandre and Cookson ; Wall, p. 300–302, fig. 6.
1968 Resting spores of *Gonyaulax scrippsae* Kofoid ; Wall and Dale, p. 270–271 ; pl. 1, figs. 14, 15.
1970 ?*Spiniferites ramosus* (Ehrenberg) ; Wall and Dale, p. 49–50, pl. 1, figs. 1–15.
1981 *Spiniferites* cf. *bulloideus* (Deflandre and Cookson) ; Matsuoka, pl. 2, fig. 7.
1983 *Spiniferites ramosus* sensu Wall ; Harland, p. 342, pl. 45, fig. 8.
1984 *Spiniferites bulloideus* (Deflandre and Cookson) ; Bradford and Wall, p. 37, pl. 3, figs. 15–18.
1985a *Spiniferites bulloideus* (Delfandre and Cookson) Sarjeant, 1970 ; Matsuoka, p. 31–32, pl. 1, figs. 8–12 ; pl. 23, figs. 1–9, text-fig. 4.

Remarks : *Spiniferites* sp. cf. *S. bulloideus* including the specimens of *S. bulloideus* recorded by Matsuoka (1985a) is characterized by a small subspherical to ovoidal cyst body with somewhat larger gonal precesses and membranous parasutural septa developed around the antapical plate. Morphological variations in this species contain the following two features ; the

Table 1 Cyst-theca correlations of dinoflagellates recorded from the surface sediments of Lake Saroma and Akkeshi Bay in Hokkaido.

Paleontological name for cyst	Biological name for motile cell
Goniolacoid	
Spiniferites sp. cf. *bulloideus*	*Gonyaulax scrippsae*
Spiniferites sp. cf. *delicatus*	*Gonyaulax* sp. cf. *scrippsae*
Spiniferites elongatus	*Gonyaulax spinifera* complex
Spiniferites firigidus	*Gonyaulax* sp. (?)
Spiniferites ramosus	*Gonyaulax spinifera* complex
Nematosphaeropsis labyrinthea	*Gonyaulax spinifera* complex
Operculodinium centrocarpum	*Protoceratium reticulatum*
Lingulodinium machaerophorum	*Gonyaulax polyedra*
Tuberculodinioid	
Tuberculodinium vancampoae	*Pyrophacus steinii*
Peridinioid	
Dubridinium caperatum	*Diplopeltopsis minor*
Brigantedinium cariacoense	*Protoperidinium avellana*
Brigantedinium sp. cf. *majusclum*	*Protoperidinium* sp. (*Conica* group) ?
Brigantedinium simplex	*Protoperidinium conicoides*
Brigantedinium grande	*Protoperidinium* (*Archaeperidinium*) sp. ?
Brigantedinium asymmetricum	*Protoperidinium* (*Archaeperidinium*) sp. ?
Brigantedinium irregulare	*Protoperidinium denticulatum*
Lejeunecysta concreta	*Protoperidinium leonis*
Lejeunecysta psuchra	*Protoperidinium* sp.
Lejeunecysta ? epidoma	*Protoperidinium* sp. (*Conica* group) ?
Selenopemphix nephroides	*Protoperidinium* sp. (*Conica* group) ?
Selenopemphix quanta	*Protoperidinium conicum*
Trinovantedinium capitatum	*Protoperidinium pentagonum*
Trinovantedinium pallidifulvum	*Protoperidinium* sp. (*Conica* group) ?
Votadinium carvum	*Protoperidinium oblongum*
Votadinium spinosum	*Protoperidinium claudicans*

cyst body varies from subspherical to ovoidal, but this feature is probably more persistent. Membranous gonal processes are more variable. The parasutural septa between the 1'''' −4''', and 3''' −4''' paraplates are often highly membranous as observed in the specimens of Wall and Dale (1968, pl. 1, fig. 14) and of Matsuoka (1985a, pl. 1, figs. 8, 10 ; pl. 2, figs. 2, 7), however sometimes these features are not observed (e.g. Wall 1965, Fig. 6 ; Wall and Dale 1968, pl.

1, fig. 15 ; Matsuoka 1985a, pl. 2, fig. 5 ; this paper, Pl. 2, fig. 6), and intermediate forms are also present (e.g. Bradford and Wall 1984, pl. 3, fig. 17)

Dimensions : Cyst diameter 36–40μm, length of processes 4.5–10.0μm.

Number of specimens observed: 56.

Remarks: As discussed later, *Spiniferites bulloideus* (Deflandre and Cookson) is probably a junior synonym of *S. ramosus* (Ehrenberg). And *S. bulloideus* of Wall (1965, p. 300–301, Fig. 6) including specimens recorded herein is a different new species as suggested by Harland (1977).

Ecological distribution around the Japanese Islands :

Subtropical to warm temperate. Wall et al. (1977) suggested that this species is cosmopolian and estuarine, and Harland (1983) also considered that it is arctic to temperate and inner to outer neritic. But around the Japanese Islands, abundance of this species decreases from the south (subtropical) to the north (warm temperate) along the Tsushima Warm current (Matsuoka 1985b).

Equivalent thecate form: *Gonyaulax scrippsae* Kofoid based on cyst incubation carried out by Wall and Dale (1968).

Spiniferites sp. cf *S. delicatus* Reid 1974

Plate 2, figures 1–4 ; 8–12, plate 3, figures 7–8

1966 ?*Hystrichosphaera* cf. *tertiaria* Eisenack and Gocht ; Morzadec-Kerfourn, p. 138, pl. 1, fig. 3.

1982 *Spiniferites delicatus* Reid ; Matsuoka, pl. 2, figs. 5,6.

1985a *Spiniferites* sp. cf. *delicatus* Reid ; Matsuoka, p. 33–34, pl. 1, figs. 1–7, text-figs. 5, 6.

Dimensions: Cyst length 32–39μm, width 27–37μm, length of large process 15μm, length of other processes 4.5–10.5μm.

Number of specimens observed: 16.

Remarks: This species is characterized by possessing some hollow processes with petaloid distal extremities, and distinguishable from *S. delicatus* in lack of the high parasutural flange at the hypocyst.

Geographical distribution around the Japanese Islands :

Spiniferites sp. cf. *S. delicatus* has been recorded in surface sediments of Yakiuchi Bay, Kuji Bay and Shinokawa Bay in the Amami Islands (Matsuoka, 1985d), and of Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga, Lake Kamo, Off Honjo, and Funakawa Bay (Matsuoka, 1985b).

Equivalent thecate form: *Gonyaulax* sp. cf. *G. scrippsae* Kofoid based on incubation experiment by Matsuoka (personal observation).

Spiniferites elongatus Reid 1974
Plate 1, figures 9, 10

1968 Resting spore of *Gonyaulax* sp. 1 in Wall and Dale, p. 271, pl. 1, fig. 16.
1971 *Spiniferites* sp. of Shimakura, Nishida and Matsuoka, pl. 1, fig. 1.
1974 *Spiniferites elongatus* Reid, p. 602–603, pl. 3, figs. 23–24.
1980 *Spiniferites elongatus* Reid ; Harland and Reid in Harland et al., Fig. 2, K-L.
1982 *Spiniferites elongatus* Reid ; Matsuoka, pl. 2, figs. 1–2.
1982 *Spiniferites elongatus* Reid ; Harland, pl. 1, figs. 9, 10.
1983 *Spiniferites elongatus* Reid ; Matsuoka, p. 137, pl. 13, fig. 8.
1986 *Spiniferites elongatus* Reid ; Harland and Sharp, pl. 1, figs. 1–8, pl. 2, fig. 9.

Dimensions: Cyst length 48–50μm, width 32–34μm, length of processes 12–15μm.

Number of specimens observed: 16.

Remarks: The morphological differences between *S. elongatus* and *S. frigidus* are discussed in the section of *S. frigidus*. The diagnostic feature of *S. elongatus* is to have a membranous parasuture on the hypocyst.

Ecological distribution in previous record:

Arctic to temperate; inner neritic to oceanic (Harland 1983), but around the Japanese Islands, this species has been recorded from the region influenced by the warm water Tsushima current (Matsuoka, 1985b).

Equivalent of thecate form: *Gonyaulax* sp. 1 by Wall and Dale (1968) and later Dale (1976) pointed out that this species is a cyst of *Gonyaulax spinifera* complex.

Spiniferites frigidus Harland and Reid 1980
Plate 1, figures 1–8

1980 *Spiniferites frigidus* Harland and Reid in Harland et al., p. 213, figs. 2A-J, 3.
1980 *Rottnestia amphicavata* Dobell and Norris in Harland et al., p. 218, figs. 4–9.
1984 *Spiniferites frigidus* Harland and Reid ; Bujak, p. 191, pl. 3, fig. 3.
1986 *Spiniferites frigidus* Harland and Reid ; Harland and Sharp, pl. 2, figs. 1–8, 10–11.

Dimensions: Cyst length 49–51μm, width 30–36μm, length of processes

11–16μm.

Number of specimens observed: 18.

Remarks: *Spiniferites frigidus* is similar to *Spiniferites elongatus* Reid in possessing an elongate cyst body with membranous parasutures, but differs from the latter in bearing a well-developed antapical membranous extension sometimes forming an antapical pericoel. But sometimes it is difficult to distinguish on each other, because intermediate forms are present (e.g. this paper, Pl. 1, figs. 9, 10).

Geographical distribution:

Beaufort Sea (Sub-Recent; Harland et al. 1980), southern Barents Sea (Recent; Harland 1982, Recent; Harland and Sharp 1986), Bering Sea (Late Pleistocene; Bujak 1984).

Equivalent thecate form: Unknown, but this cyst is closely related to the genus *Gonyaulax*.

Spiniferites ramosus (Ehrenberg 1837) Loeblich and Loeblich 1966
Plate 2, figure 7; Plate 3, figures 1–6

1964 *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel; Rossignol, p. 85–86, pl. 1, fig. 11; pl. 3, fig. 9.

1966 *Hystrichosphaera bulloidea* Deflandre and Cookson; Morzadec-Kerfourn, p. 138, pl. 1, fig. 4.

1967 *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel; Wall, p. 99–100, pl. 14, figs. 1, 2, text-fig. 2.

1966 *Spiniferites ramosus* (Ehrenberg) Loeblich and Loeblich, p. 56–57.

1968 *Hystrichosphaera ramosa* var. *ramosa* (Ehrenberg) O. Wetzel; Harland, p. 540–541, fig. 21.

1968 *Hystrichosphaera bulloidea* Deflandre and Cookson; Harland, p. 544, fig. 20.

1974 *Spiniferites bulloideus* (Deflandre and Cookson) Sarjeant; Reid, p. 600–601, pl. 2, figs. 17–19.

1976 *Spiniferites bulloideus* (Deflandre and Cookson); Dale, pl. 1, fig. 4.

1977 *Spiniferites ramosus* (Ehrenberg); Harland, p. 102–103, pl. 1, figs. 5–6.

1977 *Spiniferites ramosus* (Ehrenberg); Reid and Harland, pl. 1, fig. 5.

1985a *Spiniferites* sp. cf. *ramosus* (Ehrenberg); Matsuoka, p. 38–39, pl. 4, figs. 1–3, ; pl. 6, figs. 3–4.

Description: The proximochorate cyst is ovoidal to subspherical in shape. In polar view, the outline is nearly circular and in equatorial view, ovoidal to subcircular. The cyst wall comprises granular periphragm and smooth endophragm adpressed between processes. Parasutural septa are low, but distinct and membranous at the proximal base of processes. Processes are only gonal, solid, rigid, and slenderly tapering with trifurcate branches carrying bifid tips. Paratabulation is 4′, 6″, 6c, 6‴, 1p, 1⁗ and Xs. The parasuture between the 1′ and 4′ paraplates is usually reduced and therefore these two paraplates are amalgamated, but the 4′ paraplate is always smaller than the 1′. The 6″ paraplate is triangular. The 1⁗ paraplate possesses six sides and contacts 1p, 2‴, 3‴, 4‴, 5‴ and 6‴ paraplates. The paracingulum is strongly helicoid.

Dimensions: Cyst diameter 44–57μm, 40–45μm, length of processes 8–18μm.

Number of specimens observed: 14.

Remarks: As Harland (1977) already discussed, the classification of *Spiniferites ramosus* and *S. bulloideus* of the Pleistocene and Recent specimens is especially confused. According to Deflandre and Cookson who elected this species under the name *Hystrichosphara bulloidea* from the Tertiary of Australia in 1955, the diagnostic features for this species are as follows ; small spherical or subspherical cyst body, circular in outline, and slender trifurcate processes with bifid tips. Since in the holotype (Deflandre and Cookson 1955, pl. 5, figs. 3, 4) the orientation is probably polar and so its seems to become circular and the lateral shape is unknown. Other features concerning processes are common to those of *S. ramosus*. Consequently, it is probable that *S. bulloideus* described by Deflandre and Cookson (1955) is probably a junior synonym of *S. ramosus*.

However, *Spiniferites bulloideus* which was described as a resting cyst of *Gonyaulax scrippsae* by Wall and Dale (1968) is characterized by a small ovoidal cyst body with membranous parasutural septa in the hypocyst. Especially the specimens of Wall and Dale (1968) differ from the holotype of *S. bulloideus* described from the Balcombian of Australia by Deflandre and Cookson (1955, pl. 5, figs. 3, 4) in having larger processes and membranous parasutural septa especially in the antapical area.

Therefore, these morphological differences probably suggest that *Spiniferites bulloideus* of Deflandre and Cookson (1955) is a junior synonym of *Spiniferites ramosus* including *Hystrichosphaera furcata* of Deflandre and Cookson (1955), and *Spiniferites bulloideus* of Wall and Dale is a different from *Spiniferetes bulloideus* of Deflandre and Cookson (1955) and probably a new species.

This interpretation is similar to that of Harland (1977).

Ecological distribution around the Japanese Islands :

Subtropical to warm temperate region (Matsuoka, 1985b)

Equivalent thecate form: A species of *Gonyaulax spinifera* complex based on cyst incubation by Wall and Dale (1970).

Genus *Operculodinium* Wall 1967

Type species : *Operculodinium centrocarpum* (Deflandre and Cookson 1955) Wall 1967

Operculodinium centrocarpum (Deflandre and Cookson 1955) Wall 1967
Plate 4, figures 1–12

1945 Cyst of *Protoceratium reticulatum* (Claparéde and Lachmann) Bütschli ; Braarud, p. 15–17, pl. IV, figs. d, e, text-fig. 6.

1953 *Hystrichosphaeridium* sp. a ; Cookson, p. 115, pl. II, figs. 26, 27.

1955 *Hystrichosphaeridium centrocarpum* Deflandre and Cookson, p. 272–273, pl. 8, figs. 3, 4.

non 1961 *Baltisphaeridium centrocarpum* (Deflandre and Cookson) Gerlach, p. 192–193, pl. 28, fig. 9.

non 1966 *Cordosphaeridium tiara* (Klumpp 1953) subsp. *centrocarpum* (Deflandre and Cookson) Morgenroth, p. 26, pl. 5, fig. 12 ; pl. 6, fig. 1.

1967 *Operculodinium centrocarpum* (Deflandre and Cookson) Wall, p. 111, pl. 16, figs. 1, 2, 5.

1967 Cyst of *Gonyaulax grindleyi* Reinecke, p. 158–160, pl. 1, figs. A-C.

Dimensions : Cyst diameter 35–43μm, length of processes 5.6–7.5μm.

Number of specimens observed: 116.

Remarks: *Operculodinium centrocarpum* (Deflandre and Cookson) differs from similar spherical cyst with numerous processes in possessing a non-pigmented cyst wall, slender processes with a capitate distal extremity and a precingular archeopyle.

Ecological distribution in previous record:

Cosmopolitan ; neritic (Wall et al. 1977) and temperate to tropical ; inner to outer neritic and oceanic (Harland 1983).

Equivalent thecate form: *Protoceratium reticulatum* (Claparéde and Lachmann) Diesing by Wall and Dale (1968). This thecate species is a senior synonym of *Gonyaulax grindleyi* Reinecke, because the plate distribution of *Protoceratium reticulatum* differs from the *Gonyaulax,* especially in apical and sulcal areas, and the cyst form is also different from the typical *Spinif-*

erites type of *Gonyaulax spinifera.*

Family Pyrophacaceae Lindemann, 1928

Genus *Tuberculodinium* Wall 1967

Type species : *Tuberculodinium vancampoae* (Rossignol 1962) Wall 1967

Tuberculodinium vancampoae (Rossignol 1962) Wall 1967
Plate 18, figures 1–2

1962 *Pterospermopsis? vancampoae* Rossignol, p. 134, pl. 2, fig. 1.
1967 *Tuberculodinium vancampoae* (Rossignol) Wall, p. 114, pl. 16, figs. 15, 16.
1971 Cyst of *Pyrophacus vancampoae* (Rossignol) Wall and Dale, p. 234–235, figs. 10–25.
1985c Cyst of *Pyrophacus steinii* subsp. *vancampoae* (Rossignol) Balech ; Matsuoka, p. 252–253, pl. 1, figs. 6–7.

Dimensions of figured specimen: Cyst diameter 84.3μm, length of processes ca. 13μm.

Number of specimens observed: 7.

Ecological distribution in previous record:

Tropical-subtropical; estuarine (Wall et all. 1977) and tropical to temperate ; inner to outer neritic (Harland 1983).

This species abundantly occurs in inner bay areas influenced by the warm Tsushima current around Japan (Matsuoka, 1985b). There are two possible interpretations for the rare ocurrence of this species in Lake Saroma. One of them is that these specimens might be ineffectively dispersed by the Soya current which is a branch of the Tsushima current. Alternatively these speciems are reworked from the older sediments which probably deposited during the middle Holocene when the Soya current might be stronger than the present.

Equivalent thecate form: *Pyrophacus steinii* (Schiller) Wall et Dale by Wall and Dale (1971), which includes *P. steinii* subsp. *vancampoae* (Rossignol) Balech by Matsuoka (1985c).

Order Peridiniales Taylor, 1980

Family Protoperidiniaceae Bujak and Davies, 1983

Subfamily Diplopsaloideae Bujak and Davies, 1983

Genus *Dubridinium* Reid 1977

Type species : *Dubridinium cavatum* Reid, 1977

Dubridinium caperatum Reid 1977

Plate 13, figures 10–11

1968 Resting spore of *Diplopeltopsis minor* (Paulsen) Pavillard ; Wall and Dale, p. 280, pl. 4, figs. 21, 22, text-fig. 7.

1977 *Dubridinium caperatum* Reid, p. 451–452, pl. 4, figs. 38–41, 44.

Description: Intermediate subspherical cysts are dark brownish in color, and consist of two nearly adpressed layers. The endophragm is brownish, thick and smooth, and the periphragm is non-pigmented to light brown, thin membranous and somewhat chagrinate on surface. Paracingulum is weakly indicated by folding of the wall, but discontinuous. Parasulcus is reflected by no feature. The archeopyle is theropylic with a relatively smooth principal archeopyle suture, and the operculum is adnate and probably composed of the whole epicyst.

Dimensions of figured specimen: Cyst diameter 43.5μm.

Number of specimens observed: 19.

Remarks: *D. caperatum* is similar to other species of *Dubridinium* in having a large theropylic archeopyle, but this species is characterized by possessing a relatively thick endophragm and lacking a capsule. This species is also distinguishable from species of *Brigantedinium* in bearing a theropylic archeopyle and bi-layered cyst wall.

Geographical distribution in previous record:

West and east coasts of the Irish Sea, north coast of Ireland and the Dee around the British Isles (Reid 1977).

Omura Bay, Senzaki Bay, Lake Hiruga, Off Honjo and Off Oga around the Japanese Islands (Matsuoka 1985b).

Equivalent thecate form: *Zygabikodinium lenticulatum* (Paulsen) Loeblich and Loeblich [=*Diplopeltopsis minor* (Paulsen) Pavillard] by the incubation experiment of Wall and Dale (1968) and the observation on the thecate specimens including cysts of Reid (1977).

Dinoflagellate cyst type D

Plate 19, figures 3–6 ; 11–12

1982 Cyst of *Diplopsalis* sp. ? of Matsuoka, pl. 2, fig. 11.
1985a Dinoflagellate cyst type A of Matsuoka, p. 65, pl. 15, fig. 15.

Dimensions : Cyst diameter 39.2–48.5μm, length of processes 7.8–11.2μm.

Number of specimens observed : 62.

Descriptive remarks : The cyst is small to intermediate in size and originally spherical, but because of the relatively thin autophragm and large archeopyle, the cyst body is often deformed. The cyst surface is smooth to slightly granular. Processes are nontabular, hollow and acuminate distally. The archeopyle is of a theropylic type, but it is difficult to determine the position of the principal archeopyle suture. The operculum is adnate and probably polyplacoid.

The cyst of *Diplopelta parva* is similar to Dinoflagellate cyst type D in possession of a brownish cyst wall and nontabular acuminate processes, but good preserved specimens of the cyst of *Diplopelta parva* have typically a theropylic apical archeopyle, whereas Dinoflagellate cyst type D seems to possess a theropylic epicystal archeopyle similar to other species of *Dubridinium.*

Geographical distriburion around the Japanese Islands :

This cyst has been recorded in surface sediments of Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga, Lake Kamo, Off Honjo and Funakawa Bay (Matsuoka 1985b) and Yakiuchi Bay, Kuji Bay and Shinokawa Bay of the Amami Islands (Matsuoka 1985d).

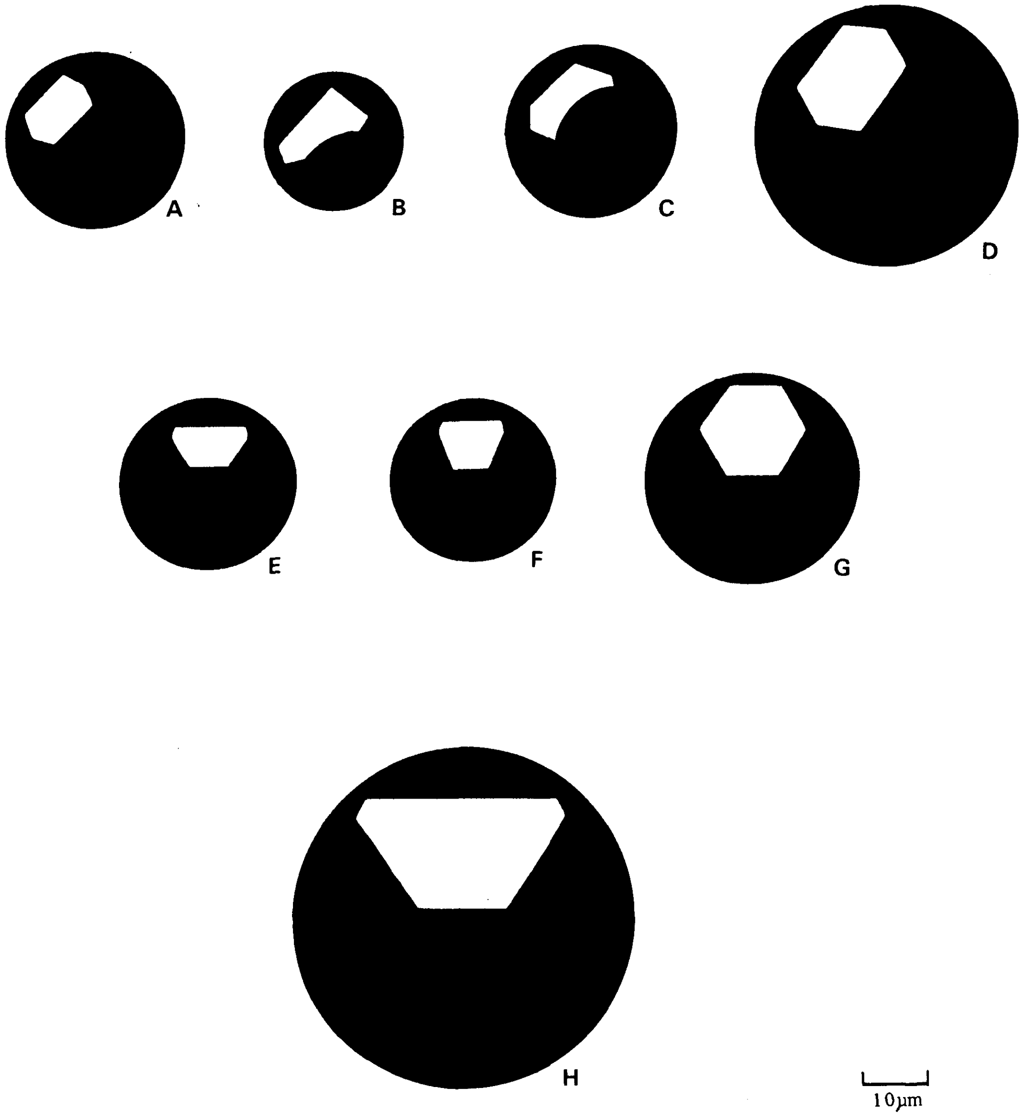
Equivalent thecate form: This species is probably a cyst form of the Diplopsaloideae based on its theropylic archeopyle and possession of spinous ornaments.

Subfamily Protoperidinioideae Bujak and Davies, 1983

Genus *Brigantedinium* Reid 1977

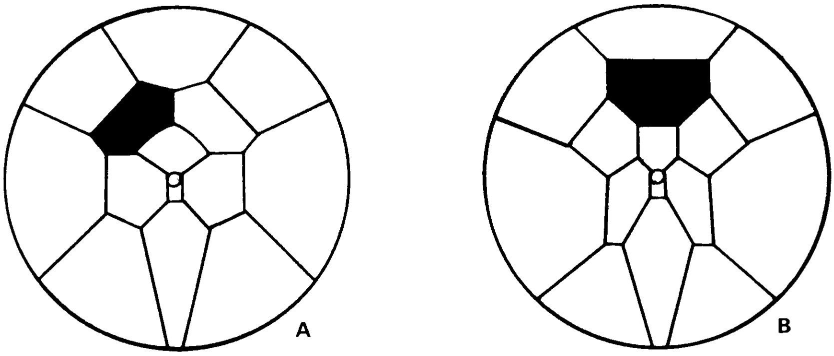
Type species : *Brigantedinium simplex* (Wall 1965) Reid 1977

Remarks : It is almost impossible to distingush species which are attributed to the genus *Brigantedinium* on each other except for the cyst diameter and an exact topology of the intercalary archeopyle. Practically these cysts are grouped as brown spherical cysts (*Brigantedinium* spp.) which probably include some cysts of the Diplopsaloideae.



Text-fig. 4 Semi-diagramatic illustrations of brown and spherical cyst species of the genus *Brigantedinium*.

A-D : Cyst species attributable to the thecate subgenus *Archaeperidinium*. A ; *B.* sp. (*Protopericlinium ?punctulatum*) B ; *B. asymmetricum*, C ; *B. irregulare*, D ; *B. grande*. E-H : Cyst species attributable to the thecate subgenus *Protoperidinium*. E ; *B.* sp. cf. *majusculum*, F ; *B. simplex*, G ; *B. auranteum* based on the holotype designated by Reid (1977), H ; *B. majusculum* based on the holotype designated by Reid. Except for A, G and H, other figures based on the specimens from Lake Saroma and Akkeshi Bay, Hokkaido, and Omura Bay, West Japan.



Text-fig. 5 Thecal plate tabulations of the subgenus *Archaeperidinium* (A) and the *Conica* group of the subgenus *Protoperidinium* (B).

Brigantedinium cariacoense (Wall 1967) Reid 1977 emend.
Plate 5, figures 5–9

1967 *Chytroeisphaeridia cariacoensis* Wall, p. 113–114, pl. 16, fig. 14, non fig. 13.
1968 Resting spore of *Peridinium avellana* (Meunier) Lebour ; Wall and Dale, p. 277, pl. 3, fig. 29, pl. 4, figs. 1, 2.
1977 *Brigantedinium cariacoense* (Wall) Reid, p. 434 (in part).
1977 *Brigantedinium cariacoense* (Wall) Reid ; Harland, p. 104, pl. 3, figs. 10, 11, 13.
1984 *Protoperidinium avellana* (Meunier) Balech ; Matsuoka, p. 38–39, pl. 2, figs. 5–7.

Emended diagnosis : Spherical cysts with smooth autophragm. Intercalary archeopyle apparently hexagonal, consisting one long and straight, four short and one curved principal archeopyle suture.

Holotype : Wall (1967), pl. 16, fig. 14, Pleistocene, Caribbean Sea.

Dimensions : Cyst diameter 35.8–48.5μm.

Number of specimens observed : 26.

Remarks : This species is characterized by a hexagonal archeopyle. Based on this feature, Reid (1977) considered that the thecal affinity of this species are assignable to *Protoperidinium avellana* (Meunier) Balech, *P. punctulatum* (Paulsen) Balech and probably *P. dinticulatum* (Gran and Baraarud) Balech. But according to detailed observation of good specimens, the type of their archeopyles is distinguishable on each other. For example, the archeopyle of the cyst of *P. punctulatum* is a lati-thetaform without arched principal archeopyle suture, whereas that of the cyst of *P. avellana* has one distinctively curved princepal archeopyle suture. Furthermore, the cyst of *P. denticulatum* possesses an irregularly hexagonal archeopyle.

Geographical distribution in previous record:

Pleistocene of the Caribbean Sea (Wall 1967), and Recent and late Quaternary sediments around the British Isles (Reid 1977 and Harland 1977).

Omura Bay and Senzaki Bay in West Japan (Matsuoka 1984, 1985a).

Equivalent thecate form: *Protoperidinium* (*Archaeperidinium* sect. *Fuscusphaeridium*) *avellana* (Meunier) Balech based on cyst incubation by Wall and Dale (1968) and Matsuoka (1984).

Brigantedinium sp. cf. *B. majusculum* Reid 1977
Plate 11, figures 6, 7 ; Text-fig. 4E

1985a *Brigantedinium majusculum* Reid ; Matsuoka, p. 49. pl. 15, figs. 1–4.

Dimensions: Cyst diameter 39.2–44.8μm.

Number of specimens observed: 10.

Remarks: The species is similar to *Brigantedinium simplex* (Wall), but differs from the latter in possessing a large hexagonal (iso-to lati-deltaform) archeopyle and larger cyst body. Its archeopyle ratio is approximately 0.65. The present specimens differs from the sepecimens recorded from the British Isles by Reid (1977) in having smaller cyst diameter, but are identical to the species of Matsuoka (1985a).

Equivalent thecate form: Unknown, but this cyst may be related to the *Conica* group of the subgenus *Protoperidinium*.

Brigantedinium simplex (Wall 1965) Reid 1977
Plate 6, figures 1–14 ; Plate 14, figures 6–7 ; Text-fig. 4F

1965 *Chytroeisphaeridia simplica* Wall, p. 308, figs. 7, 20.

1968 Resting spore of *Peridinium conicoides* Paulsen ; Wall and Dale, p. 277, pl. 2, figs. 29–30 ; pl. 3, figs. 27–28.

1977 *Brigantedinium simplex* (Wall) Reid, p. 435–436, pl. 1, figs. 3–4.

1982 *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech 1974 ; Harland, p. 382, 383, text-fig. 18.

Remarks: The archeopyle of this species is nearly trapezoidal (steno-deltaform) in shape, but actually it consists of four long and two very short archeopyle sutures. According to this, the archeopyle ratio is approximately 1.0.

Dimensions : Cyst diameter 33.5–43.5μm.

Number of specimens observed: 150.

Ecological distribution in previous record:

Cosmopolitan: estuarine to neritic as 'grouped *Peridinium* species' (Wall et al. 1977) and temperate: inner neritic (Harland 1983).

Around the Japanese Islands; *Brigantedinium simplex* and *B. cariacoense* are abundant in the northern part of the areas influenced by the Tsushima current (Matsuoka 1985b).

Equivalent thecate form: *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech 1974 based on the cyst culture by Wall and Dale and by observation of Matsuoka (1976).

Brigantedinium grande sp. nov.
Plate 5, figure 1–2; Text-fig. 4D

1976b *Peridinium* sp. cf. *P. punctulatum* Paulsen; Matsuoka, p. 361–362, pl. III, fig. 11.

Derivation of name; Latin *grandis,* large; with reference to the large cyst body.

Diagnosis: Large to intermediate chorate cyst brownish-pigmented, consisting of smooth autophragm, without any ornament on surface. Except for archeopyle, no feature indicating paratabulation. Archeopyle intercalary, broadly hexagonal (lati-thetaform), formed by loss of the 2a paraplate. Archeopyle ratio: 0.6–0.7.

Testa quae est globularis et grandis vel intermedia in magnitudine et brunnea in colore consistit ex levi autophragmate sine ullo ornamento in superficie. Archeopyla excepta nullus vultus indicat paratabulationem. Archeopyla quae formatur remotione secundae anterioris et intercalaris paraplattae est late hexagonalis.

Holotype: Slide no. SR8–2 (15.2/143.0), Pl. 5, figs. 1–2, sample no. SR8, Recent sediment in Lake Saroma, Hokkaido, North Japan.

Dimensions: Cyst diameter 59.7–66.0μm (Holotype 60.0μm).

Number of specimens observed: 8.

Remarks: This spherical cyst is different from *Brigantedinium cariacoense* (Wall) in possessing larger cyst body and a broadly hexagonal archeopyle. This species is also similar to *B. majusculum* in its larger cyst body, but differs from the latter in bearing a lati-thetaform (hexagonal) archeoyle.

Geographical distribution around the Japanese Islands:

Off Hachinohe in North Japan by Matsuoka (1976).

Equivalent thecate form: Probably a species of the subgenus *Archaeperidinium* in the genus *Protoperidinium* based on its hexagonal archeopyle, but the thecate species corresponding to this cyst has been unknown.

Brigantedinium asymmetricum sp. nov.
Plate 5, figures 10–12; Text-fig. 4B

Derivation of name: Latin *a+symmetricus*, non+symmetry; with reference to the asymmetrical archeopyle.

Diagnosis: Small chorate cyst brownish-pigmented, consisting of smooth autophragm, without ornament on its surface. Archeopyle intercalary, relatively large, and comprising one long, two intermediate, two short and one curved sides. Archeopyle ratio: 0.6–0.7.

Testa quae est globularis, parva vel intermedia in magnitudine et subfusca in colore consistit ex levi autophragmate sine ullo ornamento in superficie. Archeopyla quae est anterior et intercalaris et irregularis habet unum longum et flexum latus et duo intermedia et brevia latera.

Holotype: Slide no. AK2–2 (100.4/44.7). Pl. 5, figs. 10–12, sample no. AK2, Recent sediment in Akkeshi Bay, Hokkaido, North Japan.

Dimensions: Cyst diameter 30.0–32.8μm (Holotype 31.2μm).

Number of specimens observed: 7.

Remarks: This spherical cyst resembles *Brigantedinium cariacoense* (Wall) in possessing a curved principal archeopyle suture, but differs from the latter in that its archeopyle is irregularly hexagonal in shape.

The specimens of *Protoperidinium* sp. cf. *conicoides* similar to the present species are recorded from modern Carifornia Current surface sediments by Wall (1986 MS.).

Equivalent thecate form: Probably a species of the subgenus *Archaeperidinium* in the genus *Protoperidinium* based on the shape of archeopyle corresponding to the 2a plate, but its thecate species has been unknown.

Brigantedinium irregulare sp. nov.
Plate 5, figures 13–16; Text-fig. 4C

1976b *Peridinium* sp. cf. *P.* ? *denticulatum* Gran and Braarud; Matsuoka, p. 359, pl. III, fig. 10.

1983 Empty resting cyst of *Protoperidinium denticulatum* (Gran & Braarud) Balech ; Dale, Fig. 21.

Derivation of name: Latin *irregulare,* irregular, with reference to its irregularly hexagonal intercalary archeopyle.

Diagnosis : Small spherical cyst brownish-pigmented, and consisting of smooth autophragm. Except for archeopyle, neither ornament nor structure representing paratabulation. Archeopyle simple intercalary, irregularly hexagonal in shape ; consisting two long sides which are slightly curved, three intermediate sides and one short side.

Testa quae est globularis, parva vel intermedia in magnitudine et brunnea in colore consistit ex levi autophragmate. Archeopyla excepta neque ornamentum neque structura repraesentat paratabulationem. Archeopyla quae est simplex, anterior, intercalaris et inusitate hexagonalis habet duo longa et flexa, tria intermedia latera et unum breve latus.

Holotype : Slide no. Ak2–2 (85.5/31.7), Pl. 5, figs. 15–16, sample no. AK2, Recent sediment in Akkeshi Bay, Hokkaido, North Japan.

Demensions : Cyst diameter 36.0–42.8μm (Holotype 40.0μm).

Number of specimens observed: 15.

Remarks : This cyst closely resembles *Brigantedinium cariacoense* (Wall) and *B. asymmetricum* in possessing a hexagonal intercalary archeopyle. But this species differs from *B. asymmetricum* in bearing two long principal archeopyle sutures and from *B. cariacoense* in carrying one very short principal archeopyle suture, of which character has been pointed out by Dale (1983).

Geographical destribution in previous record :

Off Monhegan Island, U.S.A. by Dale (1983).

Equivalent thecate form: *Protoperidinium denticulatum* (Gran & Braarud) Balech reported by Dale (1983).

Genus *Lejeunecysta* Artzner and Dörhöfer 1978

Type species : *Lejeunecysta hyalina* (Gerlach 1961) Artzner and Dörhöfer 1978

Synonym : *Quinquecuspis* Harland 1977

Discussion: The taxonomic validity of the genus *Quinquecuspis* Harland, 1977 has been discussed by Harland (1982) and Bujak (1984). Harland (1982) pointed out that the important features for this genus are a discontinuous paracingulum, deeply indented parasulcus and a large archeopyle probably involving the 3′ paraplate. But some late Cenozoic species of *Lejeunecysta* examined in the personal observation have distinctively a deep parasulcus indicated by strong parallel ridges. And most specimens of *Quinquecuspis concretum* including the holotype possess no combination archeopyle as mentioned in its original description, but a single intercalary archeopyle with hexagonal shape. Therefore, *Quinquecuspis* is a synonym of *Lejeunecysta.* This genus also differs from *Votadinium* in possessing a paracingulum structure.

Lejeunecysta concreta (Reid 1977) comb. nov.
Plate 7, figures 9–10; Plate 8, figures 1–9; Plate 9, figures 1–4

Synonym: *Trinovantedinium subrinum* Reid 1977
=*Lejeunecysta subrina* (Reid) Bujak 1984

1964 ?*Peridinium leonis* Pavillard; Evitt and Davidson, p. 5–7, pl. 1, text-fig. 1.
1968 Resting spore of *Peridinium leonis* Pavillard; Wall and Dale, p. 276, pl. 2, figs. 18–21.
1977 *Trinovantedinium concretum* Reid, p. 438–439, pl. 1, figs. 9–11.
1977 *Trinovantedinium subrinum* Reid, p. 441–442, pl. 2, figs. 15–17.
1977 *Quinquecuspis concretum* (Reid) Harland, p. 107, pl. 3, figs. 1–6, 17–20.
1982 *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Parvillard) Balech: Harland, p. 385, text-fig. 20, pl. 41, figs. 1–14, pl. 42, figs. 7, 9.
1984 *Lejeunecysta subrina* (Reid) Bujak, p. 193.

Dimensions: Cyst length 59.7–64.8μm, width 62.7–66.8μm, thickness (a single specimen measured) 47.2μm.

Number of specimens observed: 12.

Remarks: The morphological variation of this species includes the cyst shape, horn development and paracingulum depth. The cyst shape varies from roundly pentagonal to peridinioid, depending on the development of apical and antapical horns. The paracingulum is indicated by indentation of the autophragm, but sometimes is hardly observed because of weak indentation. According to Reid (1977), *Trinovantedinium subrinum* is distinguished from the present species in possessing more distinctive antapical horns and deeper sulcus. These features, however, are variable as shown by Wall and Dale (1968; pl. 2, figs. 19–21) and Matsuoka (1985a; pl. 12, figs. 3–8, pl. 13, figs. 1–4).

Ecological distribution in previous record:

Tropical to temperate ; inner to outer neritic (Harland, 1983).

Around the Japanese Islands ; Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga, Lake Kamo, Off Honjo, and Off Oga (Matsuoka 1985b).

Equivalent thecate form: *Protoperidinium leonis* (Pavillard) Balech by incubation experiment of Wall and Dale (1968) and Matsuoka (personal observation). Reid (1977) mentioned that the thecate form of *Trinovantedinium concretum* is probably *Protoperidinium latissinum* (Kofoid) Balech, but *T. concretum* designated by Reid differs from the cyst of *P. leonis*. Harland (1977) pointed out that *Quinquecuspis concretum* is most closely comparable to the cyst of *P. leonis*.

Lejeunecysta? epidoma sp. nov.

Plate 9, figures 5–6

Deviation of name: Latin *epi+domus*, upper+dome, with reference to the dome shaped epicyst.

Diagnosis: Large proximate cysts lightly brownish-pigmented, consisting smooth to finely granular autophragm. Epicyst broad dome-shaped without apical boss or node. Hypocyst large, trapezoidal at optical cross section in dorso-ventral view, possessing two very small antapical horns with thickened distal tips. Paracingulum indicated by indentation of autophragm with some longitudinal striations. Parasulcus also shown by shallow indentation of autophragm. Sometimes two traces of flagellar pore present in the parasulcus. Archeopyle hexagonal intercalary, with four long and two short principal archeopyle suture (steno-deltaform).

Magnae cystae proximae quae sunt brunneae in colore consistuntur ex levi vel tenuiter granulato autophragmate. Epitractum formam grandis domae sine apicali nodo habet. Hypotractum quod est magnum et trapezoidale dorsoventraliter habet duo parvissima antapicalia cornua cum densis apicibus distalibus. Paracingulum indicatur indentatione autophragmatis cum aliquibus verticalibus striis. Parasulcus etiam indicatur humili indentatione autophragmatis. Parasulcus duo vestigia flagelliferi foraminis habere potest. Archeopyla hexagonalis, intercalaris cum quattuor longis et duabus brevibus et principalibus archeopylasuturis.

Holotype: Slide no. AK2–1 (15.2/131.7) ; Pl. 9, figs. 5–6, sample no. AK2, Recent sediment in Akkeshi Bay, Hokkaido, North Japan.

Dimensions: Cyst length 74.6–84.0μm, width 74.6–80.0μm, width of the paracingulum ca. 8μm (Holotype 84.0μm$\times$76.4μm).

Number of specimens observed: 3.

Remarks : This species is very distinctive and easily distinguishable from other cysts of *Protoperidinium* in possessing a broadly dome-like epicyst and a large trapezoidal hypocyst.

Equivalent thecate form: Unknown, but probably *Protoperidinium* sp. (*Conica* group), judging from its steno-deltaform intercalary archeopyle, and brownish pigmentation.

Lejeunecysta psuchra sp. nov.

Plate 9, figures 7–8 ; Plate 14, figures 11–12

Derivation of name: Greek *psuchros,* cold ; with reference to the ecology of this species.

Diagnosis : Lage pentagonal cysts lightly brownish-pigmented, and composed of thin autophragm without any ornamentation. Epicyst roundly conical with broad apical projection and hypocyst widely trapezoidal in dorso-ventral view with two broad and round antapical horns. Paracingulum weakly suggested by shallow indentation and indistinctive. Parasulcus indicated by moderate depression of the wall. Antapical depression between two horns also shallow to moderate. Archeopyle intercalary, but its shape unclear, because of the autophragm easily deformed.

Grandes cystae pentagonales sunt brunneae in colore et componuntur ex tenio autophragmate sine ullo ornamentatione. Epitractum rotunde conicale cum lata apicali proiectione et hypotractum late trapezoidale dorsoventraliter cum duobus latis et rotundis antapicalibus cornibus. Paracingulum infirme indicatur humili indentatione et indistinctum est. Parasulcus indicatur moderato depressione muri. Antapicalis depressio inter duo cornua etiam humilis vel moderata. Archeopyla intercalaris sed figura non est clara, propter autophragma facile deformatum.

Holotype : Alide no. AK2–2 (87.6/37.0) ; Pl. 9, figs. 7–8, Sample no. Ak2, Recent sediment in Akkeshi Bay, Hokkaido, North Japan.

Dimensions : Cyst length 80–84μm, width 68–72μm (Holotype 80μm× 70μm)

Number of specimens observed : 5.

Remarks : This species is somewhat similar to *Votadinium carvum,* but differs from the latter in having a paracingulum and two distinctive antapical horns. This cyst also resembles *Lejeunecysta concreta* (Reid) comb. nov. in bearing a pentagonal outline, but also differs in possessing broader antapical horns, and larger and wider hypocyst.

Equivalent thecate form: Unknown, but probably a species of *Protoperidinium,* because of its brownish pigmentation and intercalary archeopyle.

Genus *Selenopemphix* Benedek 1972 emend. Bujak in Bujak et al. 1980

Type species : *Selenopemphix nephroides* Benedek 1972

Selenopemphix nephroides Benedek 1972

Plate 10, figures 1–9

1986 *Selenopemphix nephroides* Benedek, p. 47–48, pl. 11, fig. 13, pl. 16, figs. 1–4.

1976b *Peridinium* sp. cf. *P. subinerme* Paulsen ; Matsuoka, p. 362, pl. III, fig. 1.

Description : The large, brownish-pigmented cysts are antero-posteriorly compressed. The cyst wall consists of an autophragm. The wall surface weakly wrinkles longitudinally. The epicyst is widely conical with slightly concave outline in dorso-ventral optical section and bears a single broad apical boss. The hypocyst is also conical with a truncated posterior end and without antapical horns. The paracingulum is narrow, and is well defined by deep indentation. The paracingular lists distinctively waves. The parasulcus is wide and short, and is also well indicated by indentation of the autophragm. Two flagellar pores are often reflected by two small depression in the parasulcus. The large and intercalary iso- to lati- deltaform archeopyle is shifted from the middle line, and is derived from the loss of the 2a paraplate.

Dimension : Cyst length (one specimen measured) 43μm, width 64–84μm, thickness 55.0–84.0μm.

Number of specimens observed : 19.

Remarks : *Selenopemphix nephroides* is similar to *S. alticinctum* (Bradford) Matsuoka in possessing a cyst body antero-posteriorly compressed. Bujak (1984) suggested that *S. alticinctum* is probably a junior synonym of *S. nephroides*. However, *S. nephroides* differs from *S. alticinctum* in possessing a larger cyst body with the wrinkled surface and slightly waving margines of the paracingulum.

Geographical distribution around the Japanese Islands :

Off Hachinohe in North Japan by Matsuoka (1976b). This cyst may be a cold water species.

Equivalent thecate forms : Unknown, but probably a species assignable to the *Conica* group of the genus *Protoperidinium* based on the archeopyle shape.

Selenopemphix quanta (Bradford 1975) Matsuoka 1985
Plate 11, figures 1–5

1965 *Peridinium* sp. (Cyst-form 6) Wall, p. 308, figs. 17, 23.
1968 Resting spore of *Peridinium conicum* (Gran) Ostenfeld and Schmidt ; Wall and Dale, p. 273–274, pl. 2, figs. 4–5.
1975 *Multispinula quanta* Bradford, p. 3067–3070, figs. 5–6, non. 7.
1980 *Protoperidinium conicum* (Gran) Balech ; Fukuyo, No. 59, figs. G.H.
1982 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech ; Harland, p. 384–385, text-fig. 19, pl. 39, pl. 39, figs.
1985 *Selenopemphix quanta* (Bradford) Matsuoka, p. 51–52, pl. 11, figs. 1–3, 7–9, non. 4–6.

Dimensions : Cyst diameter 80.0–82.0μm, thickness (one specimen measured) 72.0μm, length of processes 13.5–16.0μm.

Number of specimens observed: 39.

Remarks : The original specimens designated by Bradford (1975) seem to include two different cyst species ; one of them is characterized by short and many slender processes which are distributed densely along the paracingular lists (Bradford 1975, Figs. 4, 5), and another bearing a few long and stout processes in number (Bradford 1975, Fig. 6).

Kobayashi and Matsuoka (1984) also showed two different cyst types in modern sediments. They are called type A and type B based on incubation experiments of cysts of *Protoperidinium conicum* (Gran). Furthermore, Wall and Dale (1968) also reported the cyst of *Protoperidinium nudum*?, which is characterized by smaller but higher cyst body and fewer processes in number. Although the theca-cyst relationships of these cyst types have not yet been confirmed, the morphology of these cyst forms is different on each other.

The present specimens are closely similar to the specimens reported by Harland (1977, pl. 4, figs. 18, 19) in possessing shorter and curved processes more densely distributed along the paracingulum.

Ecological distribution in previous record:

Temperate ; inner neritic (Harland 1982).

Genus *Trinovantedinium* Reid 1977

Type species : *Trinovantedinium capitatum* Reid 1977

Trinovantedinium capitatum Reid 1977
Plate 12, figures 1–6

1908 Bestachelte Cyste Paulsen, pl. 11, fig. 8.
1968 Resting spore of *Peridinium pentagonum* Gran ; Wall and Dale, p. 274–275, pl. 2, figs. 9–10.
1968 Resting spore of *Peridinium* sp. cf. *P. pentagonum* Gran ; Wall and Dale, p. 274–275, pl. 2, figs. 11–12.
1976b *Peridinium* sp. aff. *P. pentagonum* Gran ; Matsuoka, p. 361, pl. III, fig. 8.
1977 *Trinovantedinium capitatum* Reid, p. 437–438, pl. 1, figs. 6–8.
1977 *Lejeunecysta applanata* Bradford, p. 47–49, fig. 2 ; 1–8.
1982 *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech 1974 ; Harland, p. 386, text-fig. 22, pl. 39, figs. 7–11, pl. 42, fig. 8.

Dimensions : Cyst length 76.0–90.0μm, width 76.0–84.0μm, length of processes ca. 4μm.

Number of specimens observed : 9.

Remarks : The archeopyle of this species is a large intercalary (lati deltaform) type formed by the loss of the 2a paraplate. This species is also characterized by lack of pigmentation in the cyst wall.

Ecological distribution in previous record :

Cosmopolitan ; estuarine to neritic (Wall et al., 1977) and temperate ; inner to outer neritic (Harland, 1983).

Around the Japanese Islands ; Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga, Off Honjo (Matsuoka, 1985b).

Equivalent thecate form : *Protoperidinium pentagonum* (Gran) Balech by incubation experiments of Wall and Dale (1968) and Matsuoka (1982).

Trinovantedinium pallidifulvum sp. nov.
Plate 13, figures 1–9

Derivation of name : Latin *pallidus+fulvus*, lightly brownish ; with reference to the lightly brownish-pigmented cyst wall.

Diagnosis : Intermediate pentagonal cysts slightly brownish-pigmented, consisting of thin autophragm, and covered with very short and apparently nontabular spines. Epicyst large conical with a small apical horn and straight outline in dorso-ventral view, and hypocyst trapezoidal in dorso-ventral view, relatively small, and bearing two small antapical horns. Paracingulum represented by two parallel rows of spines and shallow indentation of wall, avoiding spines and hardly displaced at the ventral area.

Parasulcus indicated by shallow indentation without spine and widenning toward the antapex. Archeopyle intercalary, basically hexagonal, steno delta-form and formed by the loss of the 2a paraplate.

Pentagonales cystae quae consistuntur ex tenui autophragmate est intermediae in magnitudine et pallidifulvae in colore et conteguntur spinis quae sunt brevissimae et non ut videtur habent tabulationem. Epitractum est grande conicale cum parvo apicali cornu et rectum lineamentum dorsoventraliter. Hypotractum quod est trapezoidale dorsoventraliter et parvum habet duo brevia et antapicalia cornua. Paracingulum repraesentatur duobus parallelis ordinibus spinarum et humili indentatione muri sine spina, et vix disceditur in ventrali area. Parasulcus indicatur humili indentatione sine spina et amplificat ad antapicem. Archeopyla quae intercalaris et hexagonalis est stenodeltaforma et formatur remotione secundae paraplattae.

Holotype: Slide no. AK2–2 (87.4/27.6) ; Pl. 13, figs. 7–9 ; Sample no. AK2, Recent sediment in Akkeshi Bay, Hokkaido, North Japan.

Description: The epicyst is always larger than the hypocyst. The cyst wall thickened at the apex and antapex. Two antapical horns are sometimes lacking. The paratabulation is represented by no feature. Two small depressions which probably represent the flagellar pores are sometimes present in the parasulcus.

Dimensions: Cyst length 52.2–70.8μm, width 56.0–63.4μm, width of paracingulum 4.9–6.3μm, length of processes ca. 2.5μm (Holotype ; cyst length 58.0μm, width 56.0μm, width of paracingulum ca. 6μm).

Number of specimens observed: 12.

Remarks: This species resembles *Trinovantedinium capitatum* in possessing a pentagonal body covered with many short spines, but differes from the latter in bearing a slightly brownish-pigmented cyst wall and in that the epicyst is always larger than the hypocyst.

Equivalent thecate form: Unknown, but probably a species assignable to the *Conica* group of the *Protoperidinium,* based on its brownish-pigmented cyst wall and intercalary archeopyle.

Genus *Votadinium* Reid 1977

Type species : *Vatadinium carvum* Reid 1977

Votadinium carvum Reid 1977

Plate 7, figures 1–8

1966 *Peridinium* sp. (Cyst-form 4) Wall, p. 307, text-figs. 14, 15, 22.

1968 Cordate resting spore of *Peridinium oblongum* (Aurivillius) Paulsen ; Wall and Dale, pl. 272–273, pl. 1, figs. 25–28.

1976b *Peridinium oblongum* (Aurivillius) ; Matsuoka, p. 560, pl. III, figs. 2, 3 ; pl. IV, figs. 4, 5.

1977 *Votadinium calvum* Reid, p. 444–445, pl. 2, figs. 21–23.

1982 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech ; Harland, p. 380–381, text-fig. 14, pl. 40, figs. 10–12.

1985a *Votadinium calvum* Reid ; Matsuoka, p. 57–57, pl. 12, figs. 1–2.

Dimensions : Cyst length 69.0–76.5μm, width 63.4–82.0μm.

Number of spicimens observed: 76.

Remarks : This species equivalent to the cordate resting spore of *Protoperidinium oblongum* has a single intercalary archeopyle with six-sided principal archeopyle sutures. According to Wall and Dale (1968), however, its thecate form, *Protoperidinium oblongum* which includes several variations in the morphology of the second intercalarly plate, is fundamentally classified under the Ortho-Quadra type by Balech (1974).

Votadinium carvum is similar to a round form of *Lejeunecysta concreta* (Reid) comb. nov., but differs in lacking a paracingular feature.

Ecological distribution in previous record :

Temperate ; inner neritic (Harland, 1983).

Around the Japanese Islands ; Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga, Off Honjo and Off Oga (Matsuoka 1985b).

Equivalent thecate form : *Protoperidinium oblongum* (Aurivillius) Balech by incubation experiment of Wall and Dale (1968).

Votadinium spinosum Reid 1977
Plate 14, figures 1–5

1965 *Peridinium* sp. (Cyst-form 5) Wall, p. 307, fig. 16.

1968 Resting spore of *Peridinium claudicans* Paulsen ; Wall and Dale, p. 273, pl. 2, figs. 1, 2.

1977 *Votadinium spinosum* Reid, p. 445–446, pl. 2, figs. 24–26.

1982 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech ; Harland, p. 380, text-fig. 13.

1985a *Votadinium spinosum* Reid ; Matsuoka, p. 58–59, pl. 14, figs. 1–6.

Dimensions : Cyst length 57.2–71.2μm, width 56.0–64.0μm, length of processes ca. 6μm.

Number of specimens observed: 5.

Remarks: The variations of this cyst is recognized in the cyst shape and hypocystal lobs; the former feature varies from roundly pentagonal (Pl. 14, figs. 4–5) to broadly cordate (Pl. 14, figs. 1–3), and therefore the cordate form has a parasulcus deeply indented, whereas this feature in the roundly pentagonal form (e.g. Wall and Dale 1968; pl. 1, fig. 29) is not distinct. The broadly cordate forms have also been recorded from Senzaki Bay by Matsuoka (1985a).

Ecological distribution in previous record:

Temperate; inner neritic (Harland, 1983).

Around the Japanese Islands; Nagasaki Bay, Omura Bay, Senzaki Bay, Lake Hiruga and Lake Kamo (Matsuoka 1985b).

Equivalent thecate form: *Protoperidinium claudicans* (Paulsen) Balech by incubation experiment of Wall and Dale (1968).

Subfamily Uncertain

Dinoflagellate cyst type A

Plate 3, figures 9–11; Plate 14, figures 13–14; Plate 17, figures 1–15

Description: Small spherical chorate cyst is brown in color. The cyst wall consists of two layers, which are loosely adpressed. The coarsely granular endophragm is relatively thicker than the periphragm. The periphragm is thin and menbranous, sometimes wrinkled. Except for the archeopyle, no ornament and suclpture represent the paratabulation.

The large polygonal field formed by the periphragm are always developed on the surface, but they do not represent paraplates because these are not regular in size and position as like as paraplates. The archeopyle probably consists of two intercalary paraplate (Pl. 17, fig. 3) and sometimes of one hexagonal intercalary paraplate (Pl. 14, fig. 13). The opeculum is rarely attached (Pl. 17, fig. 14).

Dimensions: Cysts diameter 33.2–41.0μm, thickness of endophragm ca. 1μm.

Number of spicimens observed: 50.

Remarks: Dinoflagellate cyst type A is closely similar to *Ataxiodinium choanum* Reid in possessing two layers which are roughly adpressed. But this cyst differs from the latter in having a brownish-pigmented wall and an intercalary archeopyle. This cyst also resembles the phycoma of *Protosperma cuboides* Gaarder and *P. nationalis* Lemmermann, both of which are assigned to the Prasinophyceae, but differs in bearing irregular polygonal field in size and position and an archeopyle.

Equivalent thecate form : Unknown, but probably a species related to the Protoperidiniaceae, but bi-layered cyst with an intercalary archeopyle has never been recorded in modern sediments.

Order Gymnodiniales Lemmermann, 1910

Family Polykrikaceae Lindemann, 1928

Genus *Polykrikos* Bütschli 1873

Type species : *Polykrikos schwartzii* Bütschli 1873

Polykrikos schwartzii Bütschli 1873

Plate 15, figure 1–10

1887 Umrindete cysts Hensen, p. 80, pl. 4, figs. 32a, b ; pl. 6, figs. 67–68.
1968 ?Resing spore of naked dinoflagellate ; Wall and Dale, p. 281, pl. 4, fig. 28.
1978 Resting cyst of *Polykrikos schwartzii* Bütschli ; Reid, p. 227, pl. 1, figs. 1–9.
1982 Cyst of *Polykrikos kofoidii* Chatton ; Fukuyo, p. 208–209, pl. IV, figs. 1–3.
1985a *Polykrikos schwartzii* Bütschli ; Matsuoka, p. 61–62, pl. 16, figs. 4–10.

Dimensions : Cyst length 89.6–108.2μm, width 60.0–62.5μm, height of ornament ca. 9μm.

Number of specimens observed : 84.

Ecological distribution in previous record :
Temperate ; inner neritic (Harland 1983).

Polykrikos sp. cf. *P. kofoidii* Chatton 1914

Plate 16, figures 1–9

Compare with :

1980 Cyst of *Polykrikos kofoidii* Chatton ; Morey-Gains and Ruse, p. 230–231, fig. 4.
1980 "Acritarch" species ; Arends and Damassa, pl. 2, figs. 1–2, 12–13.
1982 Cyst type PS–1 ; Fukuyo, p. 209, pl. IV, figs. 7–8.
1985a *Polykrikos* sp. cf. *kofoidii* Chatton ; Matsuoka, p. 62–63, pl. 16, figs. 1–3.
non 1982 Cyst of *Polykrikos kofoidii* Chatton : Fukuyo, p. 208–209, pl. IV, figs. 1–3.

Dimensions: Cyst length 106.7–114.2μm, width 55.9–67.2μm, length of processes 23.3–26.2μm.

Number of specimens observed: 84.

Remarks: The present specimens possess no shelf-like ornament but short infundibular processes with recurved distal parts. Sometimes these processes connect adjacent ones and makes incomplete shelf like ornaments. Five rows of processes or shelf-like ornaments are present.

These specimens are similar to the cysts of *Polykrikos kofoidii* described by Morey-Gains and Ruse (1980) in possessing hollow processes, but differ from the latter in that processes are not cylindrical rather than infundibular with recurved distal extremities. These features are also different from those of the specimens of *P.* sp. cf. *kofoidii* shown by Matsuoka (1985a).

Geographical distribution around the Japanes Islands:

This type cyst may occur in the region effected by the cold current.

Order Uncertain

Dinoflagellate cyst type B

Plate 18, figures 3–11; Plate 19, figures 11–14

Description: The spherical proximochorate cyst is small to intermediate in size and lightly brownish in color. The cyst body may be composed of two layers closely adpressed over all, autophragm with a smooth to faintly granular surface, and is covered with many solid and somewhat flexous processes with acicular extermities. No feature represent the paratabulation. The archeopyle is usually indistinctive, and probably a chasmic type formed by the slit on the cyst.

Dimensions: Cyst diameter 40.0–49.2μm, length of processes 6.0–8.4μm.

Number of spcimens observed: 132.

Remarks: The present cyst form is similar to Dinoflagellate cyst G of Reid and Harland (1977) and the cyst of *Pheopolykrikos hartmannii* (Zimmermann). Although this cyst differs from Dinoflagellate cyst G of Reid and Harland (1977) in possessing a larger cyst body and longer processes, these differences are possibly included within a species variation.

This cyst is also distinguishable from the cyst of *Pheopolykrikos hartmannii* in lack of processes with short striations at the proximal base.

Equivalent thecate form: Unknown, but the chasmic archeopyle and brownish cyst body suggests that this cyst is closely related to the Gymnodiniales.

Dinoflagellate cyst type C
Plate 19, figures 1–2, 7–10

Description : The small to intermediate spherical cyst is proximochorate, and lightly to dark brownish in color. The cyst wall comprises two closely adpressed layers. The periphragm is relatively thin and smooth to slightly granular surface. Processes are many, nontabular, solid, slender and flexous with corynate to capitate distal extremities. No feature suggests the paratabulation. The archeopyle is unclear but probably chasmic and formed by the slit on the cyst.

Dimensions : Cyst diameter 26.0–42.9μm, length of processes 8.4–10.1μm.

Number of specimens observed : 5.

Remarks : This cyst is characterized by the processes providing with corynate to capitate distal tips.

Operculodinium centrocarpum is similar to this species, but differs in having a precingular archeopyle and a non-pigmented cyst wall.

Dinoflagellate cyst type C closely resembles Dinoflagellate cyst D of Reid and Harland (1977, pl. 2, fig. 10), but apparently differs in having more stout processes.

Equivalent thecate form : Unknown, but this cyst is probably related to the Gynmodiniales based on its chasmic archeopyle.

Dinoflagellate cyst type E
Plate 14, figures 8–9

Description : The small proximochorate cyst is spherical and lightly brownish in color. The cyst wall consists of two layers closely adpressed between processes. The periphragm is slightly granular. Processes are nontabular, relatively long, hollow, flexous and acuminate distally. No feature suggests the paratabulation. The archeopyle is indistinct but probably chasmic and formed by the slit on the cyst.

Dimensions : Cyst diameter 22.4–30.0μm, length of processes 6.7–8.6μm.

Number of specimens observed : 66.

Remarks : Dinoflagellate cyst type E resembles Dinoflagellate cyst type A in this paper and Dinoflagellate cyst B of Reid and Harland (1977, pl. 2, figs. 6, 7), but differs from Dinoflagellate cyst type A in its smaller cyst body and

Table 2 Absolute numbers and relative frequencies of dinoflagellate cysts recovered from the surface sediemnts of Lake Saroma (SR) and Akkeshi Bay (AK) in Hokkaido.

Species / Sample	AK 1		AK 2		AK 3		AK 4		SR 1		SR 5		SR 8		SR 11		SR 16		SR 17	
Gonyaulacoid Lineage																				
Gonyaulacaceae		%		%		%		%		%		%		%		%		%		%
Spiniferites sp. cf. *bulloideus*	4	1.8	4	1.0	4	1.7	3	1.2	5	3.4			9	4.3	1	0.6	6	2.6	20	16.9
Spiniferites sp. cf. *delicatus*	2	0.9	2	0.5			2	0.8	5	3.4	1	1.0	9	4.3			7	3.0		
Spiniferites elongatus	4	1.8	2	0.5	3	1.3			2	1.4									5	4.2
Spiniferites frigidus													7	3.3	3	1.7	3	1.3	5	4.2
Spiniferites ramosus			2	0.5	2	0.9	3	1.2	2	1.4			2	1.0	2	1.2	1	0.4		
Spiniferites spp. indet.	5	2.3	6	1.4	1	0.4	2	0.8	3	2.0	6	5.7	5	2.4	2	1.2	8	3.4		
Operculodinium centrocarpum	24	10.8	24	5.8	19	8.3			3	2.0	6	5.7	5	2.4	2	1.2	4	1.7	29	24.6
Nematosphaeropsis labyrinthea									1	0.7									1	0.8
Protogonyaulax affinis + spp.	5	2.3	1	0.2			1	0.4	46	31.3	11	10.5	6	2.9	61	35.3				
Lingulodinium machaerophorum											1	1.0								
Tuberculodinium Lineage																				
Pyrophacaceae																				
Tuberculodinium vancampoae									1	0.7							1	0.4	5	4.2
Peridinioid Lineage																				
Diplopsaloideae																				
Dubridinium caperatum	2	0.9	17	4.1																
Dinoflagellate cyst type D	3	1.4	1	0.2			2	0.8	5	3.4	12	11.4	17	8.1	10	5.8	12	5.2		
Protoperidinoideae																				
Brigantedinium spp.	95	42.8	228	54.7	134	58.5	161	63.9	60	40.9	38	36.2	97	46.2	68	39.3	105	45.3	22	18.6
Lejeunecysta concreta	19	8.6	4	1.0	14	6.1	25	9.9											1	0.8
Lejeunecysta psuchra	1	0.5	4	1.0	2	0.9	1	0.4									1	0.4	1	0.8
Lejeunecysta? *epidoma*	1	0.5					2	0.8												
Selenopemphix nephroides	5	2.3	3	0.7	10	4.4	1	0.4												
Selenopemphix quanta	6	2.7	7	1.7	5	2.2	5	2.0			7	6.7			6	3.5	3	1.3		
Trinovantedinium capitatum	2	0.9	1	0.2			1	0.4											5	4.2
Trinovantedinium pallidifulvum	4	1.8	2	0.5	3	1.3	2	0.8					1	0.5						
Votadinium carvum	4	1.8	33	7.9	12	5.2	16	6.3	1	0.7			2	1.0	1	0.6	2	0.9	5	4.2
Votadinium spinosum	4	1.8							1	0.7										
Dinoflagellate cyst type A	2	0.9	4	1.0	2	0.9	12	4.8	1	0.7	2	1.9	14	6.7	2	1.2	10	4.3	1	0.8
Gymnodinioid Lineage																				
Gymnodiniales																				
Polykrikos schwartzii	5	2.3	7	1.7	8	3.5			4	2.7			14	6.7	7	4.0	21	9.1	18	5.3
Polykrikos sp. cf. *kofoidii*	5	2.3	4	1.0	1	0.4	2	0.8			5	4.8	3	1.4			5	2.2		
Lineage indet.																				
Dinoflagellate cyst type B & C	19	8.6	53	12.7	4	1.7	8	3.2	1	0.7	4	3.8	11	5.2	2	1.2	26	1.2		
Dinoflagellate cyst type E	1	0.5	8	1.9	5	2.2	3	1.2	6	4.1	12	11.4	8	3.8	6	3.5	17	7.3		
Total count	222		417		229		252		147		105		210		173		232		118	
Total number/1ml	740		13900		1145		1260		490		350		875		480		1289		393	

possessing more slender processes and from Dinoflagellate cyst B of Reid and Harland, 1977 in bearing a granular periphragm and fewer processes in number.

Equivalent thecate form: Unknown.

Note on the dinoflagellate cyst assemblages in Akkeshi Bay and Lake Saroma

Akkeshi Bay

Protoperidiniacean cysts are dominant in all four samples of Akkeshi Bay. These cysts comprise various cyst genera and species including six new cyst species at least. Undifferentiated sperical and brown cysts which are attributed to *Brigantedinium* occupy mostly half of the assemblage, from 40 to 60 percent of total cyst number. *Lejeunecysta concreta* is also diagnostic for this assemblage, but is not abundant.

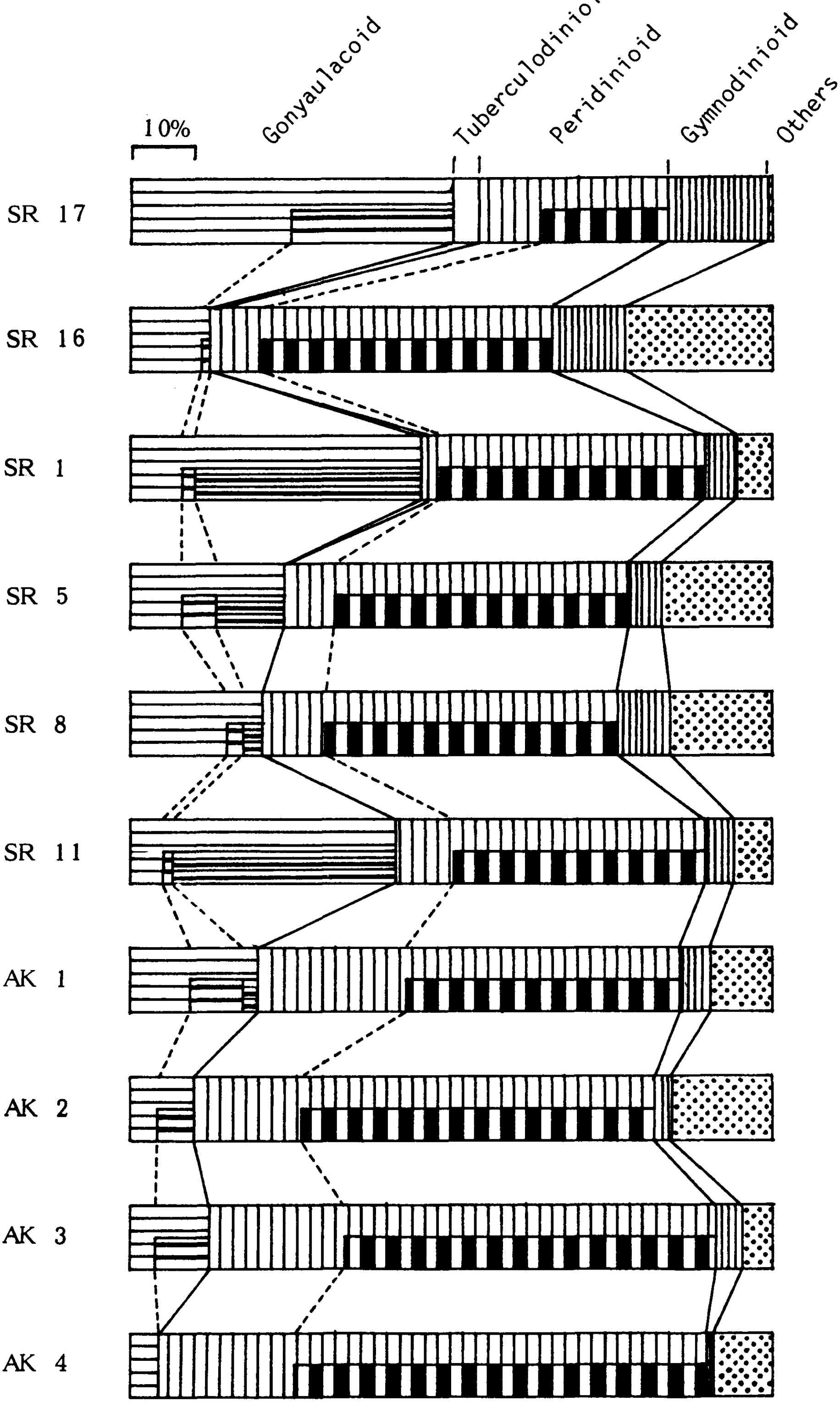
The gonyaulacacean cyst assemblage mostly comprising several species of *Spiniferites* is rare or lack in typical subtropical to warm water species such as *Spiniferites ramosus* and *S. bentori*. *Operculodinium centrocarpum* is common. Ellipsoidal and smooth-walled cysts of *Protogonyaulax* are also common in AK 1. These are probably assignable to *P. tamarensis* based upon its ecological distribution previously recorded by Fukuyo (1985).

The gymnodiniacean cyst assemblage consists mainly of two species as *Polykrikos schwartzii* and *P.* sp. cf. *kofoidii,* and other cysts such as *Pheopolykrikos hartmannii* which is common in warm water to subtropical area are not present in this area. Spinous and brownish-pigmented cysts with a simple slit (probably chasmic archeopyle) which are attributed to the unknown group are probably members of the Gymnodiniaceae.

Consequently, the dinoflagellate cyst assemblage in Akkeshi Bay is characterized by predominance of protoperidiniacean cysts, especially *Brigantedinium* and very scarcity of Gonyaulacoid cysts such as *Spiniferites* and *Tuberculodinium* except for *Operculodinium centrocarpum.*

Lake Saroma

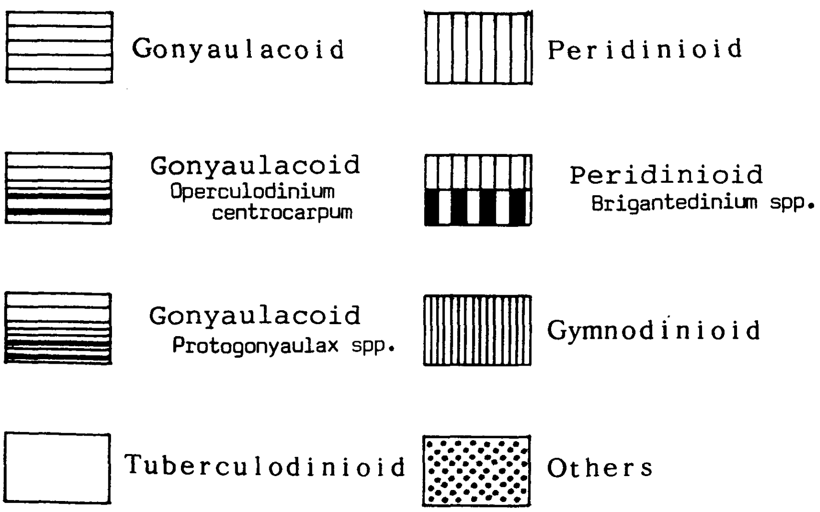
Protoperidiniacean cysts are abundant through all samples, especially brown spherical *Brigantedinium* spp. being predominant except for Sample SR 17 which abundantly contains *Spiniferites* sp. cf. *bulloideus* and *Operculodinium centrocarpum.* Other species of the protoperidiniacean cysts are less common in both diversity and individuals. Spinous and brownish spherical


10%
Gonyaulacoid
Tuberculodinioid
Peridinioid
Gymnodinioid
Others
SR 17
SR 16
SR 1
SR 5
SR 8
SR 11
AK 1
AK 2
AK 3
AK 4

cysts which is probably assignable to the Diplopsaloideae are considerably abundant in samples of SR 5, 8, 11 and 16.

In comparison with Akkeshi Bay, the cyst assemblage of Lake Saroma is characterized by occurrence of two ecologically different types of *Spiniferites* ; *S.* sp. cf. *bulloideus* (=*S. bulloides* of Matsuoka 1985a) and *S. frigidus* respectively. According to Matsuoka (1985a, b), *Spiniferites bulloideus* dominantly occurrs in inner bay sediments of Southwest Japan and then is considered to be a warm water species. Whereas Harland and Reid (in Harland et al., 1980), Harland (1982), and Harland and Sharp (1986) reported *Spiniferites frigidus* from the Beaufort Sea, Norwegian Sea and south Barents Sea. Based on this, Harland (1983) regarded that this cyst is a cold water species. The occurrence of both species in Lake Saroma supports that this lake is influenced by two different water mass ; warm and cold currents. The oceanographic data also suggest that the warm Soya current, which is a branch of the Tsushima current appeares along the south coast of the Sea of Okhotsk in summer, but in winter disappears and the lake is freezed over. The rare occurrences of *Tuberculodinium vancampoae* which is dominant in inner bay of the subtropical to warm temperate sea waters around Japan (Matsuoka 1985a, b) also suggests the development of the warm water current in summer.

In the samples of SR 1, 5 and 16, spherical cysts with a transparent wall abundantly occur. This cyst is probably identical with *Protogonyaulax*



Text-fig. 6 Percentage frequency of dinoflagellate cysts recovered from the surface sediments of Lake Saroma (SR) and Akkeshi Bay (AK) in Hokkaido.

affinis Inoue and Fukuyo, because Fukuyo et al. (1985) reported the presence of globular resting cysts of *P. affinis* from surface sediments of this lake.

In the gymnodinialian cysts, *Polykrikos schwartzii* is more abundant in the samples of SR 8 and 16 of Lake Saroma than in Akkeshi Bay. This cyst is also predominant in lagoonal sediments of Lake Kamo in the Sado Island, North Honshu (Matsuoka 1985b). These data strongly support that the cyst of *Polykrikos schwartzii* characterizes the inner bay to lagoonal environments around the Japanese Islands.

Comparison with other dinoflagellate cyst aeesmblages around the Japanese Islands

For the distribution of modern dinoflagellate cysts, several works have been published around the Japanese Islands.

Harada (1974) investigated dinoflagellate cysts in surface sediments on the continental margin from off-Choshi to off-Muroran along the Pacific coast in North Japan. But unfortunately he did not fully discuss the characteristics of these assemblages except for clarifying that *Operculodinium centrocarpum* which is a dominant species in above-mentioned areas differs from the Atlantic Ocean in the ecological distribution.

Matsuoka (1976b) studied the distribution of both dinoflagellate thecae and cyst in four stations of off-Hachinohe in North Japan. According to this, peridiniacean thecate cells are dominant in all surface plankton assemblages and their cysts dominantly occur in near-shore samples, whereas Gonyaulacoid cysts (*Spiniferites* spp.) and Tuberculodinioid cysts (*Tuberculodinium vancampoae*) are very rare and *Operculodinium centrocarpum* is abundant in more off shore sediments.

In Southewest Japan, the dominance of Gonyaulacoid cysts, especially *Spiniferites bulloideus, S. hyperacanthus* and *S. mirabilis* characterizes the warm temperate to subtropical inner bay dinoflagellate cyst assemblage (Matsuoka 1985a). In the coastal areas influenced by the Tsushima current, *Spiniferites bulloideus, S.* sp. cf. *delicatus, S. mirabilis* and *Tuberculodinium vancampoae* decrease, whereas *Brigantedinium* spp. and other Peridinioid cysts increase with going up the north of the current (Matsuoka, 1985b).

As above mentioned, the dinoflagellate cyst assemblage of Lake Saroma is characterized by an abundance of Peridinioid cysts accompanied with a small amount of Gonyaulacoid and Tuberculodinioid cysts such as *Spiniferites* spp. and *Tuberculodinium vancampoae.* This assemblage reflects the mixed condition of two different water masses. These are the warm water (Soya current) from the Tsushima current mainly appearing in summer and the cold water derived from the Sea of Okhotsk in winter around Lake Saroma.

On the other hand, in Akkshi Bay Peridinioid cysts of *Brigantedinium* spp. and other protoperidiniacean cysts are predominat and show a high cyst-species diversity. The extremely abundant number of cysts in a unit volum (e.g. 13,900 cells per 1ml wet sediment in maximum at AK 2) indicates the high primary production as later discussed. These characteistics are common to those of the assemblage of off-Hachinohe where the cold Oyashio current is flowing from the north. Furthermore the occurrence of the cold water species, *Spiniferites frigidus* also support this interpretation.

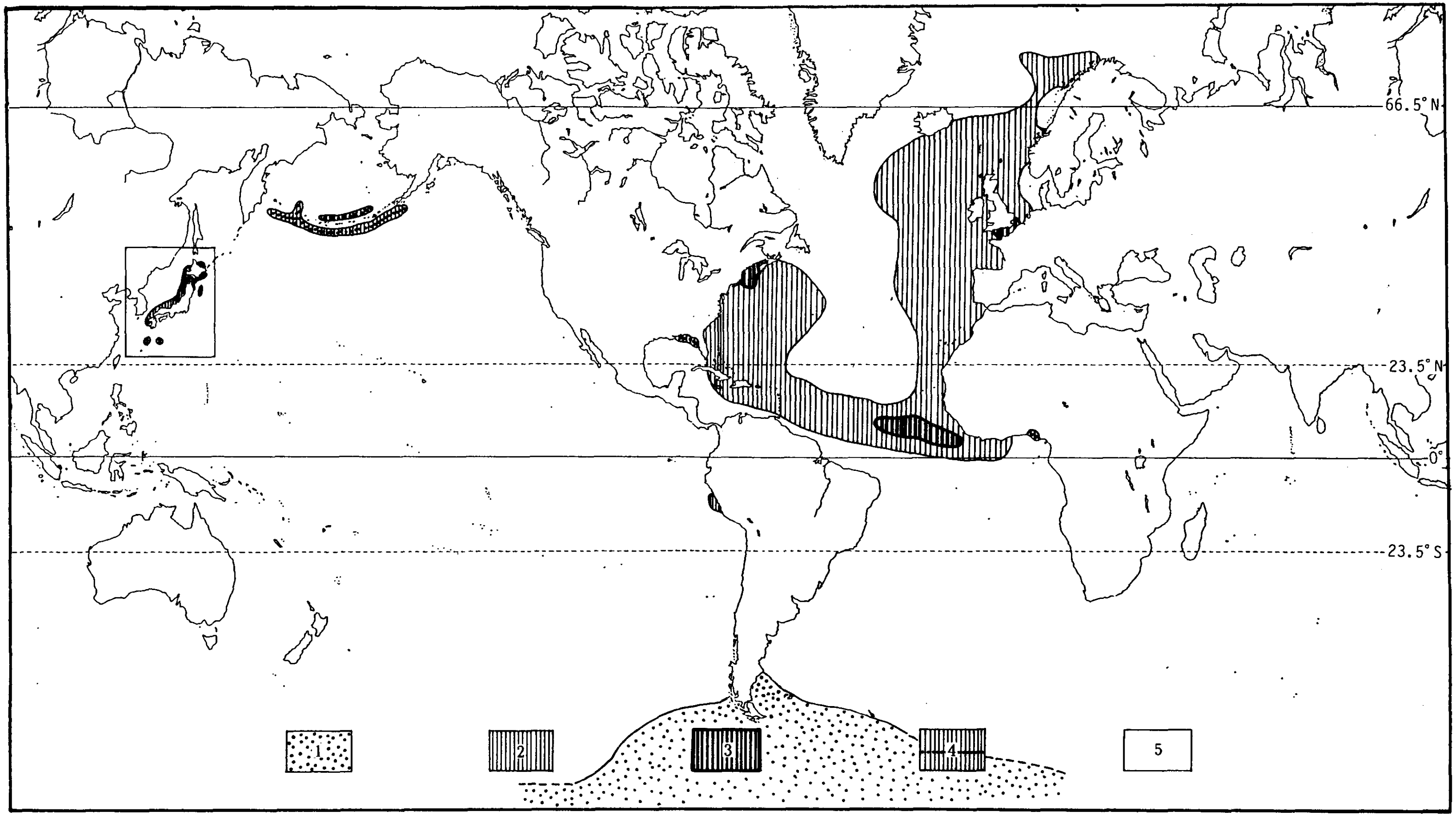
Consequently the predominance of Peridinioid cysts, especially *Brigantedinium* spp. is the most important character for the cold water dinoflagellate cyst assemblage around the Japanese Islands.

Significance of the abundance of protoperidiniacean cyst

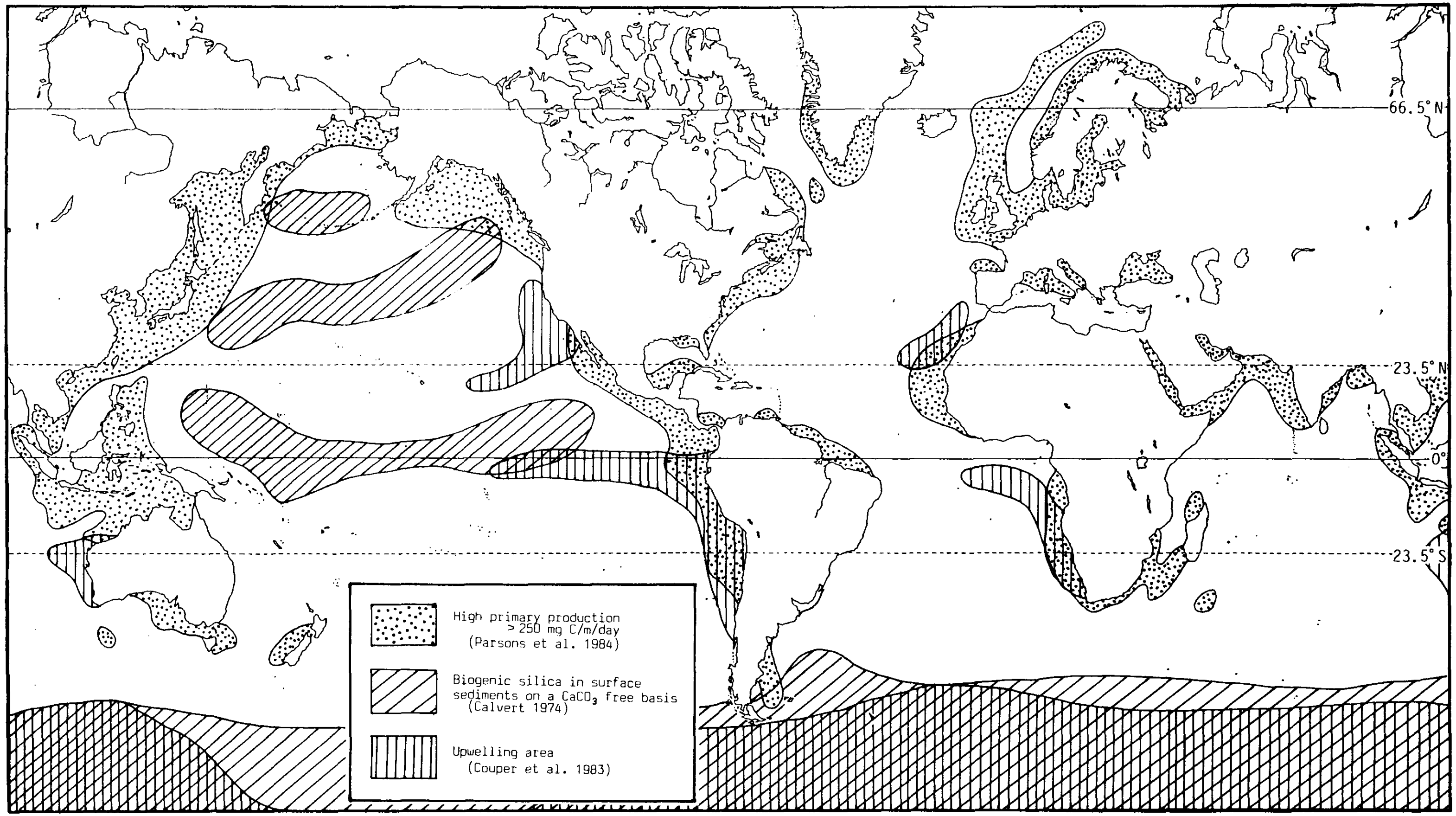
The modern dinoflagellate cyst assemblage dominated by protoperidiniacean cysts has been known from the following areas ; Gulf of Main, off western South Africa, off West Africa (Wall et al. 1977) and Dover straight (Harland 1983) in the Atlantic region, and off Hachinohe (Matsuoka 1976b), southern part of the Sea of Japan (Matsuoka 1985b), Akkeshi Bay in Hokkaido (this paper), around the Amami Island (Matsuoka 1985d), and off Pisco of Peru (Wall et al. 1977) in the Pacific region (Text-fig. 7).

Bujak (1984) reported the Late Miocene to Pleistocene fossil dinoflagellate cyst assemblage dominated by *Brigantedinium* spp. in the northern North Pacific and the Bering Sea. Matsuoka et al. (in press) recorded the Neogene to Quaternary dinoflagellate cyst assemblage including the protoperidiniacean cysts such as *Brigantedinium, Lejeunecysta* and *Selenopemphix* in North Japan. Duffield and Stein (1986) and Wrenn and Kokinos (1986) also recognized the dinoflagellate cyst assemblage which is abundant in the protoperidiniacean *Lejeunecysta, Selenopemphix* and *Sumatradinium* in the Miocene sediment of the Gulf of Mexico. Biffi and Grignani (1983) described the Oligocene protoperidiniacean cyst assemblage in the Niger Delta, central Africa (Text-fig. 7).

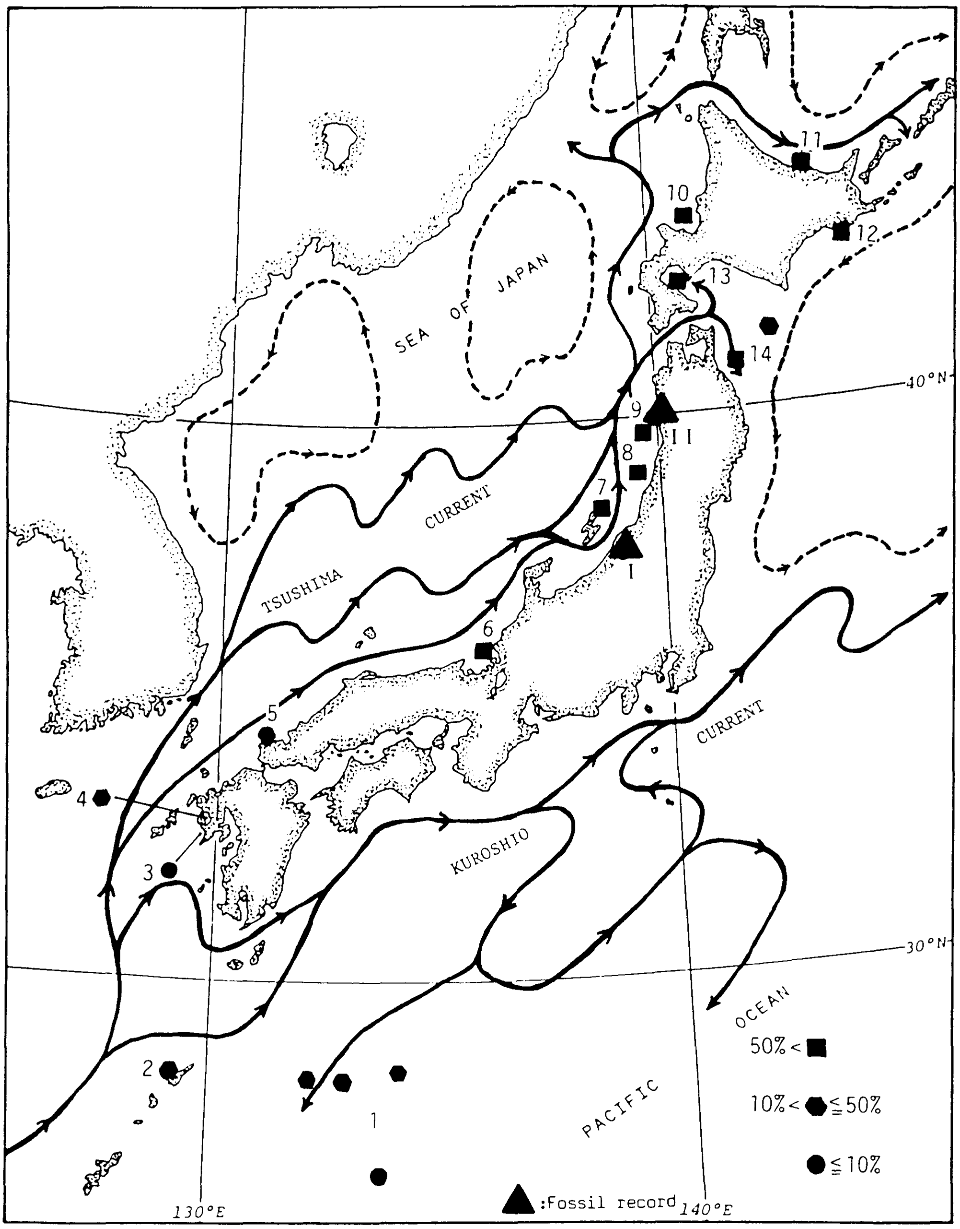
Bujak (1984) dissussed the paleoecological significance of the protoperidiniacean-rich assemblage in relation with diatomaceous sediments and concluded that protoperidiniacean dinoflagellate abundance is associated



Text-fig. 7 Distribution map of *Brigantedinium*- and *Protoperidinium*-rich areas. 1 : *Protoperidinium*-dominated area ; Weddel Sea by Balech et al. (1968). 2 : *Brigantedinium*-rich areas by Wall et al. (1977), Harland (1983), and Matsuoka (1976b, 1981, 1985a, b) showing the relative abundance of *Brigantedinium* spp. less than 50% in the total cysts. 3 : The relative abundance of *Brigantedinium* spp. more than 50% in the total cysts. 4 : Fossil protoperidiniacean cyst-rich assemblages in North Japan (Matsuoka et al. in press), Bering Sea (Bujak 1984), Gulf of Mexico (Duffield and Stein 1986) and (Wrenn and Kokinos 1986), and the Niger Delta (Biffi and Grignani 1983). 5 : Enlarged area around the Japanese Islands (see Text-fig. 9).



Text-fig. 8 Map showing upwelling area, high primary production area and biogenic silica-rich area.



Text-fig. 9 Distribution map of *Brigantedinium*-rich areas around the Japanese Islands. 1 : North Philippine Sea (Matsuoka 1981), 2 : Amami Island (Matsuoka 1985d), 3 : Nagasaki Bay, 4 : Omura Bay, 5 : Senzaki Bay, 6 : Lake Hiruga, 7 : Lake Kamo, 8 : Off Honjo, 9 : Off Oga (3–9 ; Matsuoka 1985a, b), 10 : Ishikari Bay (unpublished data), 11 : Lake Saroma (this paper), 12 : Akkeshi Bay (this paper), 13 : Funka Bay (unpublished data), 14 : Off Hachinohe (Matsuoka 1976b), I : Niigata area (Matsuoka 1983), II : Akita area (Oga Peninsula) (Matsuoka et al. in press).

with high diatom productivity and closely related with rich dissolved nutrients coming from upwelling areas.

Text-fig. 8 shows the areas of high productivity of phytoplankton (Persons et al. 1984), and high concentration of biogenic silica in surface sediments (Calvert 1974). The abundant occurrence of protoperidiniacean cysts is extended to areas in not only high concentration of biogenic silica but also high productivity of phytoplankton such as Gulf of Main, Dover straight and around the Japanese Islands.

These evidences suggest that the modern dinoflagellate cyst assemblage dominated by protoperidiniacean cysts is closely related with high productivity of not only diatom but also probably other phytoplankton groups. From the ecological view point, the relationship between protoperidiniacean dinoflagellates and other phytoplankton is explained as the follows :

Most protoperidiniacean species which produce a resting cyst are non-photosynthetic and holozoic, because they lack chloroplasts. Recently their feeding mechanism has been progressively clarified. According to Gains and Taylor (1984), a species of *Protoperidinium* attacks and then encloses other small organisms such as diatom and other flagellates, and after taking some or all of the contents withdraws the remnant part. Therefore, abundance of these dinoflagellages are supported by high phytoplankton productivity such as diatoms, silicoflagellates and probably other organic-walled phytoflagellates.

Consequently, the dominance of protoperidiniacean cysts indicates the high productivity of phytoplankton, which is introduced by dissolved nutrient rich water such as deep sea and terrestrial waters.

Based on this consideration, the areas dominated by protoperidiniacean cysts are devided into two major categories. One of them is related to the upwelling area, for example the regions of off Pisca of Perue, off West Africa and off western South Africa. Although there is no evidence concerning upwelling off eastern North Japan, these areas including Akkeshi Bay and Off Hachinohe are strongly influenced by the Oyashio current which abundantly contains dissolved nutrient originally transported from the probable upwelling zone along the Alutian Islands in the North Pacific. Another is probably related with terrestrially originated nutrients which are transported by river. These areas include Gulf of Main, Dover straight, Gulf of Mexico, off western North Japan and around the Amami Island of West Japan.

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Plate 1

Figs. 1–8. *Spiniferetes frigidus* Harland and Reid in Harland et al. 1980.

1 : Ventral surface of ventral view showing a parasulcal area, 2 : Optical cross section, 3 : Dorsal surface of dorsal view showing a precingular archeopyle (1–3 : ×710, same specimen Slide SR17–5, 16.5/138.0). 4 : Ventral surface of dorsal view, 5 : Optical cross section showing apical and antapical pericoels (arrows), 6 : Dorsal surface of ventral view showing a precingular archeopyle, 7, 8 : Well-developed antapical pericoel (4–8 : Same specimen, Slide SR8–3, 5.5/137.3 ; 4–6 : ×760, 7–8 : ×1010).

Figs. 9–10. *Spiniferites elongatus* Reid 1974.

[Cyst of *Gonyaulax spinifera* complex]

9 : Ventral surface of dorsal view, showing a triangular 6" paraplate, 10 : Optical cross section, showing parasutural septa on the hypocyst (9–10 : ×710, same specimen, No. AK2w–1).

K. MATSUOKA

PLATE 1

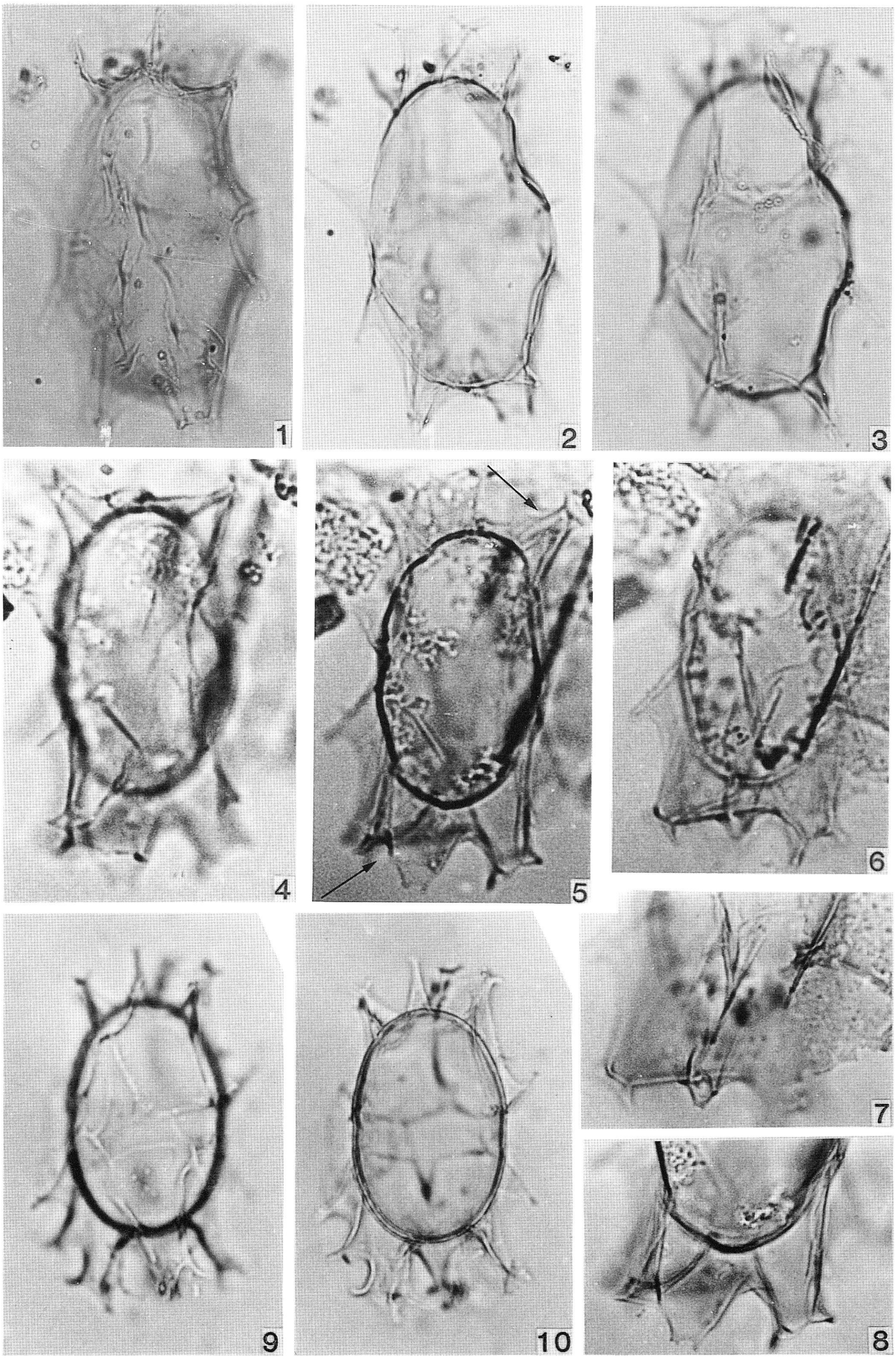

Plate 2

Figs. 1–4, 8–12. *Spiniferites* sp. cf. *S. delicatus* Reid 1974.

1 : Optical cross section, 2 : Lateral view, 3 : Lateral view, 4 : Petaloid-shaped gonal processes (1–4 : × 845, same specimen, Slide SR8–3, 9.6/138.3). 8 : Ventral surface of ventral view, 9 : Opeical cross section, 10 : Dorsal surface of dorsal view showing normal trifurcate processes (8–10 : × 710, same specimen, Slide SR16–1, 15.8/145.0). 11 : Optical cross section, showing petaloid-shaped processes, 12 : Oblique dorsal surface (11–12 : × 710, same specimen, Slide SR8–1, 13.2/144.0).

Figs. 5–6. *Spiniferites* sp. cf. *S. bulloideus* (Deflandre and Cookson) Sarjeant, 1970.

5 : Oblique ventral view, 6 : Oblique dorsal view (5–6 : × 860, same specimen, Slide AK2–2, 93.2/35.0).

Fig. 7. *Spiniferites ramosus* (Ehrenberg) Loeblich and Loeblich 1966. Dorsal surface of dorsal view, showing a reduced archeopyle (× 860 Slide AK2–2, 95.1/34.0).

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PLATE 2

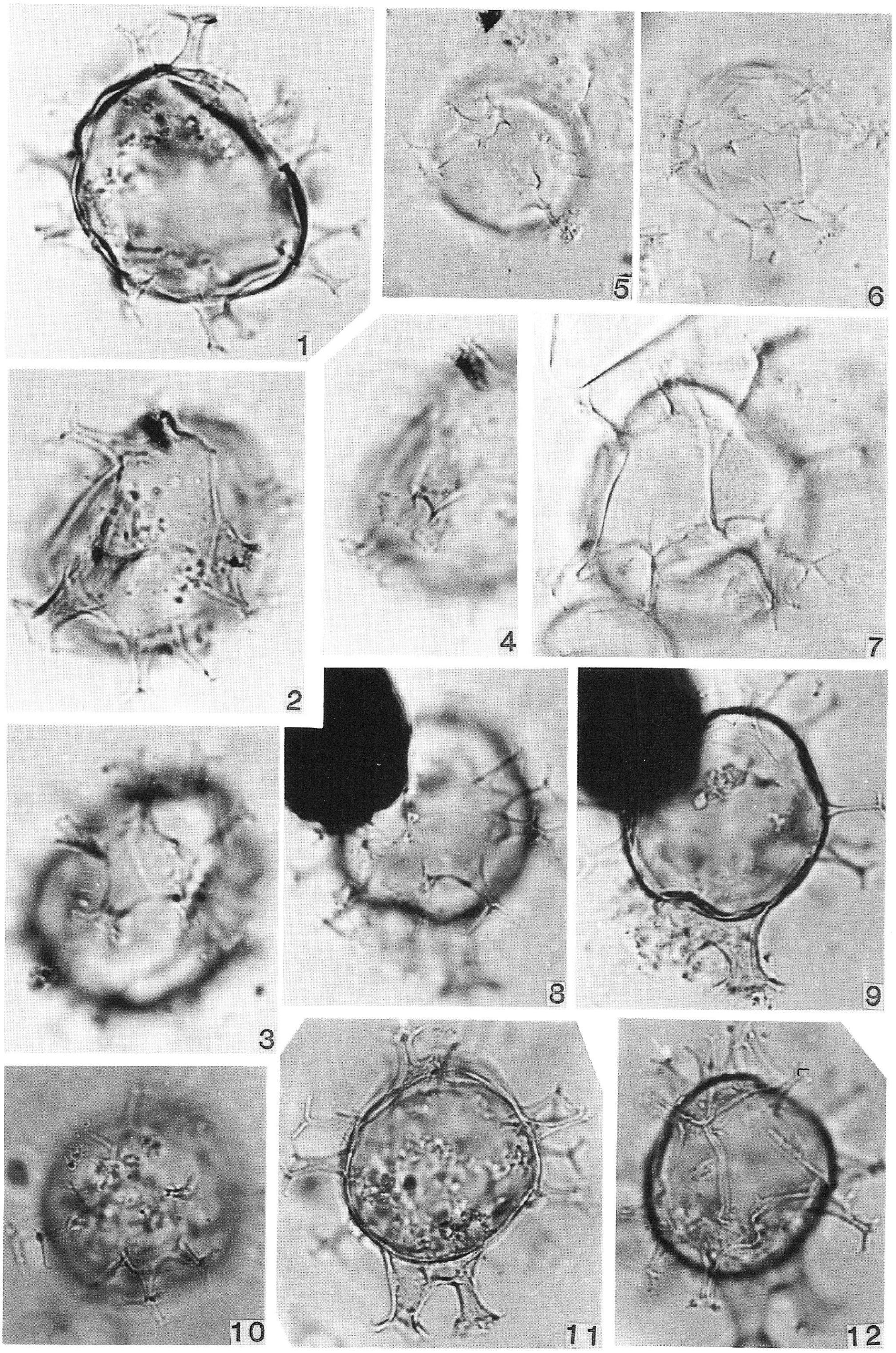

Plate 3

Figs. 1–6. *Spiniferites ramosus* (Ehrenberg) Loeblich and Loeblich 1966.

1 : Apical surface of antapical view, showing reduced parasutures between 1′ and 4′, and apical process (arrow). 2 : Optical cross section, 3 : Antapical surface of apical view (1–3 : × 750 same specimen No. AK2w–2). 4 : Lateral view, 5 : Oblique antapical view (Slide AK2–1, 93.5/31.5). 6 : Optical cross section (× 710, Slide AK2–2, 11.5/131.8)

Figs. 7–8. *Spiniferites* sp. cf. *S. delicatus* Reid 1974.

7 : Oblique ventral surface, 8 : Optical cross section of dorso-ventral view (7–8 : × 710, same specimen, Slide SR17–3, 20.3/143.4).

Figs. 9–11. Dinoflagellate cyst type A.

9 : Showing a granular surface of the endophragm, 10 : Optical cross section, showing a thick endophragm and a thin membranous periphragm, 11 : Showing a smooth periphragm (9–11 : × 860, same specimen, Slide AK2–3, 95.0/31.1).

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PLATE 3

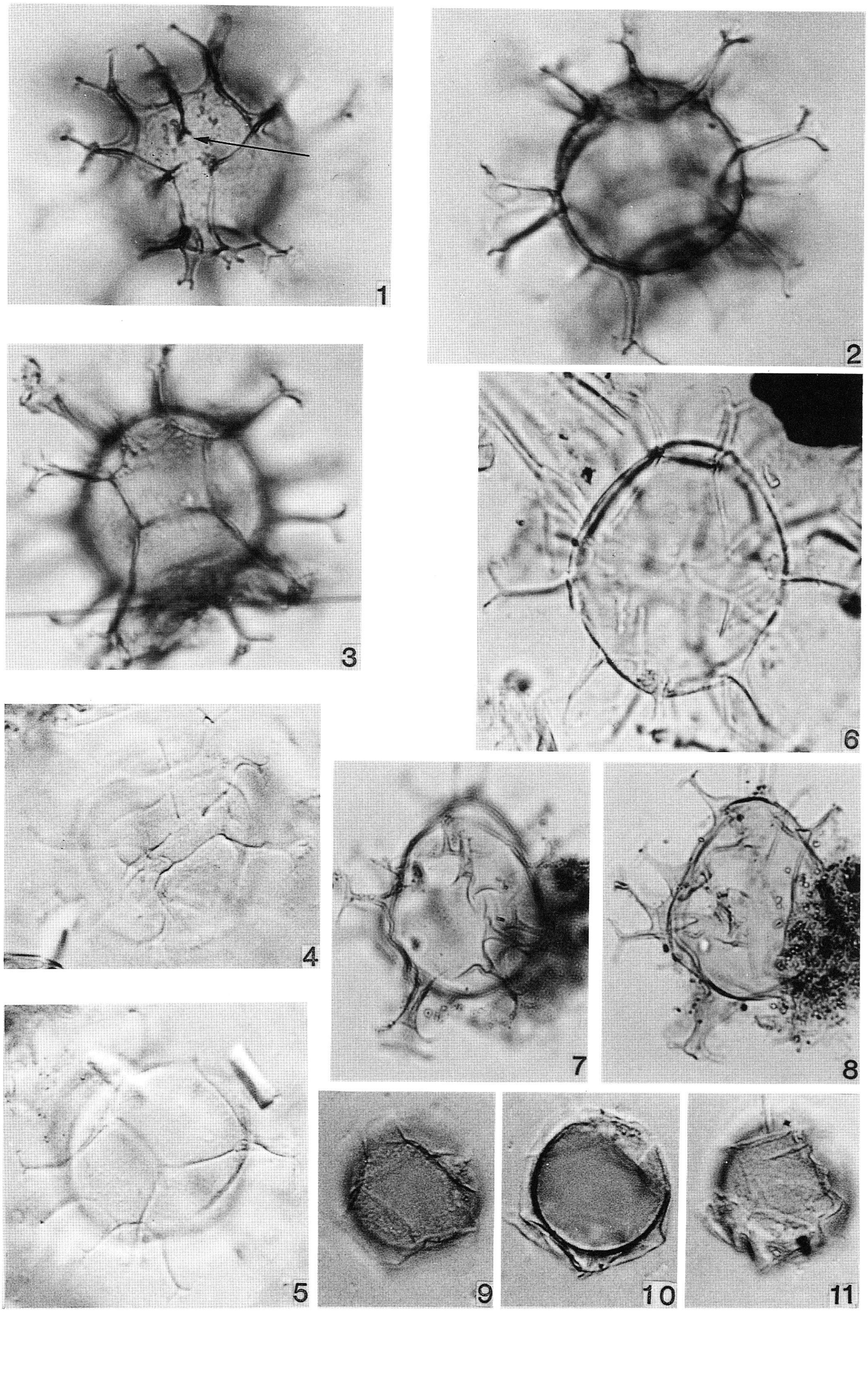

Plate 4

Figs. 1–12. *Operculodinium centrocarpum* (Deflandre and Cookson) Wall 1967.

1 : Dorsal surface showing a precingular archeopyle, 2 : Optical cross section (1–2 ; × 860, same specimen, Slide AK4–1, 95.2/42.2). 3 : Showing a granulate surface of the periphragm, 4 : Optical cross section showing capitate distal extremities of processes (3–4 ; × 710, same specimen, Slide SR8–2, 4.7/129.3).

5 : Lateral view showing a precingular archeopyle (× 710, Slide SR17–7, 12.4/136.0).

6 : Optical cross section showing a free operculum within a cyst body, 7 : Optical surface (6–7 : × 860, same specimen, Slide AK2–1, 96.5/35.5). 8 : Oblique lateral view, 9 : Optical cross section of lateral view (8–9 : × 710, same specimen, Slide SR8–3, 5.9/131.1). 10 : Showing a free operculum (arrow) within a cyst cavity, 11 : Optical cross section of lateral view, 12 : Dorsal surface, showing a precingular archeopyle (10–12 : × 860, same specimen Slide AK4–1, 84.3/34.7).

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PLATE 4

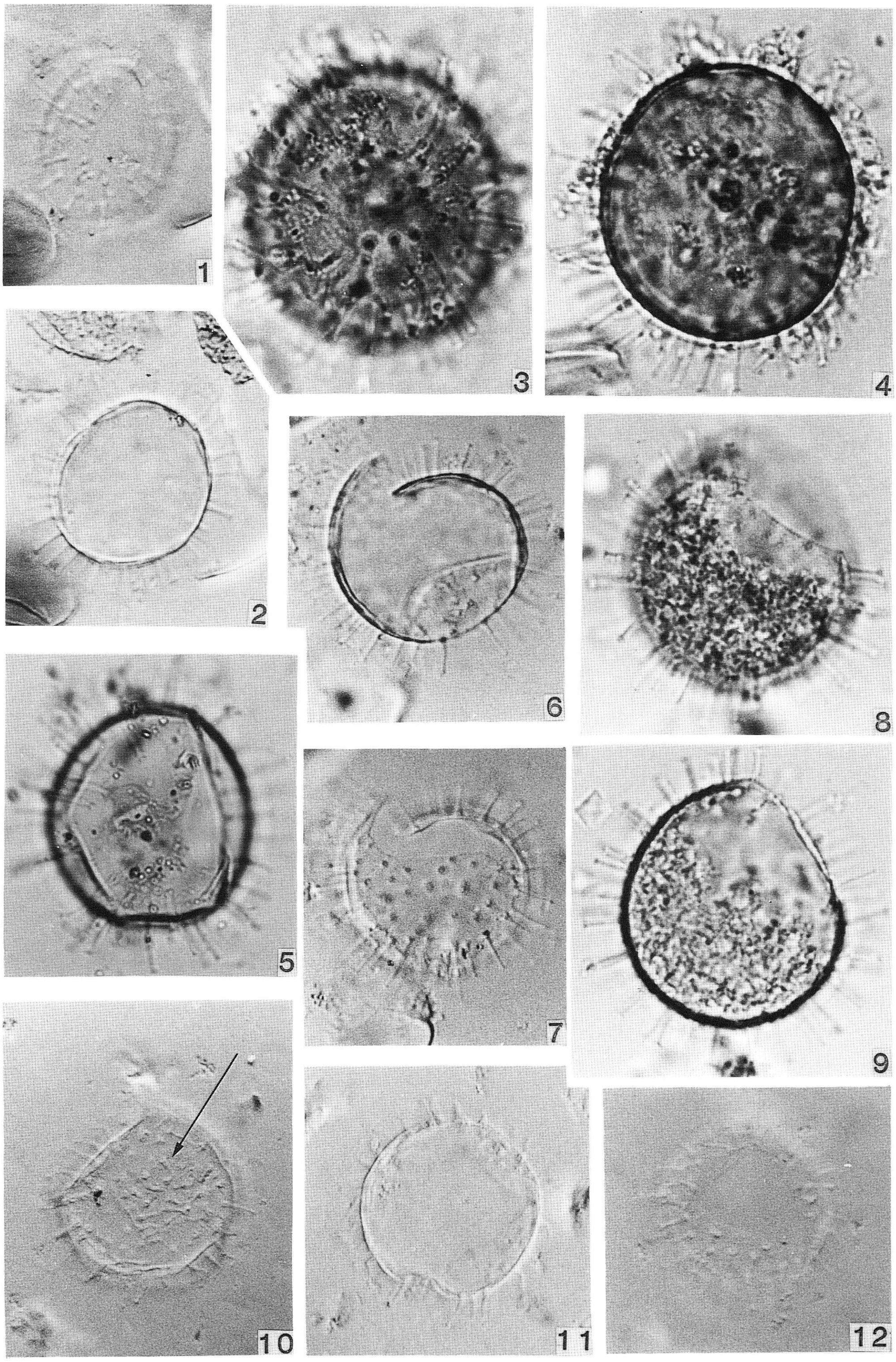

Plate 5

Figs. 1–2. *Brigantedinium grande* sp. nov.

Oblique apical surface, showing a large hexagonal (lati-thetaform) intercalary archeopyle (1–2 : × 710, same specime, Holotype, Slide SR8–2, 15.8/143.0).

Figs. 3–9. *Brigantedinium cariacoense* (Wall) Reid 1977.

3, 4 : Oblique apical surface, showing a hexagonal (lati-thetaform) intercalary archeopyle (3–4 : × 860, same specimen, Slide AK2–1, 91.4/25.7). 5 : Apical surface showing a hexagonal (lati-thetaform) intercalary archeopyle, 6 : Optical cross section of apical-antapical view (5–6 : × 710, same specimen, Slide SR8–2, 11.0/135.6). 7 : Apical surface showing an intercalary archeopyle (× 710, Slide SR8–2, 12.5/141.0). 8 : Apical surface showing a hexagonal (lati-thetaform) intercalary archeopyle (× 710, Slide AK2–1, 14.0/146.1). 9 : Apical surface showing a hexagonal intercalary archeopyle (× 710, Slide SR8–4, 20.2/14.4).

Figs. 10–12. *Brigantedinium asymmetricum* sp. nov.

10 : Optical cross section of apical-antapical view, showing a smooth surface of the autophragm, 11 : Oblique apical surface showing an irregularly hexagonal intercalary archeopyle and an adherent operculum (10–11 : × 860, same specimen, Holotype, Slide AK2–2, 100.4/14.4).

Figs. 13–16. *Brigantedinium irregulare* sp. nov.

13 : Optical cross section showing a smooth surface of the autophragm, 14 : Apical surface showing a hexagonal (lati-thetaform) archeopyle and an adherent operculum (13–14 : × 710, same specimen, Slide AK2–2, 18.7/134.5). 15 : Optical cross section, 16 : Apical surface showing a hexagonal archeopyle and an adherent operculum (15–16 : × 860, Holotype, Slide AK2–2, 85.5/31.7).

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PLATE 5

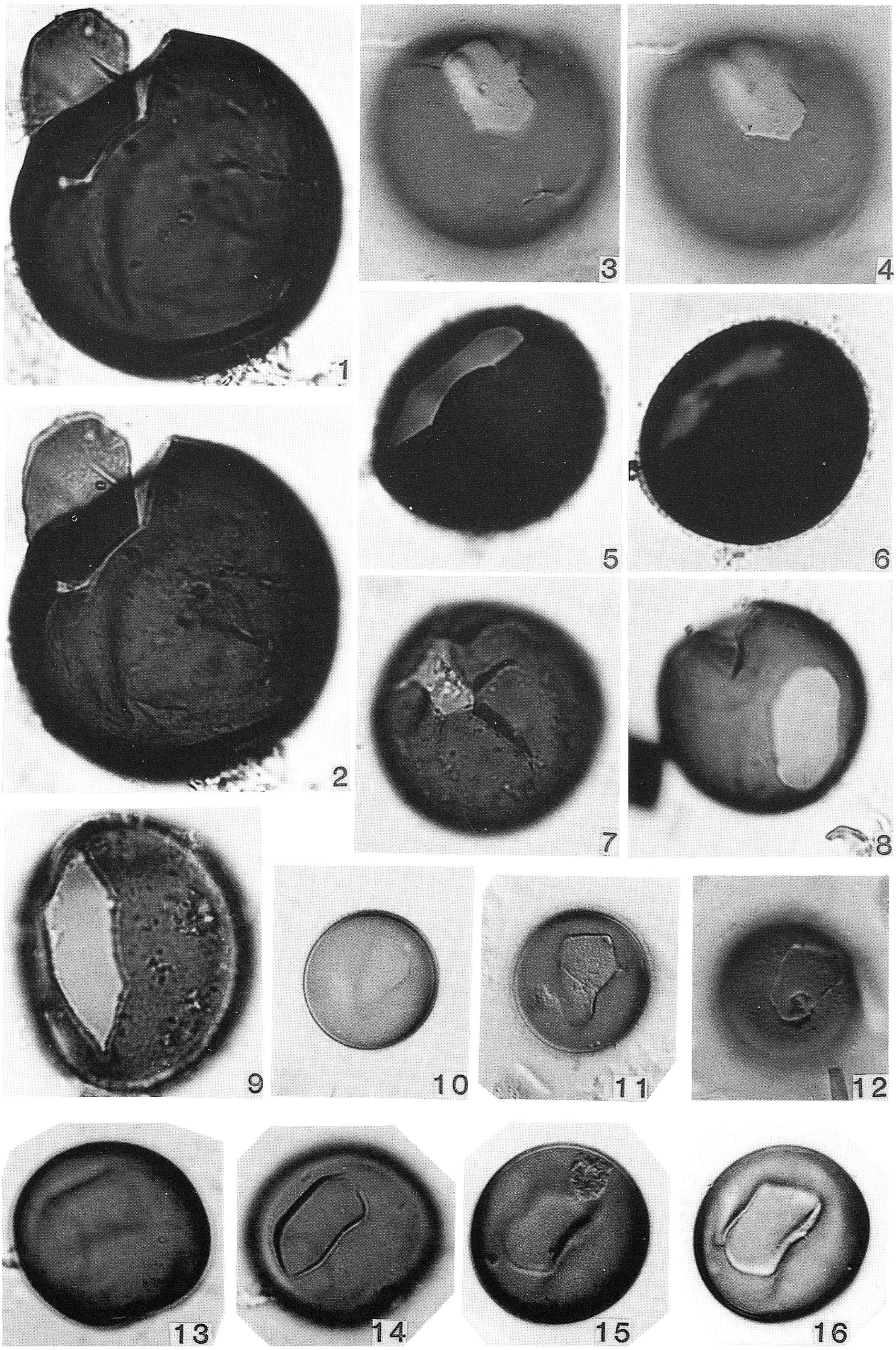

Plate 6

Figs. 1–14. *Brigantedinium simplex* (Wall) Reid 1977.

[Cyst of *Protoperidinium conidoides* (Wall) Balech 1974]

1 : Optical cross section, showing a psilate surface of the autophragm, 2 : Dorsal surface, showing a hexagonal (lati-deltaform) intercalary archeopyle (1–2 : × 710, same specimen, Slide SR8–2, 6.3/131.1). 3 : Ventral surface, showing two traces of flagellar pores (arrow), and slightly granular surface of the autophragm, 4 : Dorsal surface, showing a hexagonal intercalary archeopyle and an adherent operculum (5–6 : × 860, same specimen, Slide AK4–2, 97.3/29.5). 7 : Optical cross section, showing a contracted protoplasm (arrow), 8 : Dorsal surface showing a hexagonal intercalary archeopyle and an adherent operculum (7–8 : × 860, same specimen, Slide AK2–1, 96.1/27.3). 9 : Optical cross section, 10 : Dorsal surface, showing a hexagonal intercalary archeopyle (9–10 : × 760, same specimen, Slide AK2–3, 15.0/142.0). 11 : Dorsal surface, showing a granular surface of the autophragm, intercalary archeopyle, and an adherent operculum (× 710, Slide SR8–3, 16.0/129.0). 12 : Dorsal surface, showing a hexagonal intercalary archeopyle (× 710, Slide AK2–1, 98.1/24.3). 13 : Oblique dorsal surface, showing a hexagonal intercalary archeopyle (× 710, Slide SR16–1, 10.4/145.5). 14 : Dorsal surface, showing a hexagonal intercalary archeopyle and a wrinkled autophragm (× 860, Slide AK2–3, 15.3/132.0).

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PLATE 6

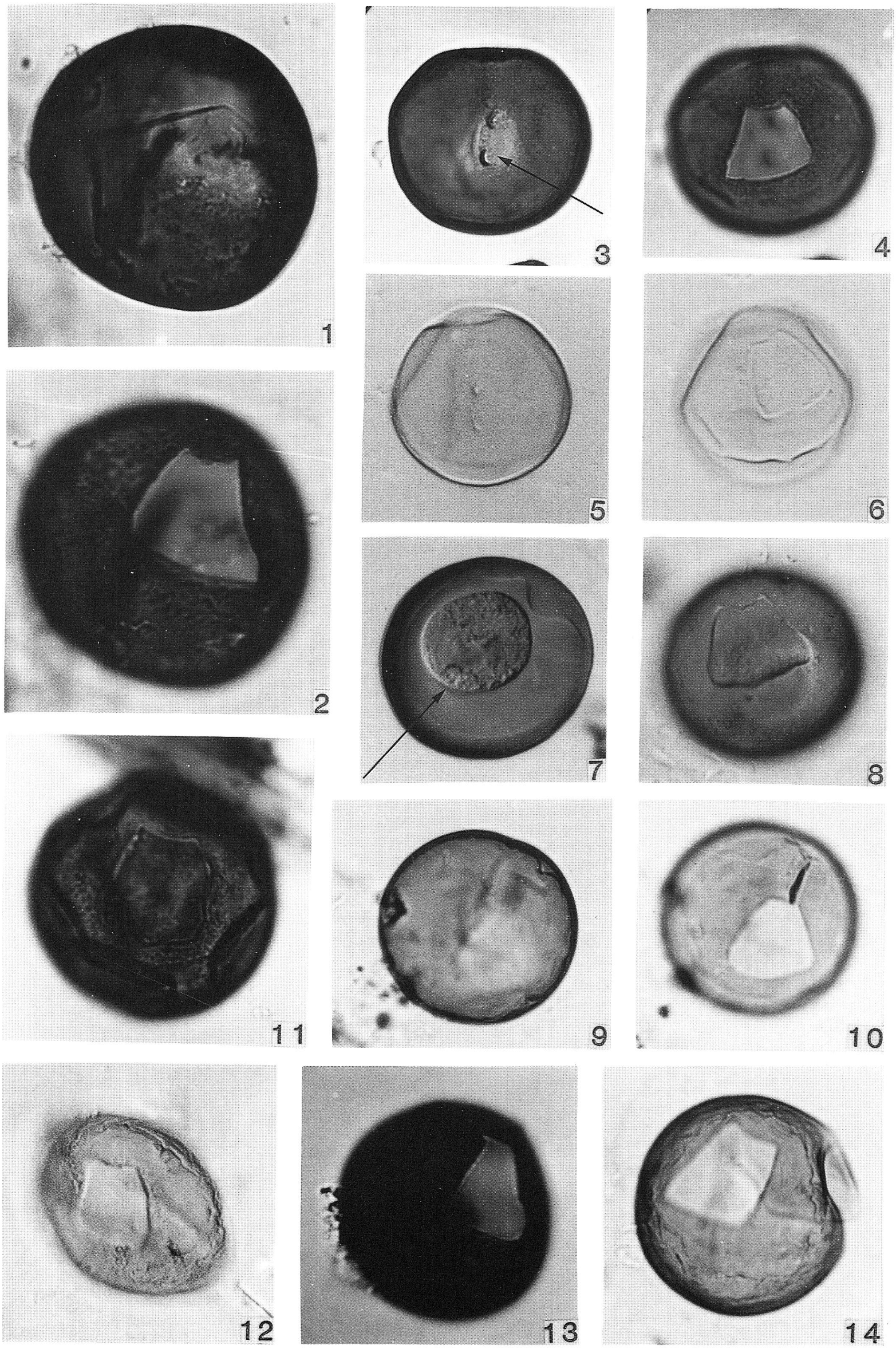

Plate 7

Figs. 1–6. *Votadinium carvum* Reid 1977.

[Cordate cyst of *Protoperidinium oblongum* (Aurivillius) Balech 1974]

1 : Dorsal surface, showing an enlarged intercalary archeopyle, 2 : Ventral surface, showing a parasulcus indicated by shallow indentation of the autophragm (1–2 : ×860, same specimen, Slide AK4–1, 89.5/29.0). 3 : Ventral surface, showing a smooth surface of the autophragm, 4 : Dorsal surface, showing an enlarged intercalary archeopyle (3–4 : ×860, same specimen, Slide AK2–2, 98.8/30.0). 5 : Optical cross section of dorso-ventral view, 6 : Ventral surface, (5–6 : ×860, same specimen, Slide AK2–1, 94.0/27.4). 7 : Ventral surface showing the folding at the apex, probably apical paraplate area (arrow), 8 : Optical cross section, showing an enlarged intercalary archeopyle (7–8 : ×710, same specimen, Slide AK2–1, 12.0/145.5).

Figs. 9–10. *Lejeunecysta concreta* (Reid) comb. nov.

[Cyst of *Protoperidinium leonis* (Pavillard) Balech 1974]

9 : Oblique dorsal surface, showing a paracingulum and two antapical projections (arrows), 10 : Optical cross section, showing an intercalary archeopyle (9–10 : ×710, same specimen, Slide AK2–3, 6.7/136.4).

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PLATE 7

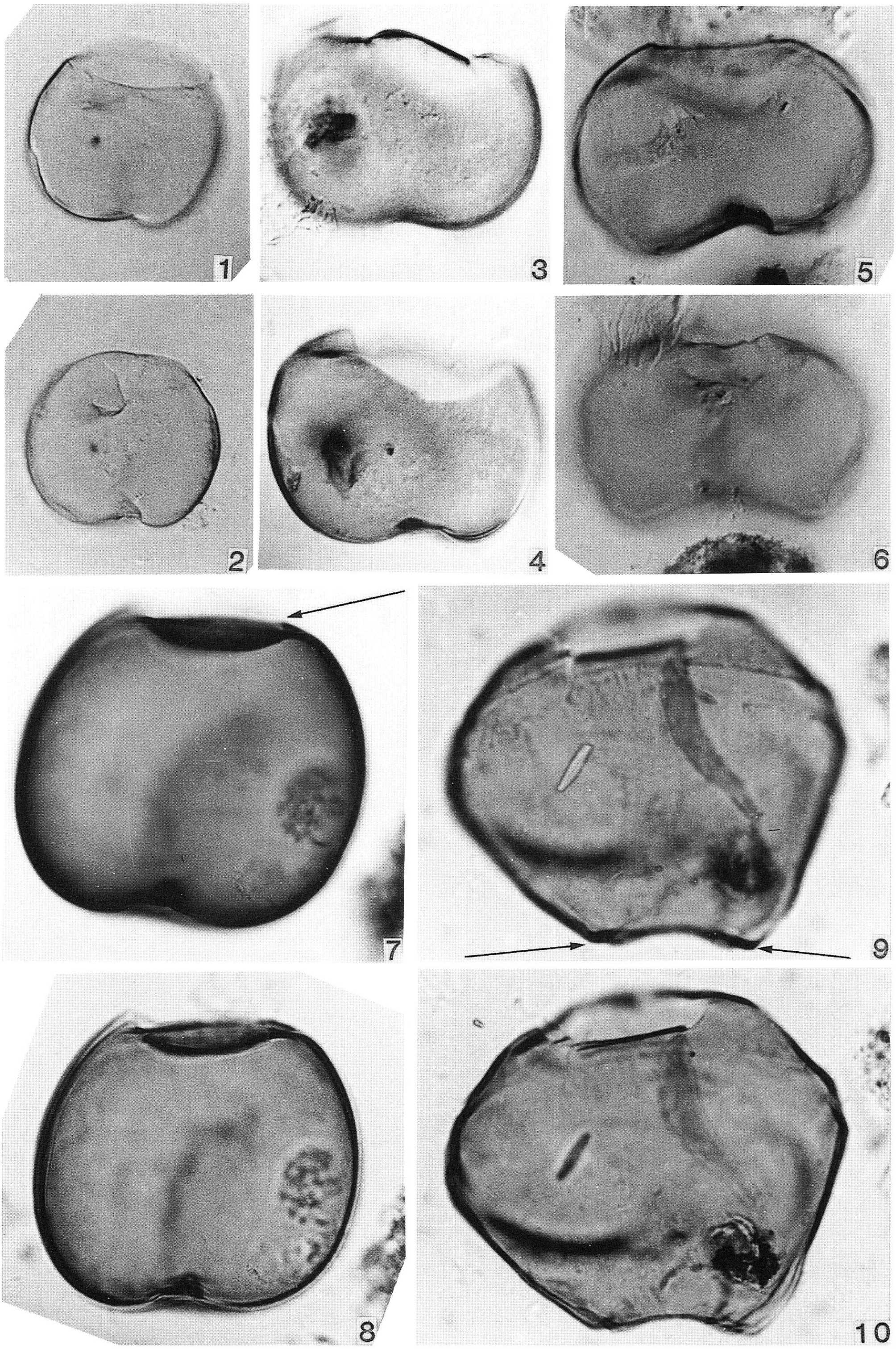

Plate 8

Figs. 1–3. *Votadinium* sp. cf. *V. carvum* Reid 1977.

1 : Ventral surface showing a parasulcus and trace of flagellar pore, 2 : Optical cross section in dorso-ventral view, 3 : Dorsal surface, showing an enlarged intercalary archeopyle (1–3 : × 710, same specimen, Slide AK2–1, 18.0/140.0).

Figs. 4–6. *Lejeunecysta* sp. cf. *L. concreta* (Reid) comb. nov.

4 : Oblique dorsal surface, showing two antapical projections (arrows), 5 : Oblique ventral surface, 6 : Oblique ventral surface, showing the parasulcus (arrow) (4–6 : × 710, same specimen, Slide AK4–1, 94.7/32.0).

Figs. 7–9. *Lejeunecysta concreta* (Reid) comb. nov.

[Cyst of *Protoperidinium leonis* (Pavillard) Balech 1974]

7 : Oblique lateral view showing two antapical projections (arrows), 8 : Lateral view showing the paracingulum and a slightly wrinkled autophragm above the paracingulum, 9 : Optical cross section of lateral view, showing an apical part and an intercalary archeopyle (arrow) (7–9 : × 710, same specimen, Slide AK2–1, 19.7/143.0).

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PLATE 8

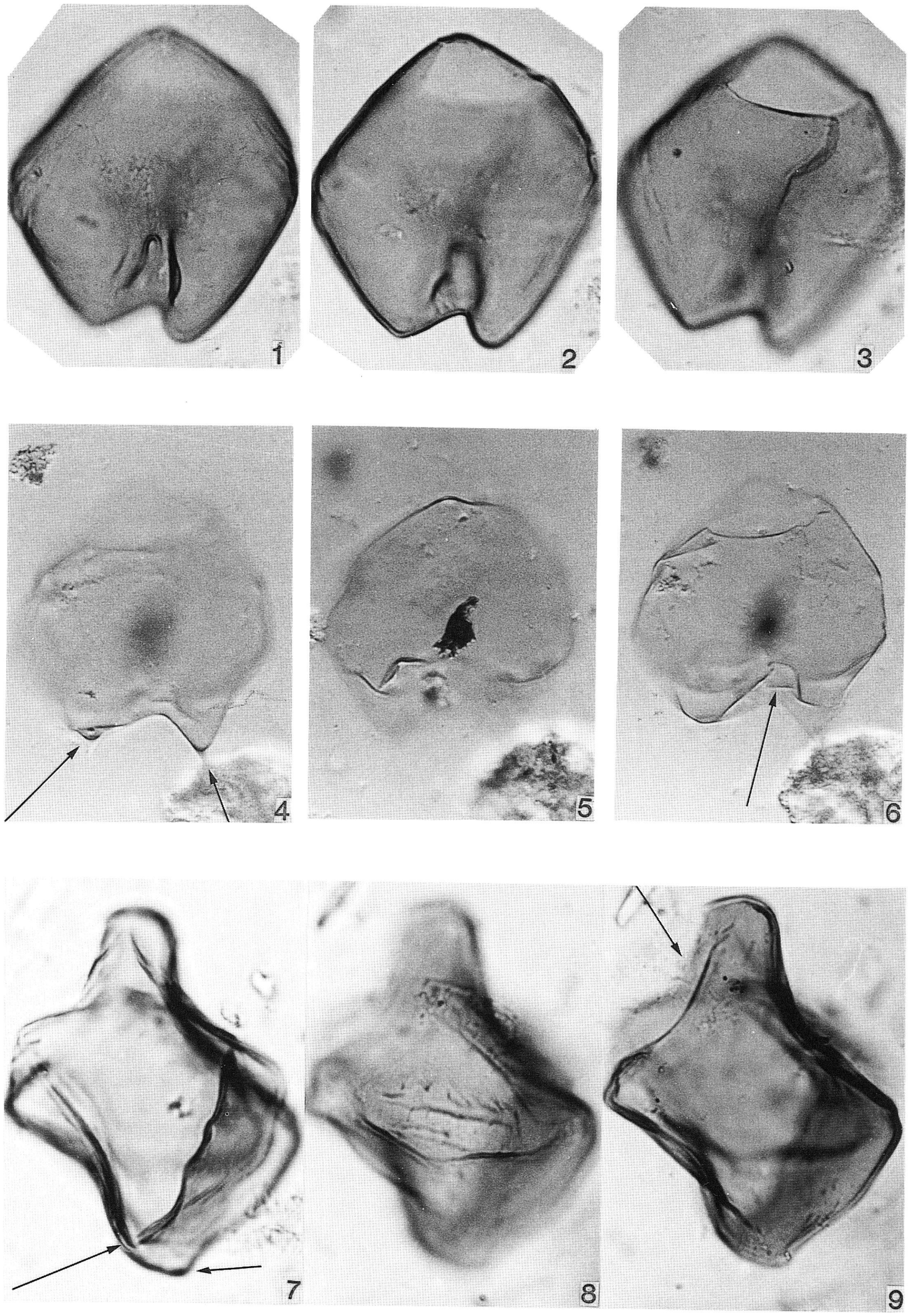

Plate 9

Figs. 1–4. *Lejeunecysta concreta* (Reid) comb. nov.

[Cyst of *Protoperidinium leonis* (Pavillard) Balech 1974]

1 : Optical cross section of dorso-ventral view, 2 : Dorsal surface showing a hexagonal (lati-deltaform) intercalary archeopyle (1–2 : ×860, same specimen, Slide AK2–1, 97.0/35.0). 3 : Ventral surface of hypocyst, showing a parasulcus, 4 : Dorsal surface of epicyst, showing a hexagonal (lati-deltaform) intercalary archeopyle (3–4 : ×860, same specimen, Slide AK2–2, 100.4/31.4).

Figs. 5–6. *Lejeunecysta? epidoma* sp. nov.

5 : Near optical cross section of dorso-ventral view, showing a smooth autophragm, 6 : Dorsal surface, showing a hexagonal (probably lati-deltaform) intercalary archeopyle, and wrinkled paracingulum (arrow) (5–6 : ×710, same specimen, Holotype, Slide AK2–1, 15.2/131.7).

Figs. 7–8. *Lejeunecysta psuchra* sp. nov.

7 : Nearly optical cross section of dorso-ventral view, 8 : Ventral surface showing the parasulcus (arrow) (7–8 : ×860, same specimen, Holotype, Slide AK2–2, 87.6/37.0).

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PLATE 9

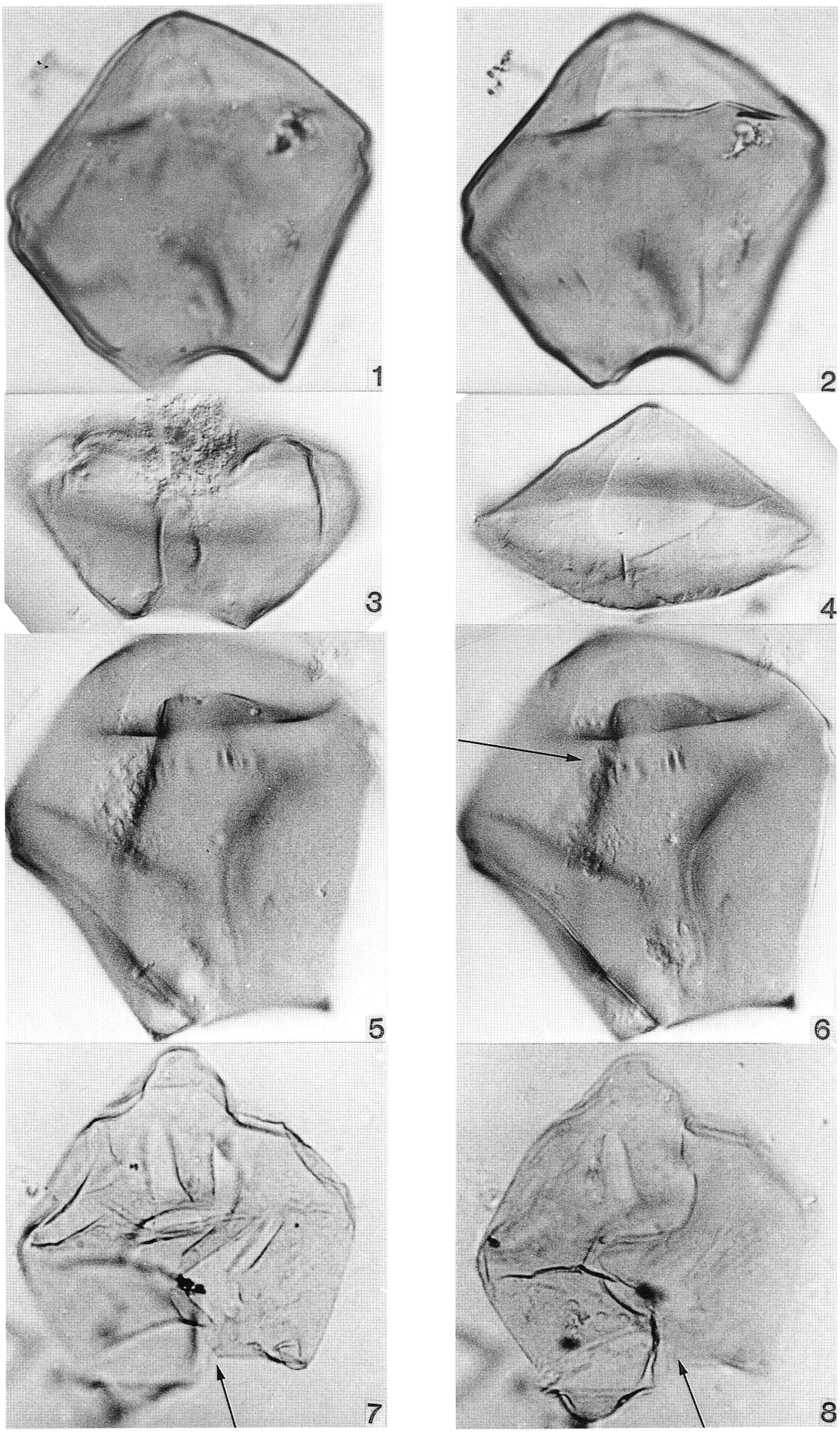

Plate 10

Figs. 1–9. *Selenopemphix nephroides* Benedek 1972.

[Cyst of *Protoperidinium* sp.]

1 : Near optical cross section of polar view, showing a roundly hexagonal (lati-delta-form) intercalary archeopyle which is asymmetrically located at the mid-dorsal line, and wrinkled paracingular lists. 2 : Apical surface showing an apical projection (arrow), 3 : Antapical surface of antapical view, showing a broad antapical projection (arrow) and striations on the hypocyst (1–3 : ×860, same specimen, Slide AK2–3, 89.3/46.0). 4 : Apical surface of apical view, showing a hexagonal intercalary archeopyle and well-developed paracingular lists. 5 : Antapical surface of antapical view, showing a broad antapical horn (4–5 : ×710, same specimen, Slide AK2–1, 8.7/144.4). 6 : Near optical cross section of polar view, showing an intercalary archeopyle and two traces of flagellar pores (arrow) (×860, Slide AK2–1, 98.7/33.5). 7 : Oblique dorsal surface of epicyst, showing an intercalary archeopyle, 8 : Oblique ventral surface of epicyst, showing an apical projection, 9 : Oblique dorsal surface of hypocyst, showing a broad antapical horn (arrow) (7–9 : ×860, same specimen, Slide AK2–1, 95.6/33.2).

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PLATE 10

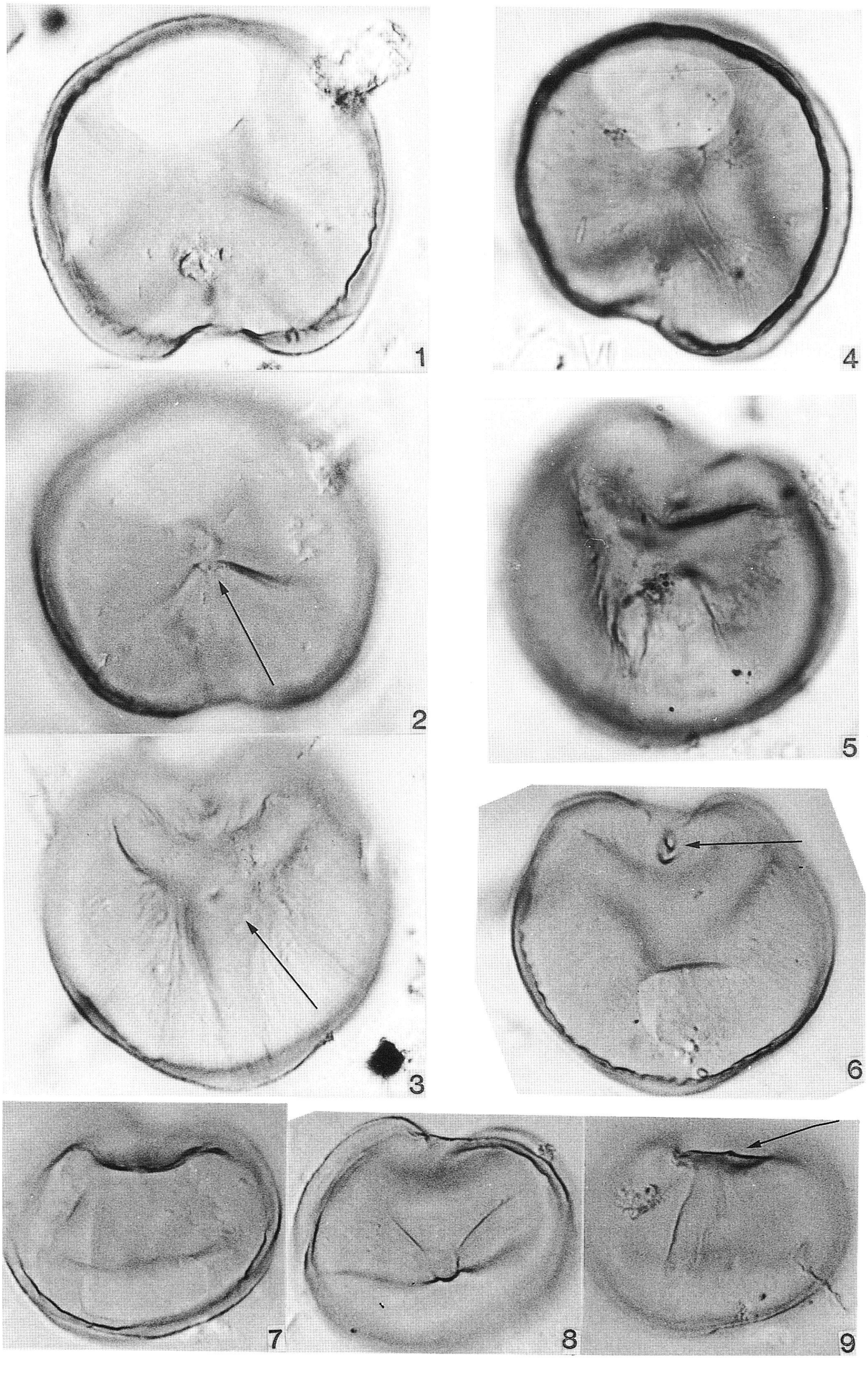

Plate 11

Figs. 1–5. *Selenopemphix quanta* (Bradford) Matsuoka 1985.

[Cyst of *Protoperidinium conicum* (Gran) Balech 1974]

1 : Near optical cross section of polar view, showing an intercalary archeopyle which is asymmetrically located at the mid-dorsal line, 2 : Apical surface, 3 : Antapical surface (1–3 : ×710, same specimen, Slide SR8–3, 20.2/142.0). 4 : Optical cross section of polar view, showing well-developed spines on the paracingular lists. 5 : Dorsal surface of hypocyst, showing parasutural features probably between the post-cingular and antapical regions, and antapical horn (arrow) (4–5 : ×860, same specimen, Slide AK2–1, 89.5/47.2).

Figs. 6–7. *Brigantedinium* sp. cf. *B. majusculum* Reid 1974.

[Cyst of *Protoperidinium* sp.]

6 : Optical cross section, 7 : Probably dorsal surface showing a hexagonal (lati-delta-form) free operculum corresponding to the 2a paraplate (arrow) (6–7 : ×710, same specimen Slide SR8–2, 19.1/140.6).

Figs. 8–9. *Selenopemphix nephroides* Benedek 1972.

[Cyst of *Protoperidinium* sp.]

8 : Lateral surface of the epicyst, showing an intercalary archeopyle and paracingulum (arrows), 9 : Lateral surface of the hypocyst, showing a broad antapical projection and parasulcus (arrow) (8–9 : ×710, same specimen, Slide SR8–3, 20.8/125.5).

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PLATE 11

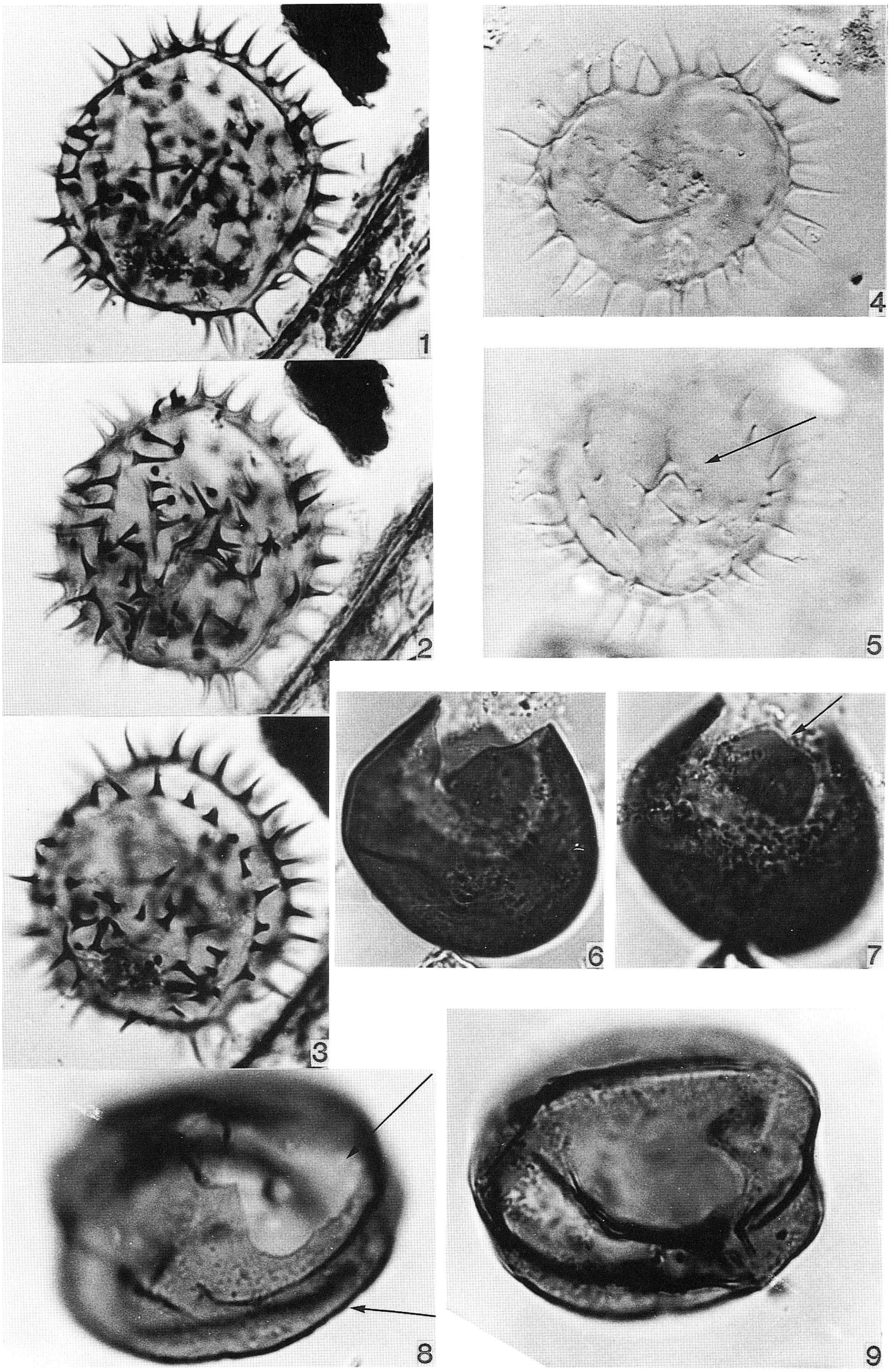

Plate 12

Figs. 1–6. *Trinovantedinium capitatum* Reid 1977.

[Cyst of *Protoperidinium pentagonum* (Gran) Balech 1974]

1 : Oblique ventral surface, showing spines with intratabular structure on the epicyst and paracingulum, 2 : Oblique dorsal surface showing well-developed right antapical horn (arrow), 3 : Oblique dorsal surface showing a hexagonal (lati-deltaform) intercalary archeopyle (arrow) (1–3 : ×860, same specimen Slide AK4–1, 92.5/40.7). 4 : Oblique ventral surface showing a shallow parasulcus and a trace of flagellar pore (arrow), 5 : Oblique ventral surface of the epicyst, showing spines with intratabular structure, 6 : Oblique dorsal surface of the hypocyst, showing two antapical horns (arrows) (4–6 : ×860, same specimen, Slide AK4–1, 84.6/34.6).

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PLATE 12

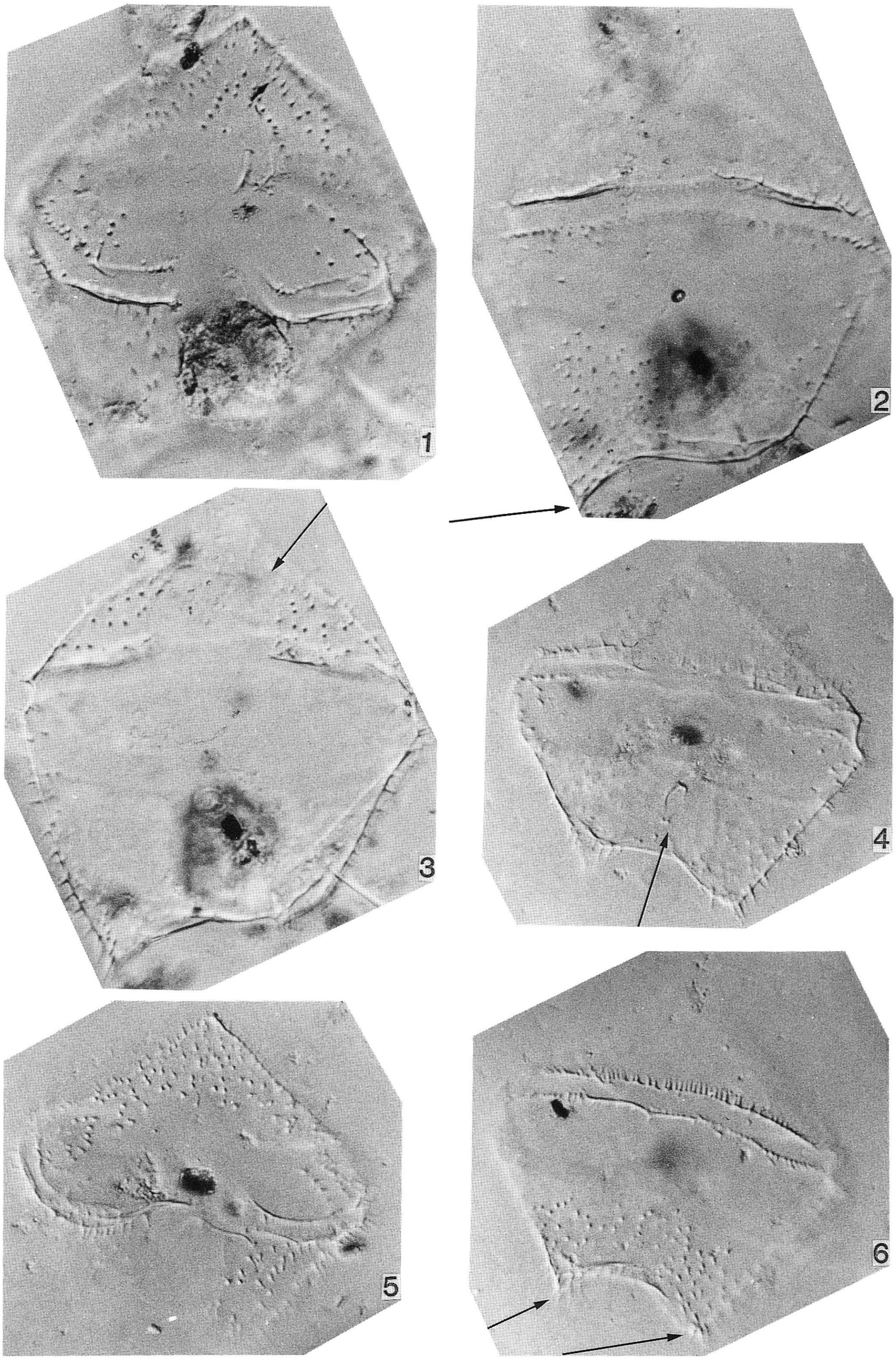

Plate 13

Figs. 1–9. *Trinovantedinium pallidifulvum* sp. nov.

[Cyst of *Protoperidinium* sp.]

1 : Ventral surface showing two traces of flagellar pores (arrow), 2 : Optical cross section, 3 : Dorsal surface showing a hexagonal (steno-deltaform) intercalary archeopyle and intratabular distribution of spines (1–3 : ×860, same specimen, Holotype, Slide AK2–2, 87.4/27.6). 4 : Ventral surface, 5 : Optical cross section, showing the 3″′ paraplate with intratabular short spines (arrow), 6 : Dorsal surface showing a hexagonal (steno-deltaform) intercalary archeopyle (arrow) (4–6 : ×710, same specimen, Slide AK2–2, 8.5/147.0). 7 : Ventral surface, showing a shallow and wide parasulcus (arrow), 8 : Dorsal surface, showing a paracingulum, 9 : Near optical cross section showing an intercalary archeopyle (arrow) (7–9 : ×860, same specimen, Slide AK2–2, 95.1/42.2).

Figs. 10–11. *Dubridinium cavatum* Reid 1977.

10 : Lateral surface of hypocyst, showing a smooth surface of the periphragm, 11 : Lateral surface of epicyst, showing a probably theropylic epicystal archeopyle (arrow) (10–11 : ×710, same specimen, Slide SR8–3, 6.8/126.6).

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PLATE 13

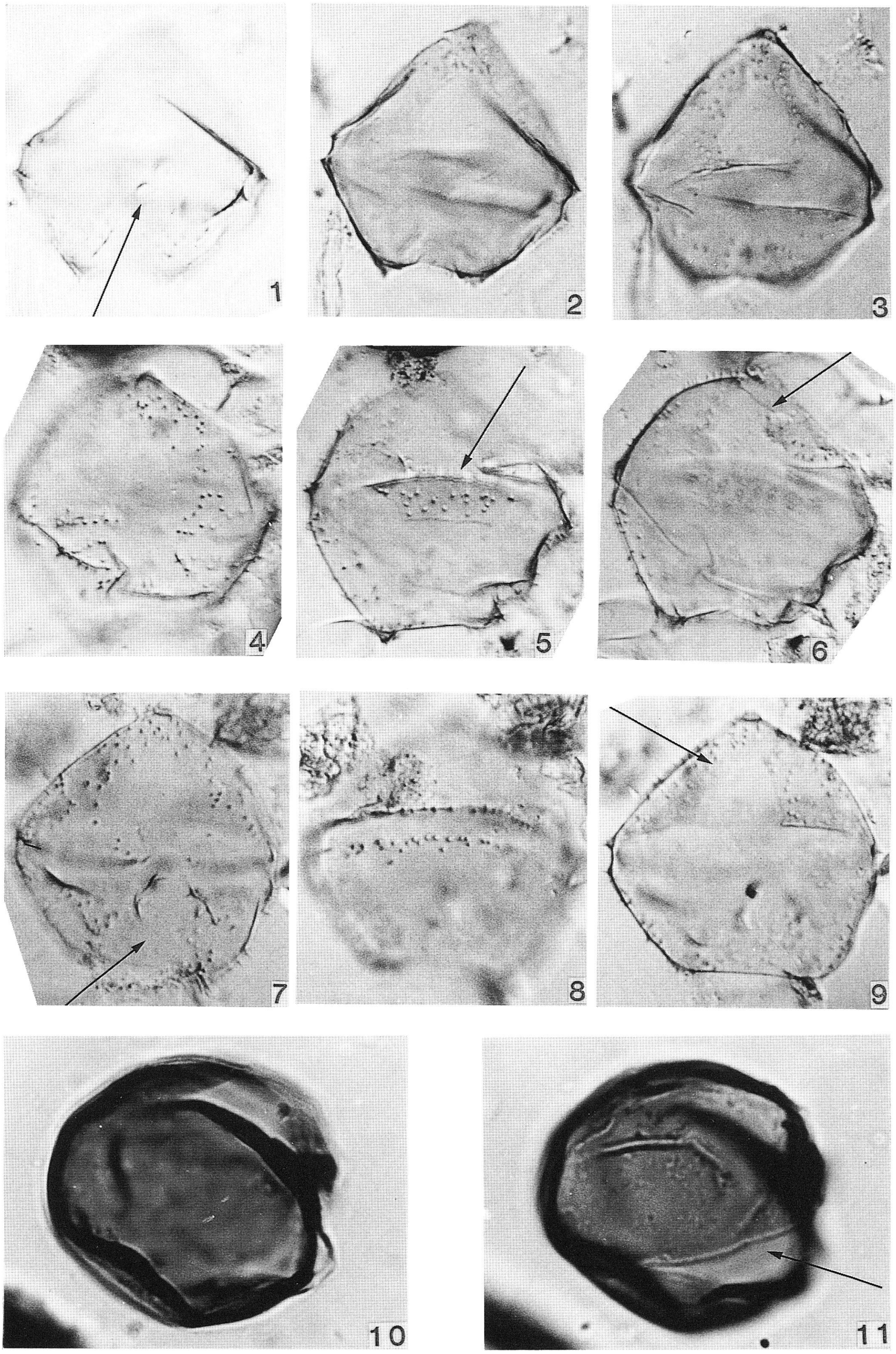

Plate 14

Figs. 1–5. *Votadinium spinosum* Reid 1977.

[Cyst of *Protoperidinium claudicans* (Paulsen) Balech 1974]

1 : Ventral surface, showing well-developed hypocyst, 2 : Optical cross section of dorso-ventral view, 3 : Dorsal surface, showing nontabular processes (1–3 : ×710, same specimen, Slide SR16–1, 5.0/130.5). 4 : Optical cross section, showing a peridinioid shape, 5 : Ventral surface (4–5 : ×710, same specimen, Slide SK2–2, 15.0/135.4).

Figs. 6–7. *Brigantedinium* sp. cf. *B. auranteum* Reid 1977.

[Cyst of *Protoperidinium* sp.]

6 : Ventral surface, showing two traces of flagellar pores, 7 : Dorsal surface showing a probably hexagonal (lati-deltaform) intercalary archeopyle and slightly granular autophragm (6–7 : ×860, same specimen, Slide AK4–2, 87.8/29.0).

Figs. 8–9. Dinoflagellate cyst ? type E.

8 : Optical cross section showing slender, flexous and aculiate processes. 9 : Surface of the cyst, showing granular structure (×860, Slide SK2–1, 93.6/27.1).

Fig. 10. *Brigantedinium* sp. indet., optical cross section (×860, Slide AK2–1, 90.8/27.0).

Figs. 11–12. *Lejeunecysta psuchra* sp. nov. (×860, Slide AK2–1, 100.2/45.5).

Figs. 13–14. Dinoflagellate cyst type A.

13 : Showing a membranous periphragm, 14 : Optical cross section (×860, Slide AK2–1, 93.6/27.1).

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PLATE 14

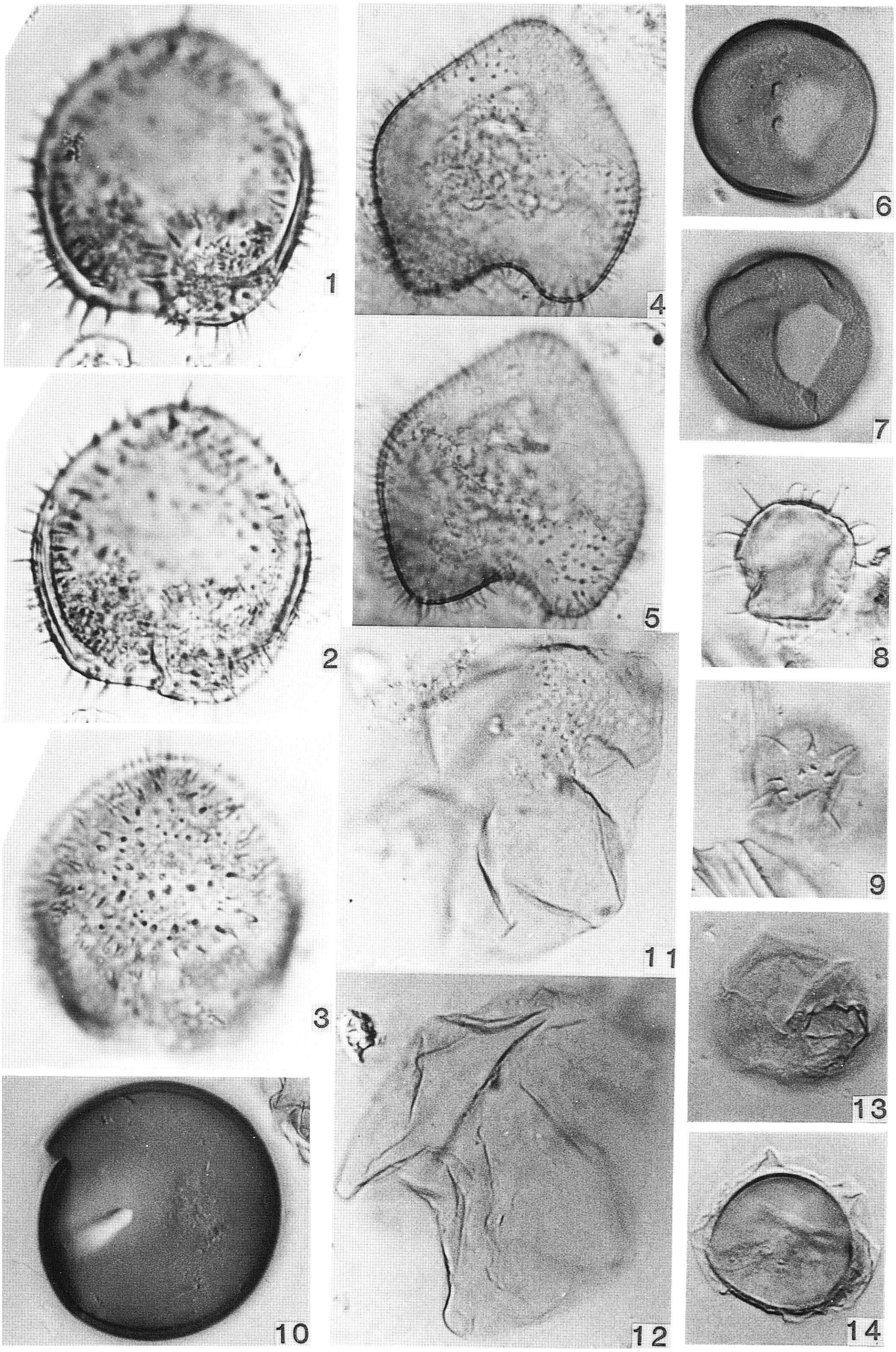

Plate 15

Figs. 1–10. *Polykrikos schwartzii* Bütschli 1873.

1 : Ventral surface, 2 : Optical cross section of dorso-ventral view, 3 : Dorsal surface (1–3 : × 704, same specimen, Slide SR8–1, 4.6/145.5). 4 : Optical cross section of dorso-ventral view, 5 : Dorsal surface? (4–5 : × 704, same specimen, Slide SR8–5, 11.6/141.6). 6 : Oblique apical surface, showing a tremic archeopyle with irregular margins (× 445, Slide SR8–3, 5.4/132.6). 7 : Lateral surface (× 445, Slide AK4–1, 86.9/29.1). 8 : Ventral surface, showing a ventral elongate network which probably indicates a parasulcus (arrow), 9 : Optical cross section of dorso-ventral view, 10 : Dorsal view (8–10 : × 445, same specimen, Slide AK2–1, 86.8/32.5).

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PLATE 15

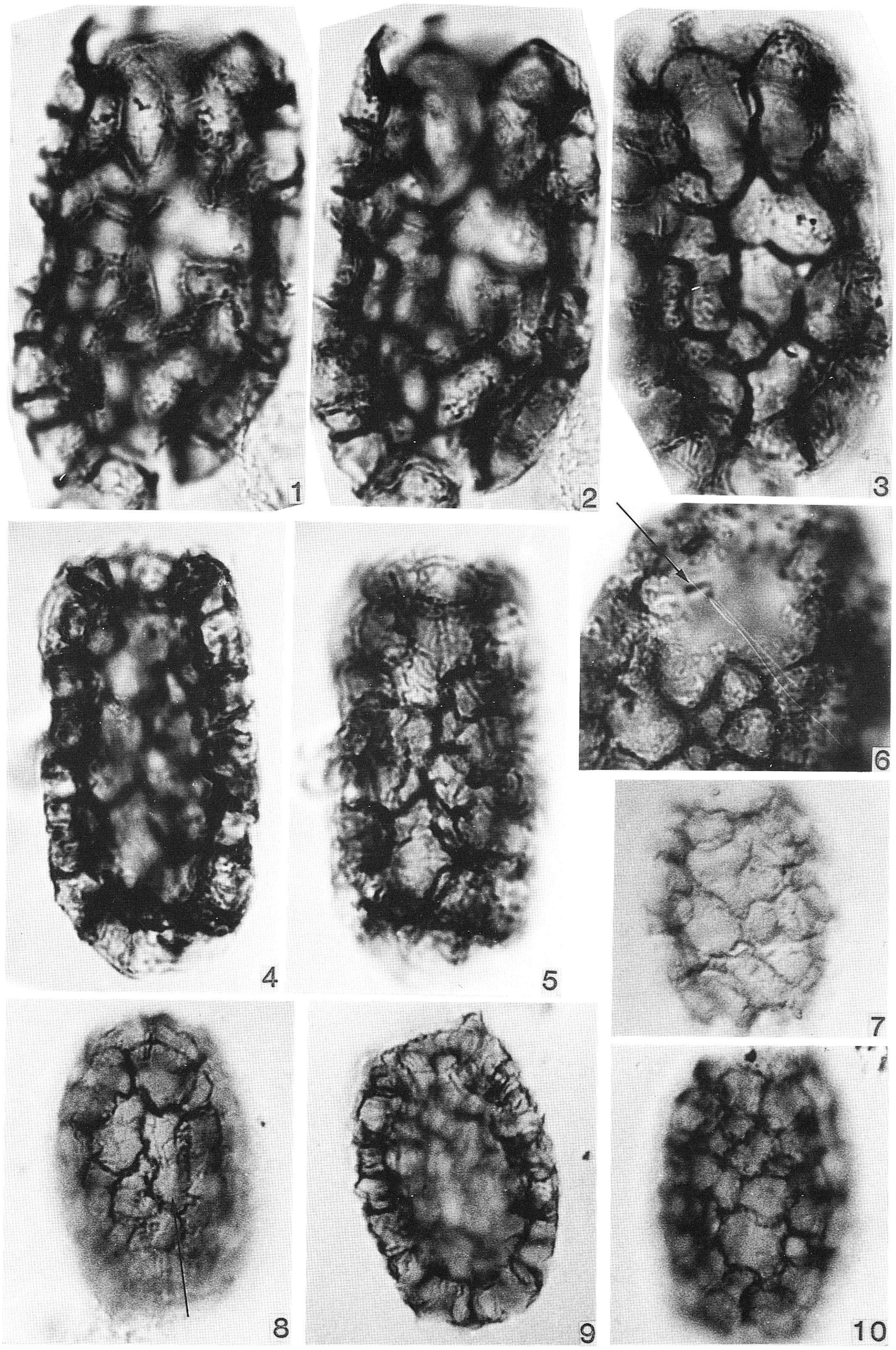

Plate 16

Figs. 1–9. *Polykrikos* sp. cf. *P. kofoidii* Chatton 1914.

1 : Probably ventral surface, showing smaller processes, 2 : Optical cross section of dorso-ventral view, 3 : Probably dorsal surface (1–3 : × 445, same specimen, Slide AK4–2, 96.4/37.8). 4 : Lateral view, 5 : Another lateral view, 6 : Optical cross section of lateral view (4–6 : × 345, same specimen, Slide SR8–2, 13.0/137.4). 7–9 : Different focuses on lateral surface (× 345, Slide SR8–2, 4.0/145.5).

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PLATE 16

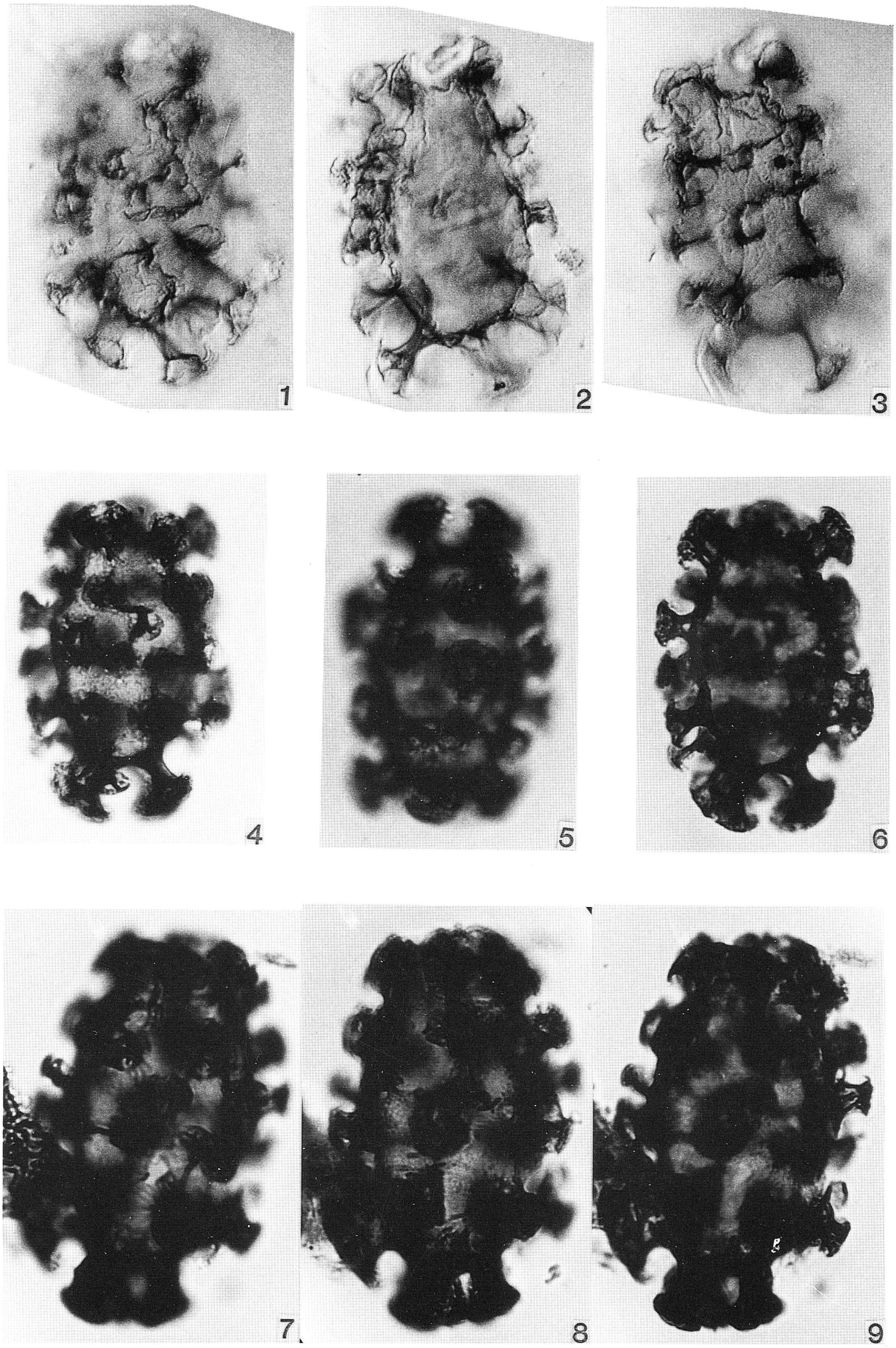

Plate 17

Figs. 1–15. Dinoflagellate cyst type A.

1 : Antapical surface, showing a granular endophragm, 2 : Optical cross section of polar view, showing a membranous periphragm, 3 : Apical surface, showing a combination (?) intercalary archeopyle probably corresponding to the 1a and 2a paraplates (arrow) (1–3 : × 710, same specimen, Slide SR8–4, 8.7/129.0). 4 : Antapical surface?, 5 : Optical cross section of polar view, 6 : Apical surface? (4–6 : × 710, same specimen, Slide SR8–4, 4.5/136.8). 7 : Antapical surface? 8 : Optical cross section of polar view, showing a thick endophragm (arrow), 9 : Apical surface? (7–9 : × 860, same specimen, Slide AK4–1, 99.1/32.2). 10 : Optical cross section, 11 : Surface of cyst, showing a thin periphragm irregularly wrinkled (10–11 : × 860, same specimen, Slide AK2–3, 98.7/35.2). 12 : Surface of cyst, 13 : Optical cross section (12–13 : same specimen, Slide AK2–3, 87.3/41.0). 14 : Apical surface?, showing an adherent operculum?? (arrow), 15 : Antapical surface? (14–15 : × 750, same specimen, Slide AK2w–2).

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PLATE 17

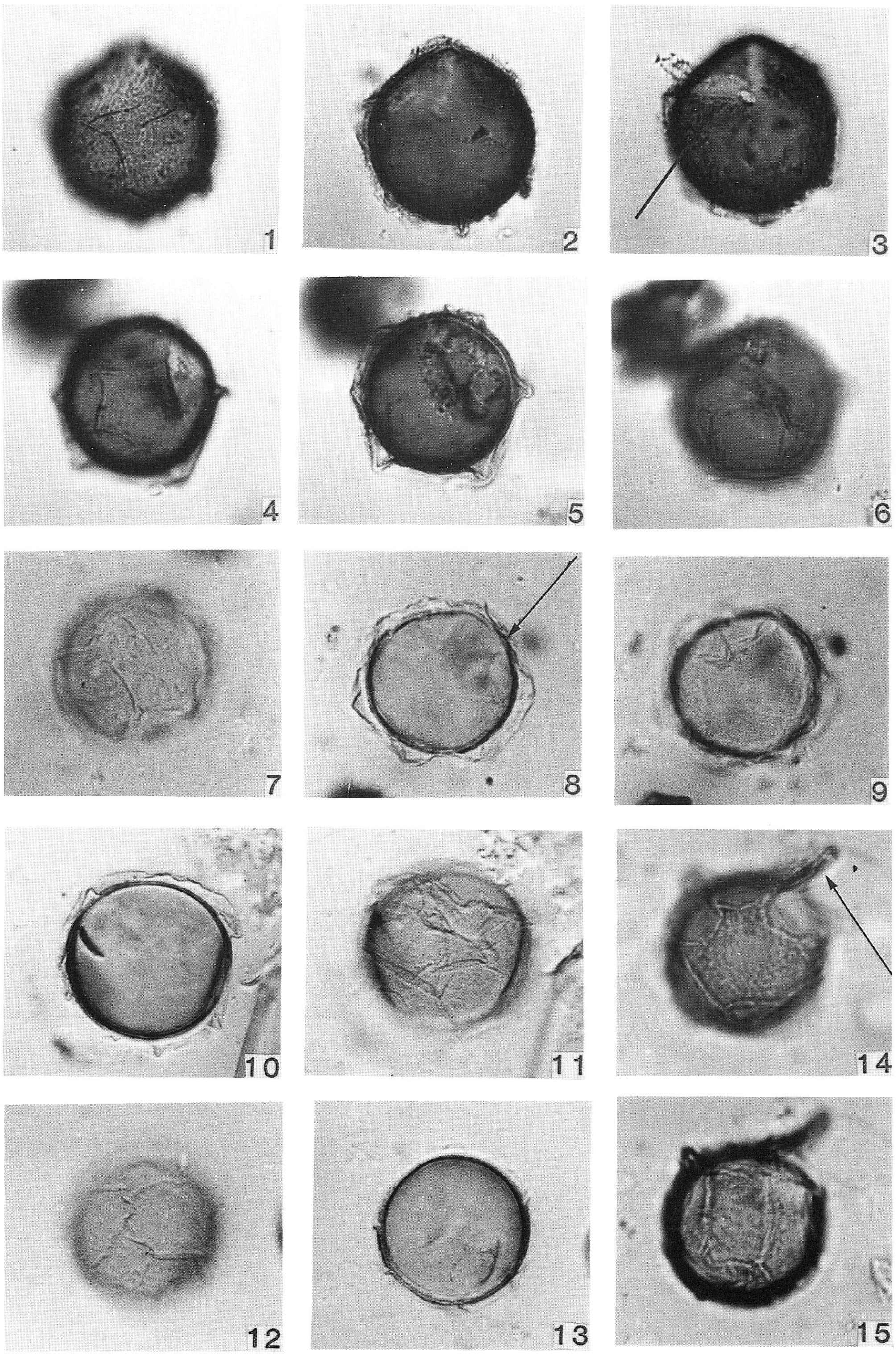

Plate 18

Figs. 1–2. *Tuberculodinium vancampoae* (Rossignol) Wall 1967.

[Cyst of *Pyrophacus steinii* (Schiller) Wall and Dale 1971]

1 : Optical cross section of apical-antapical view, 2 : Antapical surface, showing a hypocystal archeopyle (arrow) (1–2 : × 345, same specimen, Slide SR17–9, 18.8/142.4).

Figs. 3–11. Dinoflagellate cyst type B.

3 : Surface of cyst, 4 : Optical cross section, showing a thick endophragm (?) and acicular spines (3–4 : × 710, same specimen, Slide SR8–4, 20.3/138.5). 5 : Surface of cyst, showing a chasmic archeopyle (arrow), 6 : Surface of cyst showing acuminate and nontabular processes (5–6 : × 710, same specimen, Slide SR16–1, 20.3/132.0). 7 : Surface of cyst, showing a chasmic archeopyle (arrow), 8 : Another surface of the cyst (7–8 : × 710, same specimen, Slide SR8–3, 15.5/135.5). 9 : Surface of the cyst, showing a granular wall, 10 : Optical cross section (9–10 : × 710, same specimen, Slide SR8–4, 12.1/134.5). 11 : Surface of the cyst, showing a chasmic archeopyle (arrow) (× 860, Slide AK2–2, 86.7/40.4).

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PLATE 18

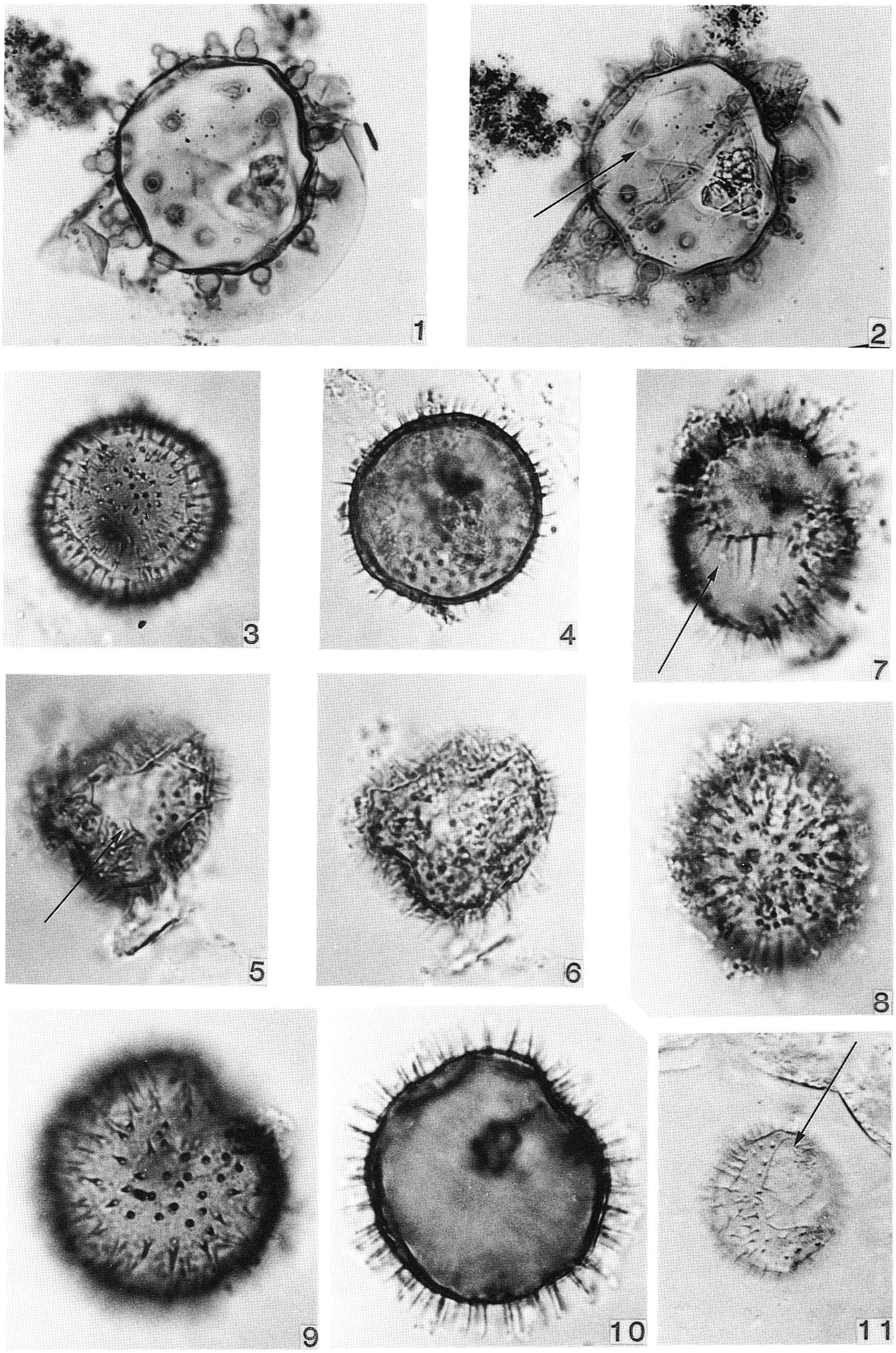

Plate 19

Figs. 1–2, 7–10. Dinoflagellate cyst type C.

1 : Surface of cyst, showing a granular wall, and nontabular and corynate processes, 2 : Optical cross section, showing corynate and slender processes (1–2 : × 710, same specimen, Slide SR16–1, 14.2/137.0). 7 : Optical cross section, showing nontabular and corynate processes, 8 : Surface of the cyst (7–8 : × 860, same specimen, Slide AK2–2, 89.0/41.0). 9 : Optical cross section, showing corynate processes, 10 : Surface of the cyst, showing a chasmic archeopyle (arrow) (9–10 : × 860, same specimen Slide AK2–1, 90.8/29.8).

Figs. 3–6, 11–12. Dinoflagellate cyst type D.

[Cyst probably attributable to the Diplopsaloideae]

3 : Oblique dorsal surface showing a theropylic epicystal (?) archeopyle (arrow), 4 : Oblique ventral surface, showing a granular autophragm and aculiate processes (3–4 : × 710, same specimen, Slide SR8–3, 15.7/126.0). 5 : Optical cross section showing theropylic epicystal archeopyle (arrow), 6 : Lateral surface, showing a probably ventral hinge and aculiate processes (5–6 : × 710, same specimen, Slide SR8–2, 15.0/128.0). 11 : Surface of the autophragm (?), 12 : Nearly optical cross section, showing nontabular aculiate processes (11–12 : × 860, same specimen, Slide AK4–2, 100.0/30.6).

Figs. 13–14. Dinoflagellate cyst type B.

13 : Surface of cyst, showing a smooth wall and nontabular processes. 14 : Optical cross section, showing a chasmic (?) archeopyle, and slender, acuminate and nontabular processes (13–14 : × 710, same specimen, Slide SR8–3, 20.8/125.5).

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PLATE 19