DINOFLAGELLATE CYSTS FROM RECENT MARINE SEDIMENTS OF THE SOUTH AND EAST CHINA SEAS

Qi Yu-zao¹, Hong Ying¹, Zheng Lei¹, David M. Kulis² and Donald M. Anderson²

- 1. Institute of Hydrobiology, Jinan University, Guangzhou, China
- 2. Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543 USA

Abstract

Sediment samples collected from forty-nine stations along the coasts of the South and East China Seas were processed to reveal living dinoflagellate resting cysts. This is the first survey of recent dinoflagellate cysts from this region. Based on morphological features of the cysts or of motile cells germinated from some specimens, twenty-two dinoflagellate species were identified; the identity of two cysts remain unknown. This survey shows that a diverse species assemblage exists in much of this area, especially in Dapeng and Daya Bays. Additional sampling and analysis is needed in the East China Sea region of this study, as the low abundance of cysts observed there may reflect sampling location selection and the small number of samples rather than absolute dinoflagellate cyst abundance. Virtually all of the cysts identified in this study could be found in Dapeng and Daya Bays, suggesting that they provide good conditions for the growth of dinoflagellates and retention of their cysts. This elevated cyst abundance is consistent with plankton surveys which show that phytoplankton biomass in general and dinoflagellate biomass in particular, are higher in Dapeng Bay than in other harbours and embayments along the coast of the South China Sea. These bays are also either connected to or are adjacent to Tolo Harbour in Hong Kong, which is well-known for the correlation of its red tide outbreaks with increased pollution. The high dinoflagellate cyst abundance and bloom frequency observed in the bays is probably linked to elevated nutrient loading. Cysts of two dinoflagellates capable of producing paralytic shellfish poisoning (PSP) toxins (Alexandrium tamarense and Gymnodinium catenatum) were detected in the cyst survey. G. catenatum was only found in Dapeng Bay, but A. tamarense was found in eight relatively contiguous locations from the mouth of the Pearl River through Guangdong and Fujian Provinces to Taizhou Bay in Zhejiang Province. This distribution is generally consistent with the region in which PSP events have been recorded in the South and East China Seas. This survey provides useful information on dinoflagellate species distribution along one section of the China Sea and accentuates the need for similar studies of other regions to the north.

Introduction

More than eighty-one marine and twenty freshwater species of living dinoflagellates are known to produce resting cysts or hypnozygotes (Matsuoka et al. 1989). Some of these resistant stages are produced during blooms and fall to the underlying sediments where they survive in a dormant, or quiescent, state until germination reintroduces the vegetative motile stage to the overlying waters. Wall (1971) and others (Dale

1983; Anderson 1984) have discussed the many roles that cysts play in dinoflagellate population dynamics. Cyst germination provides an inoculum for blooms, and cyst formation can subsequently remove substantial numbers of cells as a major factor in bloom decline (Anderson et al. 1984). Resting cysts also have important ecological roles with respect to species dispersal and survival through adverse conditions and since they result from sexual fusion of gametes (Pfiester and Anderson 1987), they represent a mechanism for

genetic recombination and evolutionary adaptation.

Knowledge of the distribution and abundance of cysts can be very useful in ecological and monitoring investigations. Numerous studies have documented the distribution (and sometimes the abundance) of cysts in sediments. Historically, such studies have been used to define the geographic range of a particular species (Anderson et al. 1982; Imai et al. 1991), to identify potential 'seedbeds' for bloom initiation (Tyler et al. 1982) and to study the dispersal of that organism from one region to another (Anderson et al. 1982; Tyler et al. 1982; Imai et al. 1991; Hallegraeff 1993). Other studies have been more general, documenting the occurrence of all cyst-producing species that occur within particular regions such as Woods Hole (Wall 1966), Bermuda and the Caribbean (Wall and Dale 1970), Japan (Matsuoka 1985b,c), New Zealand (Baldwin 1987), Spain (Blanco 1989a,b,c), Australia (Bolch and Hallegraeff 1990; McMinn 1990), Denmark (Ellegaard et al. 1994) and the North Sea (Nehring 1994). Since cysts accumulate in sediments through time, they provide an integrated record of the occurrence of a species in the plankton. These studies not only help to explain why certain species are observed in plankton samples from particular areas, but they often identify species that have not yet been observed in the water column. For example, a recent cyst survey by Ellegaard et al. (1994) revealed five species that had never been seen in plankton surveys of Danish waters. Here we present the first study of living dinoflagellate cysts in Chinese coastal waters.

Materials and methods

Between 1991–1993, samples were collected from forty-nine stations at fourteen locations in the South and East China Seas (Fig. 1, Table 1). Samples were collected from soft, depositional, locations rather than hard, sandy, areas that could be subject to erosion. A variety of sampling methods was used, depending on depth, accessibility and ongoing field programmes. At deeper, offshore, locations, box cores were taken and surface sediments removed for analysis. In

shallower waters, Van Veen or Peterson grab samplers were used, and only the top few centimetres of flocculent material and sediment were collected. At some stations, samples were obtained from sediment traps, or were scraped from the sediment surface of shallow, intertidal, locations. Samples were stored in the dark at 4 °C in tightly sealed containers to prevent germination.

Sediment processing generally followed the methods of Wall and Dale (1968). Subsamples (5-10 ml) were sonicated for 45 seconds using a Branson sonifier with a 1.3 cm disrupter horn at a setting of 3 amperes. The sonified sediment was size fractionated through Nitex screens to obtain a 20-100 µm size component. One millilitre aliquots of the processed sediment were observed in Sedgwick Rafter counting chambers under a compound microscope at a total magnification of 100x. Dinoflagellate cyst identification was based on morphological criteria; selected cysts were also isolated by micropipette and placed in separate wells of a 24 cluster tissue culture plate with each well containing 2 ml of f/2 medium (Guillard and Ryther 1962) or Erdschreiber (Starr 1964). The plates were sealed with tape to minimize evaporation while the cysts were incubated at 20°C at an irradiance of 150 $\mu Einst.$ $m^{-2} \cdot s^{-1}$ (14 h light: 10 h dark photoperiod). Isolated cysts were monitored for germination, and the motile cells to confirm species identification. Germination attempts were only successful for some cysts.

Results

Distribution

Living dinoflagellate cysts were found at all fourteen locations sampled in this study of the South and East China Seas (Fig. 1, Table 1). Dapeng Bay had the greatest diversity of species, as all cyst-types observed in this study were found there. Nearby Daya Bay also had many different species. Fewer cysts were obtained from the East China Sea sites, but this undoubtedly reflects the number and choice of sampling locations, which were often determined by logistical considerations such as either accessibility or availability of

Table 1. The distribution of dinoflagellate cysts in the South and East China Seas.

Species	Plate	Location													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Alexandrium tamarense	IA	х	х	x		х	X		х	х	X				
Cochlodinium sp.	3T		Х												
Diplopelta parva	2N		Х	X	X							X			
Gonyaulax grindleyi	ID	Х	X	X	Х	X	Х	Х					Х		
G. spinifera	ΙE	Х	Х	Χ		Х	Х		Х	Х	X			Х	
G. scrippsae	IB		Х	Χ								Х		Х	
Gymnodinium catenatum	2G-J		X												
<i>Gymnodinium</i> sp. 1	2K-L		Х	Х	Х	Х	Х			Х				X	Х
Lingulodinium polyedra	IC	Х	Χ.	Х		Х	Х		Х	Χ			Х		
Phaepolykrikos hartmannii	30		Х	Х	Х										Х
Polykrikos kofoidii	3R		Х	Χ			Х			Χ					
P. schwartzii	3S		Х	Х	Х	X	Х	Х	X	Х	Х		X		
Protoperidinium americanum	4Y					х									
P. cf. avellana	4X	Х	Х	Х			Х		X	Χ		Х			
P. claudicans	3Q		Х	Х		Х	Х			Х					
P. conicum	3P	Х	Х	Х	Х		Х			Х		X	X	X	Х
P. conocoides	4BI		X	Х											Х
P. oblongum	4U	Х	Х	Х	Х			Х	X		Х	X			
P. subinerme	4Z		X	Х											
Pyrophacus steinii	4V	Х	Х	X											
Scrippsiella precaria	2M		Х	Х	X	Х	Х		X						
S. trochoidea	4W	Х	X	Х	Χ	Х	Х	Χ	Χ	Х	X	X	X	X	Х
Unidentified A	IF		Х												
Unidentified B	4Al		X	X	X	X	X		X		X				
Number of stations		7	10	3	2	2	1	1	1	2	2	1	5	3	9

^{1:} Mouth of Pearl River; 2: Dapeng Bay; 3: Daya Bay; 4: Nanao Island; 5: Donshan Island; 6:Xiamen Harbour; 7: Meizhou Bay; 8: Mouth of Minjian River; 9: Taishan Islands; 10: Taizhou Bay; 11: Shanmen Bay; 12: Zhoushan Islands; 13: Hongzhou Bay; 14: Mouth of (Yangtze) Changjiang River.

sampling vessels. There are certainly additional species in that area that would be revealed by further study.

Approximately half of the species that were found in the samples were photosynthetic; the remainder were heterotrophic species in the genera Protoperidinium and Polykrikos. Scrippsiella trochoidea was the most common cyst observed, present at all fourteen locations. Other species that were frequently observed include Protoperidinium conicum, Polykrikos schwartzii, Gonyaulax spinifera, Lingulodinium polyedra and the toxic dinoflagellate Alexandrium tamarense. The latter species was relatively common in samples from the South China Sea, Taiwan Strait and the southern part of the East China Sea. Gymnodinium catenatum, another toxic dinoflagellate, was found only in Dapeng Bay.

Descriptions

In the sections below, the cysts identified during this study are listed according to biological species, with synonyms from the paleontological literature provided where possible.

Gonyaulacaceae

Gonyaulax grindleyi Reinecke (Plate 1D)

Synonym: Protoceratium reticulatum Claparede et Lachmann.

[Paleontological taxon: Operculodinium centrocarpum (Deflandre et Cookson) Wall]

The central body of this cyst is spherical (26–32 μ m diameter, n=17) and densely ornamented with processes 5–10 μ m long. The tips of the

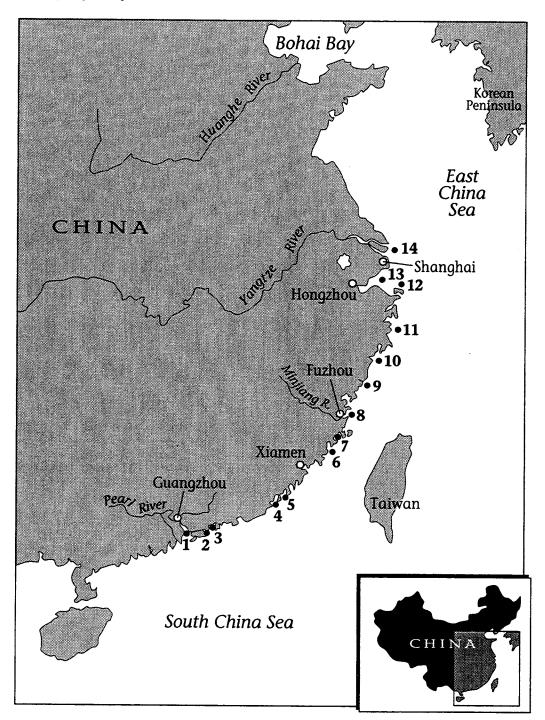


Fig. 1. Map of the study area, showing the locations sampled. 1: Mouth of the Pearl River (7 stations); 2: Dapeng Bay (10 stations); 3: Daya Bay (3 stations); 4: Nanao Island (2 stations); 5: Donshan Island (2 stations); 6: Xiamen (1 station); 7: Meizhou Bay (1 station); 8: Mouth of Minjian River (1 station); 9: Taishan Islands (2 stations); 10: Taizhou Bay (2 stations); 11: Shanmen Bay (1 station); 12: Zhoushan Islands (5 stations); 13: Hongzhou Bay (3 stations); 14: Mouth of Changjiang (Yangtze) River (9 stations).

processes are capitate and distally closed. The wall consists of two colourless layers, the outside layer being granular on the surface. The archeopyle is mid-dorsally placed and precingular, with a trapezoidal shape.

References: Matsuoka 1985d, Plate 7, figs 1–6; Baldwin 1987, figs. 4–5; Lewis and Dodge 1990, fig. 33; Bolch and Hallegraeff 1990, figs 2a–d; Ellegaard *et al.* 1994, figs. 13–16.

Lingulodinium polyedra (Stein) Dodge (Plate 1C)

Synonym: Gonyaulax polyedra

[Palaeontological taxon: Lingulodinium machaerophorum (Deflandre et Cookson) Wall]

This cyst is spherical (33–38 µm diameter, n=22) with two colourless wall layers covered with numerous processes which are flexuous, acuminate and closed at distal extremities. The compound archeopyle is similar to that of cysts of this species from Bermuda described by Wall and Dale (1968). The size and archeopyle shape representing the loss of 2, 3, and 4 plates varied among specimens. The cysts of this species from the South China Sea are generally small. This is a common species in both the South and East China Seas.

References: Wall and Dale 1968, Plate 1, figs. 17–18; Plate 3, figs. 3–6; Baldwin 1987, fig. 6; Dodge 1989, fig. 38; Ellegaard *et al.* 1994, figs. 56,57.

Gonyaulax spinifera (Claparede et Lachmann) Diesing (Plate 1E)

[Palaeontological taxon: Spiniferites hyperacanthus (Deflandre et Cookson) Cookson and Eisenack]

This is a spherical cyst (34-50 µm diameter, n=17) with a colourless, two-layered, wall. The membranous processes, particularly in the antapical area, are bifurcate or trifurcate; some are trifurcate with bifid tips. Archeopyle is trapezoidal. Many other similar cyst types including Spiniferites mirabilas (=Hystrichosphaera mirabilis Rossingnol), give rise to

Gonyaulax spinifera cells when germinated (Wall and Dale 1968). Although germination attempts were unsuccessful, morphological characteristics of this commonly found cyst type most closely resemble those described for G. spinifera.

References: Wall and Dale 1968, Plate 1, figs. 6-12; Baldwin 1987, figs. 2-3; Bolch and Hallegraeff 1990, figs. 3a-c, 4a-c; Mao and Harland 1993, Plate 2, fig. 1.

Gonyaulax scrippsae Kofoid (Plate 1B)

[Palaeontological taxon: Spiniferites bulloideus (Deflandre et Cookson) Sarjeant]

Sub-spherical to ovoid cyst (32–70 μ m long, 28–50 μ m wide, n=29). The processes are simple; relatively long (up to 15 μ m) bifurcate or trifurcate tips. Archeopyle is precingular and dorsal.

References: Wall and Dale 1968, Plate 1, figs. 13-15; Dale 1983, fig. 6; Matsuoka *et al.* 1988, figs 1-5; Bolch and Hallegraeff 1990, fig. 5; Ellegaard *et al.* 1994, fig. 59.

Alexandrium tamarense (Lebour) Balech (Plate 1A)

Elongate, ellipsoidal cyst (42–50 µm long, 30–40 µm wide, n=7). Thick, two-layered wall covered with an amorphous, transparent mucilaginous material which contains detritus. The cyst contains numerous clear starch and lipid granules and one or two orange or red pigmented bodies in a central band, with clear or brownish areas at each end containing particles in Brownian motion. Several cysts from Dapeng and Daya Bays in Guandong and from the Taishan Islands in Fujian Province were successfully germinated to yield motile cells which were identified as Alexandrim tamarense by E. Balech (pers. comm.) This species is common in the China Sea between the Zhejiang and Guandong provinces.

References: Dale 1977b, figs. 1a-c; Anderson and Wall 1978, figs. 22-50; Dale 1983, fig. 2; Fukuyo *et al* 1985, fig. 10; Fukuyo 1985, figs. 2o-p; Bolch and Hallegraeff 1990, figs. 7-10.

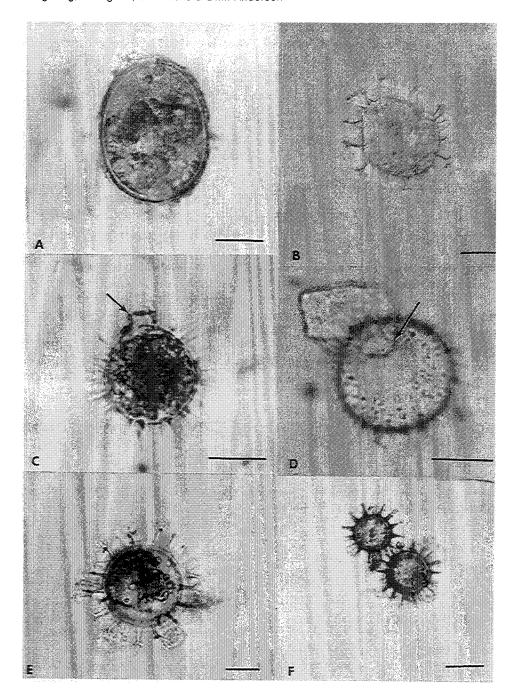


Plate 1. Dinoflagellate cysts from the South and East China Seas. A, Alexandrium tamarense. Living cyst showing thick wall, starch and lipid granules, pigmented body, and external mucilaginous material. B, Gonyaulax scrippsae. Empty cyst showing processes with bifurcate distal extremities. C, Lingulodinium polyedra. Cyst with apical operculum attached (arrow). D, Gonyaulax grindleyi Empty cyst with two colourless layers and distally closed and capitate processes. Arrow indicates archeopyle. E, Gonyaulax spinifera. Living cyst with two-layered wall and processes. F, Unidentified cyst A. Two specimens of small, unidentified cyst with numerous capitate processes. (All scale bars 20 μm.)

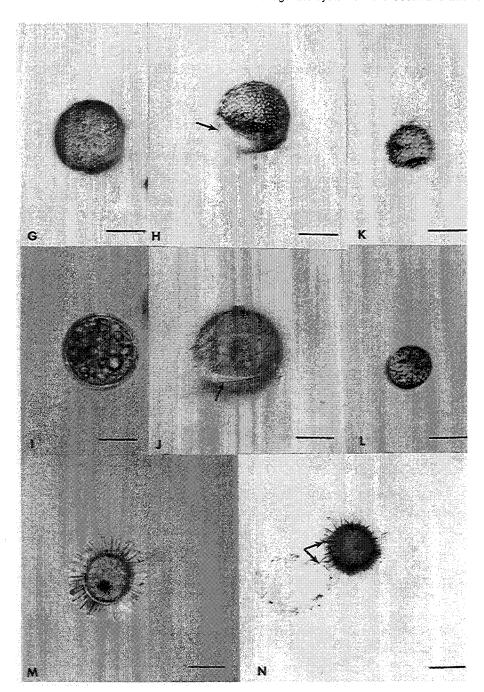


Plate 2. Dinoflagellate cysts from the South and East China Seas. G-J, Gymnodinium catenatum. G, View of cyst surface showing microreticulate markings. Outline of paracingulum visible at bottom of cyst. I, Cyst without outer wall showing starch and lipid globules. H, J, Different views of chasmic archeopyle (arrows). K-L, Gymnodinium sp.1: K, Cyst with slit-like archeopyle showing microreticulate surface; smaller size than typical G. catenatum. L, Cyst viewed with focal plane to reveal globular contents. M, Scrippsiella precaria. Living cyst with long, calcareous processes and pigmented body. N, Diplopelta parva. Newly formed cyst covered with pointed processes (arrows). (All scale bars 20 µm.)

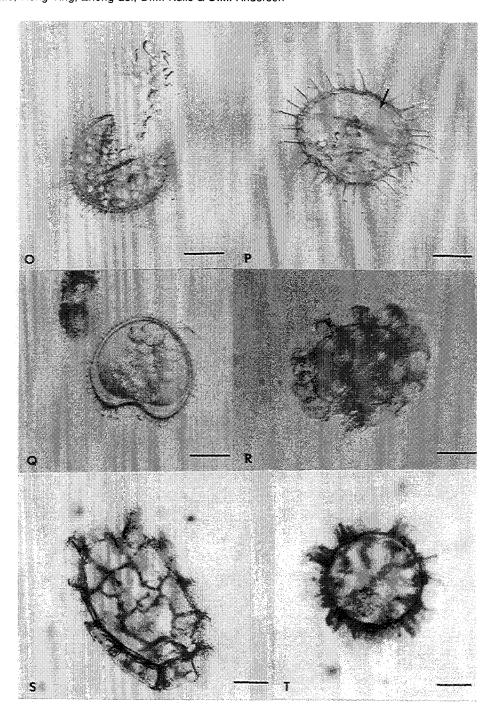


Plate 3. Dinoflagellate cysts from the South and East China Seas. O, *Phaeopolykrikis hartmannii*. Ruptured cyst covered by numerous processes. P, *Protoperidinium conicum*. Cyst with large archeopyle (arrow) and long processes. Q, *Protoperidinium claudicans*. Living cyst with starch and lipid globules and numerous short pointed spines. R, *Polykrikos kofoidii*. Cyst with fibrous processes. S, *Polykrikos schwartzii*. Empty cyst showing fibrous and flared processes which link to form a reticulate structure. T, *Cochlodinium* sp.. Spherical cyst with short, hollow and fibrous cylindrical processes. (All scale bars 20 μm.)

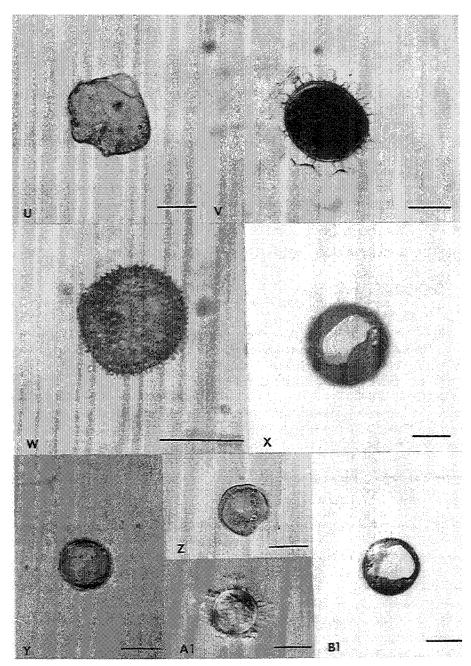


Plate 4. Dinoflagellate cysts from the South and East China Seas. U, *Protoperidinium oblongum*. Empty cyst showing a large archeopyle that truncates the apex. V, *Pyrophacus steinii*. Distinctive living cyst with bulbous and barrel-shaped processes. W, *Scrippsiella trochoidea*. Ovoid cyst with short calcareous spines and a prominent pigmented body. X, *Protoperidinium* cf. *avellana*. Empty cyst with laterally elongate and symmetrical archeopyle. Y, *Protoperidinium americanum* Empty cyst showing distinctive cloverleaf-shaped archeopyle. Z, *Protoperidinium subinerme*. Empty cyst with hexagonal intercalary archeopyle. A1, Unidentified cyst B. Spherical cyst covered by long, flexous processes and trapped detritus. B1, *Protoperidinium conicoides*. Empty cyst with trapezoidal archeopyle. (All scale bars 20 µm.)

Peridiniaceae

Protoperidinium americanum (Gran and Braarud) Balech (Plate 4Y)

Spherical brown cyst (25-30 µm diameter, n=6), with a coarse, granular wall and a folded membranous outer layer. The archeopyle has a distinctive, cloverleaf-shape, formed by the loss of 3 paraplates.

References: Matsuoka 1987, Plate 17; Dale 1976, Plate 1, Fig. 16; Bolch and Hallegraeff 1990, Figs. 29a-b; Ellegaard *et al.* 1994, figs. 53-55.

Protoperidinium cf. avellana (Meunier) Balech (Plate 4X)

[Palaeontological taxon: Brigantedinium cariacoense (Wall) Reid]

Spherical cyst (40-50 µm diameter, n=12) with a smooth, brown wall. The distinctive archeopyle is laterally elongate and symmetrical, formed by the loss of paraplate 2a. This species is common in the China Sea.

References: Wall and Dale 1968, Plate 4, figs.1-2; Bolch and Hallegraeff 1990, Figure 17; Ellegaard *et al.* 1994, fig. 44.

Protoperidinium claudicans (Paulsen) Balech (Plate 3O)

[Palaeontological taxon: Votadinium spinosum Reid]

Heart-shaped cyst (40–55 μ m long, 50–54 μ m wide, n=10), compressed dorsoventrally. Numerous short, pointed spines cover the cyst surface. This species was abundant in most of the South China Sea sites, but was not observed in samples from the East China Sea.

References: Wall and Dale 1968, Plate 2, figs. 1–2; Bolch and Hallegraeff 1990, fig. 25.

Protoperidinium conicoides (Paulsen) Balech (Plate 4B1)

[Palaeontological taxon: Brigantedinium simplex (Wall) Reid]

Dark brown, cyst (30 µm diameter, n=4), circular in dorsal view but ovoid in polar and

lateral views. Cyst wall is smooth with a middorsal, intercalary, trapezoidal archeopyle. This was not a common cyst in the China Sea.

References: Wall and Dale 1968, Plate 2, figs. 28-30; Baldwin 1987, fig. 19; Bolch and Hallegraeff 1990, fig. 26; Ellegaard *et al.* 1994, figs. 36-40.

Protoperidinium conicum (Gran) Balech (Plate 3P)

[Palaeontological taxon: Selenopemphix quanta (Bradford) Matsuoka]

Light-brown cyst (35–50 μ m long, 45–55 μ m wide, n=10), kidney-shaped and flattened anteroposteriorly. Cyst wall is smooth and covered by parallel rows of moderately long (10–15 μ m) spines, two of which delineate the girdle. This was a very common cyst in many locations.

References: Wall and Dale 1968, Plate 2, figs. 3-5; Baldwin 1987, fig. 13; Bolch and Hallegraeff 1990, fig. 14a-c; Ellegaard *et al.* 1994, figs. 28-29.

Protoperidinium oblongum (Aurivillius) Balech (Park et Dodge) (Plate 4U)

[Palaeontological taxon: Votadinium calvum Reid] Light brown cyst with rounded apices, compressed dorso-ventrally (50-65 µm long and 45-55 µm wide, n=5). The broad and large archeopyle is split around the apex on the dorsal surface, giving the cyst a truncate appearance. This is a common cyst in many locations, especially in Dapeng Bay.

References: Wall and Dale 1968, Plate 1, figs. 22-29; Dale 1983, figs. 11-13; Baldwin 1987, fig. 14; Bolch and Hallegraeff 1990, fig. 19a-b; Ellegaard et al. 1994, fig. 58.

Protoperidinium subinerme (Paulsen) Loebich III (Plate 4Z)

[Palaeontological taxon: Selenopemphix alticinctum (Bradford) Matsuokal

Light brown, kidney-shaped cyst (25-30 μ m long, 30-35 μ m wide, n=3) with a smooth wall.

Compressed slightly in the dorso-ventral direction in polar view. Dorsal, intercalary archeopyle is hexagonal. This cyst is smaller than that reported by some other workers.

References: Wall and Dale 1968, Plate 3, fig. 23; Matsuoka 1982, Plate 1, figs. 5–8; Baldwin 1987, figs. 9–11; Bolch and Hallegraeff 1990, fig. 16a–c.

Scrippsiella trochoidea (Stein) Loeblich III (Plate 4W)

Synonym: Peridinium trochiodeum (Stein) Lemmermann.

Spherical-to-ovoid, gray-coloured cyst, (25–35 µm diameter, n=15) with a prominent red body. Processes are calcareous and vary in length and in shape from blunt to pointed. When these cysts were germinated, a theropylic archeopyle (Matsuoka 1985a) was observed. The resulting vegetative cells had typical S. trochoidea morphology. This is the most common cyst in the South and East China Seas.

References: Wall et al. 1970, figs. 1-10; Baldwin 1987, fig. 23; Bolch and Hallegraeff 1990, figs. 11a-f; Lewis 1991, figs. 1-7.

Scrippsiella precaria Montresor and Zingone (Plate 2M)

Light brown, oval cyst (25–30 μ m diameter, n=9) with long (5 μ m) calcareous processes which are generally pointed but sometimes capitate. A prominent red pigmented body is visible inside the cyst. This cyst was observed in the most southern stations of the study area.

References: Montresor and Zingone 1988, figs. 8–10; Ishikwa and Taniguchi 1993, figs. 11–13.

Diplopelta parva (Abé) Matsuoka (Plate 2N)

Synonym: Dissodium parvum Abé

Brown, spherical cyst (30–37 µm diameter, n=6) covered with many pointed processes. A polygonal, apical archeopyle is reported (Bolch and Hallegraeff 1990), but was not observed. This was not a common cyst in the China Sea.

Reference: Matsuoka 1987b, fig. 5; Bolch and Hallegraeff 1990, figs. 31a-c.

Pyrophacus steinii (Schiller) Wall and Dale (Plate 4V)

[Palaeontological taxon: Tuberculodinium vancampoae (Rossignol) Wall]

Large spherical cyst (40–62 µm diameter, n=7) with bulbous and/or barrel-shaped processes. As described by Wall and Dale (1971), the polar view is circular to roundly reniform, whereas in equatorial view, it is a slightly rounded rectangle with weakly developed shoulders. The outer membrane is formed by connections between the adjacent processes. The archeopyle is reported to be hypocystal, but none was observed. This is a very common species in Dapeng and Daya Bays.

References: Matsuoka 1985b, Plates 35-40; Wall and Dale 1971.

Gymnodiniaceae Gymnodinium catenatum Graham (Plate 2G-J)

Dark brown, spherical cyst (40–45 µm diameter, n=23) containing numerous globular contents and a red pigmented body most visible when the cyst wall ruptures. The wall is covered by microreticulate surface markings, with the paracingulum and parasulcus clearly delineated. A para-acrobase (apical groove) is also visible extending from the girdle to the apex. The chasmic archeopyle is a slit along the paracingulum. This species was found only in Dapeng Bay, South China Sea. Germination attempts were not successful.

References: Anderson *et al.* 1988, figs. 1–13; Bolch and Hallegraeff 1990, figs. 33a–c; Ellegaard *et al.* 1993, figs. 20–24.

Gymnodinium sp. 1 (Bolch and Hallegraeff) (Plate 2K-L)

This cyst is similar to G. catenatum (Figs. 7-10) except for its smaller size $(20-25 \mu m, n=4)$ and its pale purple colour. Germination attempts were not successful. Similar cysts have been observed in Tasmania by Bolch and Hallegraeff (1990),

who suggest this may be related to the small, non-toxic G. catenatum cells reported from northwest Spain by Fraga and Sanchez (1985). Further germination attempts are needed to confirm the identity of this species.

Reference: Bolch and Hallegraeff 1990, figs. 34a-c.

Pheopolykrikos hartmannii (Zimmermann) Matsuoka and Fukuyo (Plate 3O)

Dark brown spherical cyst (49–60 μ m diameter, n=10) containing one or two red pigmented bodies. Wall is very thin, and covered by numerous short (6 μ m), conical processes. The archeopyle is chasmic, and after excystment, the cyst wall is light-brown in colour. This species was not very common, except in Dapeng and Daya Bays.

References: Fukuyo 1982, figs 1–6; Matsuoka 1982, fig. 13; Matsuoka and Fukuyo 1986, figs. 1–4.

Polykrikos kofoidii Chatton (Plate 3R)

Light-brown elongate-to-ovoid cyst ($50-65~\mu m$ long, $45-55~\mu m$ wide, n=8) with $12-15~\mu m$ fibrous and coarsely-wrinkled cylindrical processes which are hollow and short, and distally open. Their basis occasionally connect with adjacent ones. Sometimes even the distal extremities of processes are connected and fuse with neighboring ones forming shelf-like ornamentation. This was not a very common cyst-type in the South and East China Seas.

References: Morey-Gaines and Ruse 1980, fig. 4; Fukuyo 1982, figs. 7-9.

Polykrikos schwartzii Bütschli (Plate 3S)

Light-brown, elongate ovoid cyst $(75-100 \mu m \log, 50-65 \mu m \text{ wide}, n=14)$ with fibrous processes that flare distally. An irregular, nearly circular, tremic archeopyle is reported (Matsuoka 1985) but was not observed. This was a very common cyst in the South and East China Sea.

References: Matsuoka 1982, fig. 14; Baldwin 1987, fig. 24; Matsuoka 1987, Plate 15; Bolch and Hallegraeff 1990, figs. 32a-c; Ellegaard *et al.* 1993, figs. 25-27.

Cochlodinium sp. (Plate 3T)

Light-brown spherical cyst (55 μm diameter, n=3) with short, hollow and fibrous cylindrical processes (7μm) which are distally open. This cyst was only observed in Dapeng Bay sediments.

Reference: Fukuyo 1982, Plate 2, figs. 1-3.

Unidentified Cysts Unidentified cyst A (Plate 1F)

Spherical, brown cyst (20–25 µm diameter, n=5) with numerous long (6–7 µm) processes flared distally. Contents include starch and lipid granules and cytoplasmic particles in Brownian motion. Germination experiments were not successful. This cyst-type was only seen in Dapeng Bay.

Unidentified cyst B (Plate 4A1)

Spherical cysts (25–30 µm diameter, n=4) with a clear wall covered by numerous flexous, thin processes 5–8 µm long which collected detritus. Contents include starch and lipid granules and an orange pigmented body. Germination experiments were not successful.

Discussion

Twenty-four cyst types were identified in sediments from nearshore locations in the South and East China Seas. Most of these (22) corresponded to dinoflagellate species for which the cyst-theca relationship had been determined, but two cysts could not be identified. The species composition of Chinese cysts is broadly similar to what has been observed in Japan by Matsuoka, Fukuyo and co-workers (Matsuoka 1982, 1985c, d, 1987a; Fukuyo 1982). Many of the species have also been observed in Tasmania (Bolch and

Hallegraeff 1990) and in New Zealand (Baldwin 1987). As this is the first published study of recent dinoflagellate cysts in the China Sea, comparisons with other local studies are not possible. Mao and Harland (1993) did, however, conduct a study of fossilized dinoflagellate cysts from the South China Sea. Some of the species observed in the present study were also identified in sediment cores dating to the Upper Pleistocene e.g., Gonyaulax spinifera (= Spiniferites hyperacanthus), Protoperidinium subinerme (=Selenopemphix alticinctum), Protoperidinium conicum (=Selenopemphix quanta), Protoperidinium conicoides (=Brigantedinium simplex) and Lingulodinium polyedra (= L. machaerophorum).

Cyst abundance and diversity was greatest in Dapeng Bay in the South China Sea near Hong Kong. Virtually all of the cysts recovered in this study could be found in that bay. More samples were examined from that location (10) than for most of the other locations (typically 1-3; Table 1) but the species assemblage was diverse in all of them. We do not, therefore, believe that the number of samples biased our interpretation of the distribution of cysts within the region, as discussed below. This is supported by data from nearby Daya Bay, where a large number of species were also observed in only three samples. It thus appears that Dapeng and Daya Bays provide conditions suitable for the growth dinoflagellates and retention of their cysts. Plankton surveys by Qi and Lu (1995) also confirm that phytoplankton biomass in general, and dinoflagellate biomass in particular, are higher in Dapeng Bay than in other harbours or embayments along the coast of the south China

One motivation for this study relates to the many red tides that occur every year along the Chinese coast (Qi et al. 1993). Over sixty species of red tide organisms have been reported, and many of those are dinoflagellates. Qi et al. (1991a) described the distribution of red tide species along the coasts of China and noted that red tides are most common in Dapeng Bay. Visible red tides (mostly Noctiluca scintillans) occur 4–5 times each year. In 1991, a large

Chattonella marina bloom killed many farmed fish throughout the bay, but had no effects in adjacent waters (Qi et al. 1991b, 1994). Dapeng Bay (known as Mirs Bay in Hong Kong) is also connected to Tolo Harbour in Hong Kong, which is well-known for its red tide outbreaks, including PSP (Ho and Hodgkiss 1991). Human population within that watershed grew 6-fold between 1976 and 1986, during which time the number of observed red tide events increased 8-fold. The underlying mechanism is presumed to be increased nutrient loading from pollution that accompanied human population growth. Since Tolo Harbour empties into Dapeng Bay, the high dinoflagellate cyst abundance and bloom frequency observed there may be linked to elevated nutrient loading from both China and Hong Kong.

Dapeng Bay is also a site of recurrent paralytic shellfish poisoning (PSP) episodes (Lin et al. 1994). It is thus not suprising that cysts of two dinoflagellates capable of producing PSP toxins - Alexandrium tamarense and Gyrodinium catenatum were detected in samples from that area and nearby Daya Bay. A. tamarense cysts were germinated successfully and the species assignment confirmed (E. Balech, personal communication), but the G. catenatum cysts did not germinate. Given the unique morphology of that cyst (Anderson et al. 1988), there is no doubt that the species is present. Until cultures are established, however, its toxicity cannot be confirmed, since both toxic and non-toxic strains of G. catenatum are known to exist (Oshima et al. 1987).

Gymnodinium catenatum was only found in Dapeng Bay, but Alexandrium tamarense was found in eight relatively contiguous locations from the mouth of the Pearl River through Guandong and Fujian Provinces to Taizhou Bay in Zhejiang Province (Locations 1 – 10, Fig. 1, Table 1). This distribution is generally consistent with the region in which PSP events have been recorded in the South and East China Seas (Lin et al. 1994), but one area without PSP records but with A. tamarense cysts can be identified – the Pearl River estuary. This is a location where increased monitoring of shellfish for PSP would be justified.

Acknowledgements

This research was supported by the National Natural Science Foundation of China through a grant (No. 93890080) to Y.Z. Qi, and by the U.S. National Science Foundation (U.S./China

Cooperative Program) through a grant (INT 9201753) to D.M. Anderson. The authors thank Liang Jiawen for help in collecting the samples. Contribution No. 9308 from the Woods Hole Oceanographic Institution.

References

- Anderson, D.M. 1984. The roles of dormant cysts in toxic dinoflagellate blooms and shellfish toxicity, In Seafood Toxins. American Chemical Society Symposium Series (ed. E. Ragelis), 125-38. Washington, D.C. American Chemical Society,
- Anderson, D.M. and Wall, D. 1978. The potential importance of benthic cysts of *Gonyaulax tamarensis* and *Gonyaulax excavata* in initiating toxic dinoflagellate blooms. *Journal of Phycology* 14: 224-34.
- Anderson, D.M., Jacobson, D.M., Bravo, I. and Wrenn, J.H. 1988. The unique microreticulate cyst of the naked dinoflagellate *Gymnodinium* catenatum. Journal of Phycology 24: 255-62.
- Anderson, D.M., Kulis, D.M., Orphanos, J.A. and Ceurvels, A.R. 1982. Distribution of the toxic red tide dinoflagellate *Gonyaulax tamarensis* in the southern New England region. *Estuarine, Coastal and Shelf Science* 14: 447–58.
- Baldwin, R.P. 1987. Dinoflagellate resting cysts isolated from sediments in Marlborough Sound, New Zealand. New Zealand Journal of Marine and Freshwater Research 21: 243-53.
- Blanco, J. 1989a. Quistes de dinoflagelados de las costas de Galicia. I. Dinoflagelados Gonyaulocoides. Scienta Marina 53: 785-96.
- Blanco, J. 1989b. Quistes de dinoflagelados de las costas de Galicia. II. Dinoflagelados Peridinioides. *Scienta Marina* **53**: 787-812.
- Blanco, J. 1989c. Quistes de dinoflagelados de las costas de Galicia. III. Dinoflagelados Gymnodinoides. Scienta Marina 53: 813-9.
- Bolch, C.J. and Hallegraeff, G.M. 1990. Dinoflagellate cysts in recent marine sediments from Tasmania, Australia. *Botanica Marina* 33: 173-92.
- Bolch, C.J., Blackburn, S.I., Cannon, J.A. and

- Hallegraeff, G. M. 1991. The resting cyst of the red-tide dinoflagellate *Alexandrium minutum* (Dinophyceae). *Phycologia* **30**(2): 215-9.
- Dale, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. Review of Palaeobotany and Palynology 22: 39-60.
- Dale, B. 1983. Dinoflagellate resting cysts: 'benthic plankton'. In *Survival strategies of the algae*. (ed. G. A. Fryxell), 69-136. Cambridge: Cambridge University Press.
- Dodge, J.D. 1989. Some revisions of the family Gonyaulacaceae (Dinophyceae) based on a scanning electron microscope study. *Botanica Marina* 32: 275–98.
- Drake, J.A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137: 1-26.
- Ellegaard, M., Christensen, N.F. and Moestrup, Ø. 1993. Temperature and salinity effects on growth of a non-chainforming strain of *Gymnodinium catenatum* (Dinophyceae) established from a cyst from recent sediments in The Sound (Øresund), Denmark. *Journal of Phycology* 29: 418-26.
- Ellegaard, M., Christensen, N.F. and Moestrup, Ø. 1994. Dinoflagellate cysts from Recent Danish marine sediments. *European Journal of Phycology* **29**: 183-94.
- Fraga, S. and Sanchez, F.J. 1985. Toxic and potentially toxic dinoflagellates found in Galician rias (NW Spain). In *Toxic Dinoflagellates* (ed. D.M. Anderson, A.W. White and D.G. Baden), 51–54. Elsevier, New York.
- Fukuyo, Y. 1982. Cysts of naked dinoflagellates.

- In Fundamental Studies of the effect of marine environment on the outbreaks of red tides. Reports of Environmental Sciences, 205–14. B 148–R14–8, Monbusho, Tokyo.
- Fukuyo, Y. 1985. Morphology of *Protogonyaulax* tamarensis (Lebour) Taylor and *Protogonyaulax* catenella (Whedon and Kofoid) Taylor from Japanese coastal waters. Bulletin of Marine Research 37: 529-37.
- Fukuyo, Y., Yoshida, K. and Inoue, H. 1985. Protogonyaulax in Japanese coastal waters. In Toxic Dinoflagellates (ed. D.M. Anderson, A.W. White, and D.G. Baden), 27-32. New York: Elsevier.
- Guillard, R.R.L. and Ryther, J.H. 1962. Studies of marine planktonic diatoms. I. Cyclotella nana Hustedt and Detonula confervacea (Cleve).
 Gran. Canadian Journal of Microbiology 8: 229-39.
- Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* **32**: 79–99.
- Ho, K.C. and Hodgkiss, I.J. 1991. Red tides in subtropical waters: an overview of their occurrence. Asian Marine Biology 8:5-23.
- Imai, I. and Itakura, S. 1991. Densities of dormant cells of the red tide flagellate *Heterosigma akashiwo* (Raphidophyceae) in bottom sediments of northern Hiroshima Bay, Japan. *Bulletin of Japan Society of Microbial Ecology* 6: 1-7.
- Ishikawa, A. and Taniguchi, A. 1993. Some cysts of the genus Scrippsiella (Dinophyceae) newly found in Japanese waters. *Bulletin of Plankton Society of Japan.* 40: 1-7.
- Lewis, J. 1990. The cyst-theca relationship of *Oblea rotunda* (Diplopsalidaceae, Dinophyceae). *British Phycological Journal* 25: 339-51.
- Lewis, J. 1991. Cyst-thecal relationships in *Scrippsiella* (Dinophyceae) and related orthoperidinioid genera. *Botanica Marina* 34: 91–106.
- Lewis, J. and Dodge, J.D. 1990. The use of SEM in dinoflagellate taxonomy. In Scanning Electron Microscopy in Taxonomy and Functional Morphology. Systematics Association Special Volume No. 41 (ed. D. Claugher), 125-48. Oxford: Claredon Press.

- Lin, Y., Yang M., Chen R., Hu S. and Jin, G. 1994. Study on paralytic shellfish poison in shellfish from Guandong coast. *Oceanologia et Limnologia Sinica* 25: 220-5.
- Mao, S. and Harland, R. 1993. Quaternary organic-walled dinoflagellate cysts from the South China Sea and their paleoclimatic significance. *Palynology* 17: 47-65.
- Matsuoka, K. 1982. Dinoflagellate cysts in surface sediments of Omura Bay, West Kyushu, Japan. In Fundamental studies on the effects of marine environment on the outbreaks of red tides. Reports of Environmental Sciences. 197-204. B148 R14-8, Monbusho, Tokyo.
- Matsuoka, K. 1985a. Archeopyle structure in modern gymnodinialean dinoflagellate cysts. Review of Palaeobotany and Palynology 44: 217-31.
- Matsuoka, K. 1985b. Cyst and thecate forms of *Pyrophacus steinii* (Schiller) Wall et Dale 1971. *Transactions and Proceedings of the Paleontological Soceity of Japan. New Series* **140**: 240–62.
- Matsuoka, K. 1985c. Distribution of the dinoflagellate cyst in surface sediment of the Tsushima Warm Current. Quaternary Research 24: 1-12.
- Matsuoka, K. 1985d. Organic-walled dinoflagellate cysts from surface sediment of Nagasaki Bay and Senzaki Bay, West Japan. Bulletin of the Faculty of Liberal Arts, Nagasaki University. Natural Science 25: 21-115
- Matsuoka, K. 1987a. Organic-walled dinoflagellate cysts from surface sediments of Akkeshi Bay and Lake Saroma, North Japan. Bulletin of the Faculty of Liberal Arts, Nagasaki University. Natural Science 28: 35-123.
- Matsuoka, K. 1987b. Dinoflagellates II, Cysts. In A Guide for Studies of Red Tide Organisms (ed. Japan Fisheries Resource Conservation Association), 399–476. Tokyo: Shuwa.
- Matsuoka, K. 1988. Cyst-theca relationships in the diplopsalid group (Peridiniales, Dinophyceae). Review of Palaeobotany and Palynology 59: 95-122.
- Matsuoka, K. and Fukuyo Y. 1986. Cyst and motile morphology of the colonial dino-

- flagellate *Polykrikos hartmanii* (Zimmerman) comb. nov. *Journal of Plankton Research* 8: 811–8.
- Matsuoka, K., Fukuyo, Y. and Anderson, D.M. 1989. Methods for modern dinoflagellate cyst studies. In *Red Tides: Biology, Environmental Science and Toxicology* (ed. T. Okaichi, D.M. Anderson, and T. Nemoto), 461–80. New York: Elsevier.
- McMinn, A. 1991. Recent dinoflagellate cysts from estuaries on the central coast of New South Wales, Australia. *Micropaleontology* 37: 269-87.
- Montresor, M. and Zingone, A. 1988. Scrippsiella precaria sp. nov. (Dinophyceae), a marine dinoflagellate from the Gulf of Naples. Phycologia 27: 387-94.
- Morey-Gaines, G. and Ruse, R.H. 1980. Encystment and reproduction of the predatory dinoflagellate *Polykrikos kofoidii* Chatton (Gymnodiniales). *Phycologia* 19: 230-6.
- Nehring, S. 1995. Dinoflagellate resting cysts as factors in phytoplankton ecology of the North Sea. *Helgoländer Meeresuntersuchungen* **49**: 375-92.
- Oshima, Y., Hasegawa, M., Yasumoto, T., Hallegraeff, G. and Blackburn, S. 1987. Dinoflagellate *Gymnodinium catenatum* as the source of paralytic shellfish toxins in Tasmanian shellfish. *Toxicon* 25: 1105-11.
- Pfiester, L.A. and Anderson, D.M. 1987.
 Dinoflagellate life cycles and their environmental control. In *The Biology of Dinoflagellates* (ed. F.J.R. Taylor), 611-48.
 London: Blackwell Scientific Publications, Ltd.
- Qi, Y.Z. and Lu, S.H. 1995. The ecological characteristics of phytoplankton in Dapeng Bay, South China Sea. *Journal of Jinan University (Natural Science)* 16: 111-7.
- Qi, Y.Z., Lu, S.H. and Qian, H. 1991a. Red tides and red tide research in China a perspective. *Journal of Nanjing University* (*Natural Science*). Special edition on the Causes and Countermeasures of Natural Disasters. 353-60.
- Qi, Y.Z., Hong, Y., Lu, S.H., Zhang, J.P., Zhu, C.J. and Li, Y.Q. 1991b. A new recorded red tide species in China: *Chatonella marina*

- (Subrahamanyan) Hara et Chihara. Journal of Jinan University (Natural Science) 12: 92-5.
- Qi, Y.Z., Zhang, Z., Hong, Y., Lu, S.H., Zhu, C. and Li Y. 1993. Occurrence of red tides on the coasts of China. In *Toxic Phytoplankton Blooms in the Sea*, (ed. T. Smayda and Y. Shimizu), 43-6. Elsevier, Amsterdam,
- Qi, Y.Z., Hong, Y. Lu, S.H., Chu, J.H., Zhang J.P., Zhu, C.J. and Li, Y.Q. 1994. Outbreak of *Chatonella marina* red tide and its relation to ecological parameters in Dapeng Bay, South China Sea. Oceanologia et Limnologia Sinica 25: 132-8.
- Reid, P. C. 1972. Gonyaulacean dinoflagellate cysts from the British Isles. *Nova Hedwigia* **25**: 579-637.
- Shaozhi, M. and Harland, R. 1993. Quaternary organic-walled dinoflagellate cysts from the South China Sea and their paleoclimatic significance. *Palynology* 17:47-65.
- Starr, R.C. 1964. The culture collection of algae at Indiana University. *American Journal of Botany* 51: 1013-44.
- Tyler, M. A., Coats, D.W. and Anderson, D.M. 1982. Encystment in a dynamic environment: deposition of dinoflagellate cysts by a frontal convergence. *Marine Ecology Progress Series* 7: 163-78.
- Wall, D. 1965. Modern hystrichospheres and dinoflagellate cysts from the Woods Hole region. *Grana Palynologica* 6: 297-314.
- Wall, D. 1971. Biological problems concerning fossilizable dinoflagellates. *Geoscience and Man* III: 1-15.
- Wall, D. and Dale, B. 1966. Living fossils in western Atlantic plankton. *Nature* 5053: 1025-6.
- Wall, D. and Dale, B. 1967. The resting cysts of modern marine dinoflagellates and their paleontological significance. Review of Paleobotany and Palynology 2: 349-54.
- Wall, D. and Dale, B. 1968. Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropaleontology* 14: 265-304.
- Wall, D. and Dale, B. 1970. Living hystrichosphaerid dinoflagellate spores from Bermuda and Puerto Rico. *Micropaleontology*. 16: 47-58.
- Wall, D. and Dale B. 1971. A reconsideration of

living and fossil *Pyrophacus* Stein, 1883 (Dinophyceae). *Journal of Phycology* 7: 221–35.

Wall, D., Guillard, R.R.L., Dale, B., Swift, E. and Watabe, N. 1970. Calcitic resting cysts in *Peridinium trochoideum* (Stein) Lemmermann, an autotrophic marine dinoflagellate. *Phycologia*. 9: 151-6.