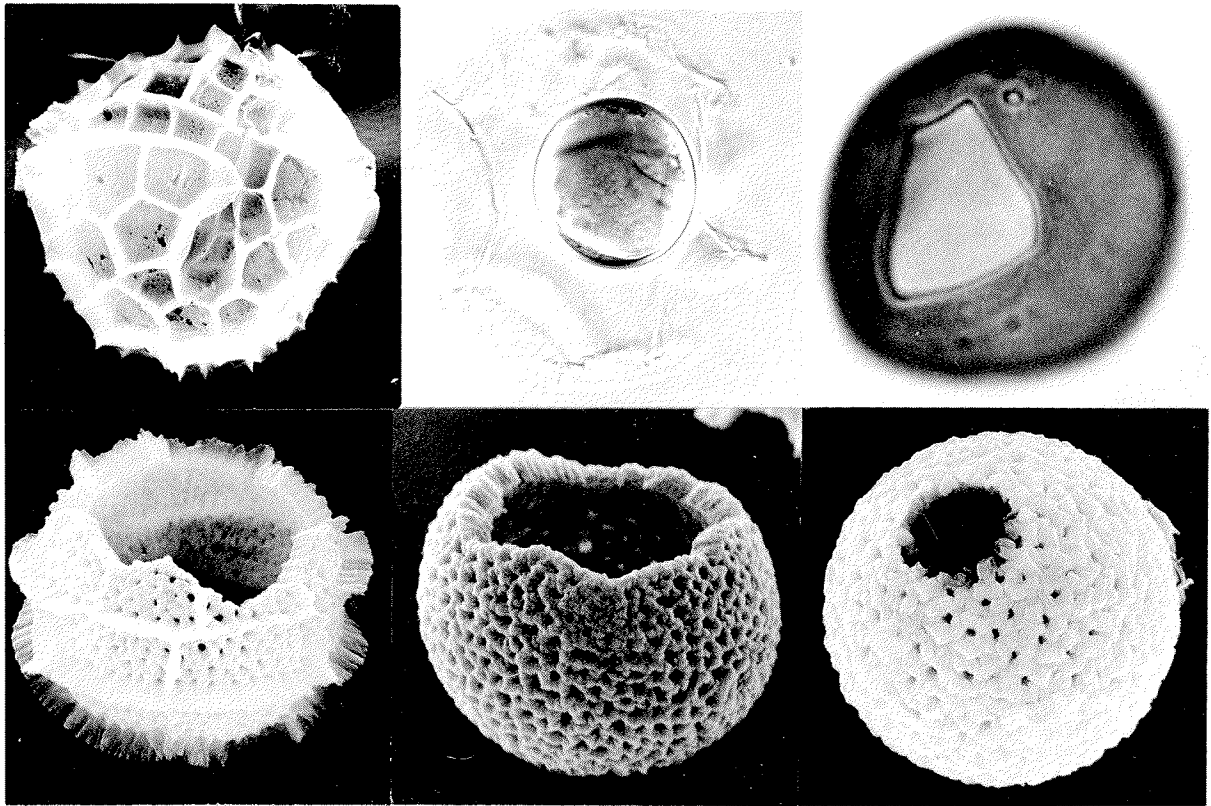


Dinoflagellate Contributions to the Deep Sea

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Explanation of Cover Photo: Dinoflagellate remains from deep sea sediment traps. Top left, *Protoceratium areolatum* theca from Station PB₁ in the Panama Basin, 667 m; top center, *Impagidinium pallidum* cyst from the Greenland Basin station (GB) in the Nordic Seas, 2,823 m; top right, *Protoperidinium conicoides* cyst from bottom sediment at Station S in the Central North Atlantic, 5,581 m; bottom left, *Calciodinellum operosum* cyst from Station P₁ in the Central Pacific, 3,000 m; bottom center, *Thoracosphaera albatrosiana* sensu Fütterer cyst from Station E in the Equatorial Atlantic, 988 m; bottom right, *Thoracosphaera heimii* from Station P₁ in the Central Pacific, 3,000 m. The top center and top right are light photomicrographs; others are SEM micrographs. Magnifications are included in the text.

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Chapter 1

Dinoflagellate Contributions to the Open Ocean Sediment Flux

Barrie Dale

Abstract

For the first time, sediment trap samples from several depths in the deep sea were analyzed to estimate both the types and amounts of mineral contributed by dinoflagellates to the deep sea sediment flux. Thecal remains of dinoflagellate motile stages were almost entirely restricted to the upper few hundred meters of the water column, supporting the generally accepted explanation of their absence in the fossil record (i.e., theca are composed of cellulosic material which is destroyed before they may be incorporated into bottom sediments). The main contribution to the sediment flux is composed of resting cysts routinely produced in the life cycles of just a few of the more obscure oceanic dinoflagellates, probably species of Scrippsiella or Ensiculifera. The cyst assemblage sedimenting out from plankton at present is overwhelmingly dominated by a few small calcareous types (up to several thousands/m²/day). If not dissolved, these may accumulate in paleontologically significant amounts in bottom sediments to give the most representative fossil record of oceanic dinoflagellates. "Oceanic assemblages" of organic-walled cysts from Recent deep-sea sediments previously described by palynologists probably represent long distance transport from more coastal regions rather than oceanic dinoflagellate production.

Introduction

Dinoflagellates are a major group of phytoplankton. They have been widely recorded from almost all present day aquatic environments, usually as characteristically biflagellated motile cells. These vegetative cells decay fairly rapidly after death and are not thought to fossilize. The extensive fossil record of dinoflagellates (at least to the Silurian) is formed from a more robust type of cell, the non-motile resting cyst, known to be produced by some living species. Most known cysts are organic-walled (called "acid resistant" cysts by

palynologists) and are thought to fossilize due to sporopollenin-like material in the cyst wall (Brooks and Shaw, 1973). However, both living and fossil calcareous cysts are known (Deflandre, 1947, 1948; Wall and Dale, 1968b; Wall *et al.*, 1970), and one group of siliceous cysts is documented from the Eocene (Dale, 1978).

The biological and paleontological significance of these two different stages in dinoflagellate life cycles (*i.e.*, motile stages and cysts) was reviewed by Dale (1983). The biological literature provides little of direct relevance to paleontology, restricted as it is almost entirely to the motile stages commonly found in plankton. The cysts, which are morphologically very different from motile stages, seldom have been recorded in biological studies of plankton. They remained largely unknown until their discovery by paleontologists looking for living counterparts of fossil dinoflagellates (Evitt and Davidson, 1964; Wall, 1965).

Within the past 15 years several paleontologists have studied living and Recent dinoflagellate cysts for comparison with the fossil record. Their main objectives have been: 1) to investigate general factors producing cyst assemblages — particularly interesting since fossil cysts have been found to have increasing application in stratigraphic palynology, *e.g.*, in oil exploration; and 2) to develop cysts as ecological indicators, particularly in Quaternary marine sediments. Two main approaches have been employed in these studies, one directed solely at Recent cysts, the other including living cysts.

Most dinoflagellate palynologists engaged in Recent studies have used standard preparation techniques (involving digestion of minerals by HCl and HF) to extract acid resistant cyst assemblages from Recent bottom sediments. The main advantage of this approach is that it produces assemblages directly comparable with fossil assemblages similarly prepared. The main limitations are that mineralized cysts are destroyed and living cysts cannot be differentiated from dead cysts in the assemblages. In some cases this is an acceptable compromise that has proved particularly useful in documenting Recent cyst distribution (*e.g.*, Rossignol, 1964; Williams, 1971; Reid, 1975; Dale, 1976; Wall *et al.*, 1977).

Wall and Dale (1968a) developed techniques for studying living cysts including mineralized forms. In a series of investigations at the Woods Hole Oceanographic Institution from 1965 to 1975, these authors showed that cysts routinely form in the life cycles of many neritic dinoflagellates, apparently serving as benthic resting stages. At least in temperate waters, cyst formation was often markedly seasonal, and the cysts provided an obvious overwintering function. However, cysts also formed in tropical waters (Wall and Dale, 1970), and Dale (1976) suggested their overall function was probably as hypnozygotes in a sexual cycle.

In a first major ecological classification of living cysts, Wall *et al.* (1977) subsequently identified several oceanic types (members of the cyst based genus *Leptodinium* Klement, 1960, since transferred to *Impagidinium* Stover and Evitt, 1978). These are acid resistant cysts with a known fossil record extending back at least to the Middle Paleogene. That they are produced today in the open ocean was first suspected from palynological preparations of bottom sediments recovered by grabs and cores. *Impagidinium* species were consistently present in outer shelf and open ocean samples while virtually absent from inner shelf and coastal samples. Attempts to recover these live proved extremely difficult, but eventually several with fresh-looking cell contents were obtained from extensive plankton tows in slope waters off the U.S. East Coast, and from surface sediments carefully collected by me from the DSRV ALVIN at water depths of 1,000–2,000 m beneath the U.S. East Coast slope

waters. Attempts to culture these in parallel experiments to those successfully used for coastal types (Wall and Dale, 1968a) all failed.

The discovery of open ocean dinoflagellate cysts raised many intriguing questions. Biologically, there are important questions concerning the function and strategy of cysts in the life cycles of oceanic dinoflagellates (discussed later). Geologically, the main questions concern which types of cysts are produced, in what amounts, their degree of preservability, and their ultimate contribution to the sediment flux. Results are presented here of an investigation aimed at answering these questions based on qualitative and quantitative microscopic examination of sediments collected by the PARFLUX project. These samples from large sediment traps placed at different depths in the deep sea provided a unique opportunity to supplement previous non-quantitative information from the two extremes of near surface plankton tows and bottom sediments. For the first time, an attempt was made to document living cysts sedimenting out through the deep sea water column today for comparison with cyst assemblages previously described from Recent deep sea sediments.

The overall aim was to provide paleontologically relevant information. Therefore, since only the cysts of dinoflagellates fossilize, the biocoenosis reported here is a biocoenosis of dinoflagellate cysts rather than their motile stages. Remains of motile stages were recorded when seen, but only limited attempts were made to identify these since they were often poorly preserved and considered outside the main scope of this work. Thoracosphaerids are described in Chapter 2 in this volume, since they are not considered to be closely related to dinoflagellate cysts reported here.

Materials and Methods

Samples

Figure 1.1 shows the location of sediment trap stations, and Table 1.1 summarizes the station data for samples used in this study. Details of the PARFLUX sediment traps, their deployments, and the collection and subdivision of samples obtained from them is presented elsewhere (Honjo *et al.*, 1980; Honjo, 1980). Samples from all depths of Station PB, and Station E, 389 m, represented 1/64 of the original trap sample; others were 1/32. A total of 15 trap samples and one bottom sediment sample were examined for dinoflagellates.

Sample Preparation and Examination

The work was carried out in two phases. The first batch of samples (from the Atlantic stations S and E) were examined in 1979 as a pilot project to assess the value of this type of sample for dinoflagellate studies. Results from this were encouraging, and in 1981 the study was extended to include samples from the Pacific stations P₁ and PB.

The samples posed several problems not usually encountered together in dinoflagellate studies. These included:

1. The bulk of cysts proved to be calcareous, precluding the use of standard palynological preparation methods involving HCl and HF.

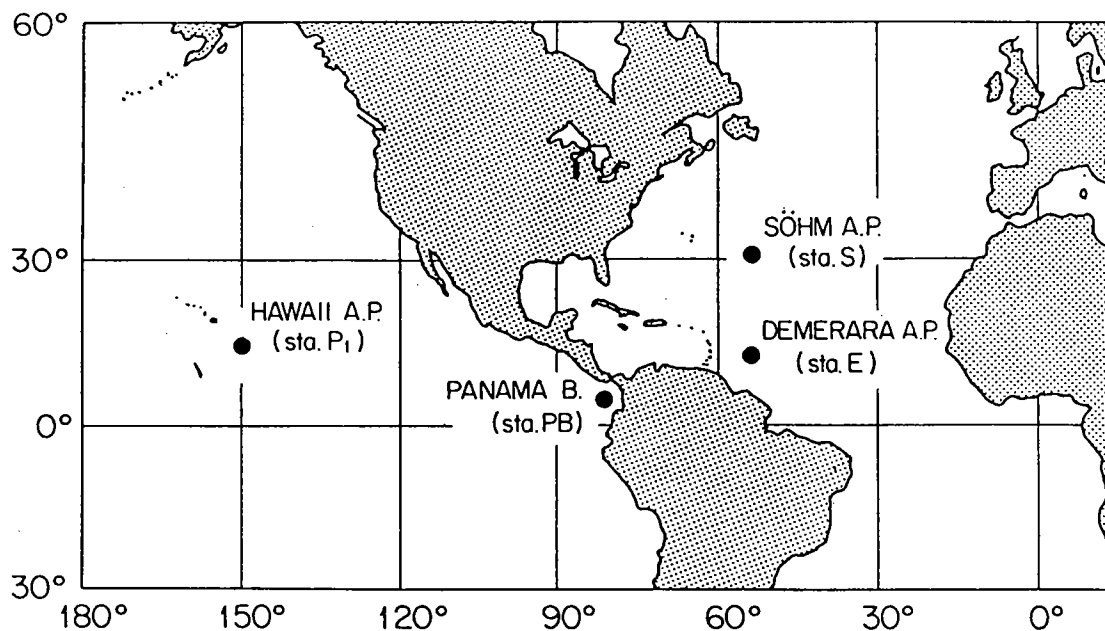


Figure 1.1: Location of PARFLUX sediment trap stations.

Table 1.1: Summary of station data and samples used for deep sea dinoflagellate studies.

Station	PARFLUX S _{1,2}	PARFLUX E	PARFLUX P ₁	PARFLUX PB
Location	31°32.5'N, 55°55.4'W	13°30.2'N, 54°00.1'W	15°21.1'N, 151°28.5'W	05°21'N, 81°53'W
Ocean/Basin	Central Sargasso Sea/ Söhm Abyssal Plain	Tropical Atlantic/ Demerara Abyssal Plain	N. Central Pacific/ E. Hawaii Abyssal Plain	Tropical Pacific/ hemipelagic Panama Basin
Term	10/76-1/77	11/77-2/78	7/78-11/78	8/79-12/79
Duration	75 days	110 days	98 days	112 days
Trap Depth (m)	(372) (976) ^a 3,694 ^a 5,206 5,367 ^a	389 ^a 988 ^a 3,755 ^a 5,068 ^a —	378 978 2,778 ^a 4,280 ^a 5,582 ^a	667 ^a 1,268 (2,265) 2,869 ^a 3,769 ^a
Ocean Depth	5,581 m	5,288 m	5,792 m	3,856 m
Sediment	Box core ^a			

^aSamples used for dinoflagellate studies. Trap samples represented size fraction < 63 μm (< 250 μm in S_{3,5,6,9}).

2. Diagnostic morphologic features of some of these calcareous cysts (*e.g.*, crystalline structure of the wall) could not be resolved by light microscopy, necessitating the use of scanning electron microscopy (SEM).
3. Valid quantitative counts for cysts could not be made from SEM preparations, due to the "diluting" effect of large amounts of other material in the samples.

The following procedure was followed to obtain both qualitative and quantitative information from the trap samples:

1. After thoroughly shaking to homogenize the sample, an aliquot portion was wet sieved with a mesh size of 25 μm routinely used for concentrating cysts.
2. The size fraction greater than 25 μm retained on the sieve was counted for particles of identifiable dinoflagellate origin (see the next section for details), using normal light microscopy. In phase 1 of the project, counting was done from open drops on microscope slides (allowing manipulation of specimens), but in phase 2 permanent mounts in glycerine jelly ringed with beeswax were used. Counts were related back to the original sample, and results were expressed (as in Honjo, 1980) as a daily flux in a square meter section of water column at a given trap (Tables 1.2 and 1.3). This was calculated by dividing the total flux by the number of days the trap was deployed and the 1.5 m^2 area of the trap opening.
3. The size fraction less than 25 μm was spot-checked microscopically to see if significant dinoflagellate remains were being lost from the counts, and then permanently mounted in reference slides.
4. Sample material not used for the quantitative count was used for detailed morphologic studies of the various types encountered. For this, individuals were picked off with a micropipette, coated with gold using standard SEM preparation methods, and examined and photographed in the SEM. Permanent reference slides were made of any > 25 μm fraction remaining after these studies.
5. The bottom sediment sample from Station S was sieved as in point 1, above, and the fraction > 25 μm was counted to obtain percentages of the various cysts making up the assemblage.

The Organisms Recorded

Organisms identified in this study as obviously of dinoflagellate affinity are discussed below under three categories: Thecae of dinoflagellate motile stages, organic-walled dinoflagellate cysts, and calcareous dinoflagellate cysts. Not so obviously of dinoflagellate affinity are calcareous organisms referable to the subfamily Thoracosphaeroideae Kamptner, 1928. Biological studies suggest that thoracosphaerids are in fact stages in the life cycle of a type of dinoflagellate (Tangen *et al.*, 1982). However, these differ significantly from dinoflagellates described here (Tangen *et al.*, 1982, created a new order, Thoracosphaerales, for these), and they are described in Chapter 2 in this volume.

Table 1.2: Fluxes of dinoflagellate thecae.

Station: and Depth (m)	Dinoflagellate Thecae (type numbers)											Total Flux (m ² /day)
	1	2	3	4	5	6	7	8	9	10	11	
S: 976	284	57	57	28					28		57	426
3,694	85											9.6
5,369												—
E: 389	50	14	8	70	12	10	31	4	17		43	259
988	39	19					10		10	10	15	137
3,755	39	10								10		59
5,068	97											97
P ₁ : 2,778	22											22
4,280	9											9
5,582	22						4				4	30
PB ₁ : 667			61									61
1,268												—
2,869		15										15
3,769			15									15
3,791								25			25	50

Type 1 = *Cladopyxis*
 Type 2 = *Dinophysis*
 Type 3 = *Heteraulacus*
 Type 4 = *Pyrophacus*
 Type 5 = *Protoceratium*
 Type 6 = *Ornithocercus*
 Type 7 = *Blepharocystis*
 Type 8 = *Protoperidinium*
 Type 9 = *Scrippsiella* and *Ensiculifera*
 Type 10 = *Gonyaulax*
 Type 11 = Unidentified thecae

Table 1.3: Fluxes of dinoflagellate cysts.

Station: and Depth (m)	Dinoflagellate Cysts							Total Flux (m ² /day)
	1 ^a	2 ^b	3 ^c	4 ^d	5 ^e	6 ^f	7 ^g	
S: 976	5,803	57	28		114			6,002
3,694	8,448		85		171			8,704
5,369	2,304		38		171	57		2,560
E: 389	5,353	128	19	2		35	14	5,551
988	5,595	112	29	10	63	24	48	5,857
3,755	12,422	184	136		78	349	48	13,217
5,068	13,750	136	58		78	524	38	14,584
P ₁ : 2,778	1,833	9			30	96		1,968
4,280	1,467	9			4	87		1,567
5,582	392				9			401
PB ₁ : 667	2,368	30					30	2,422
1,268	2,347	76				15	152	2,590
2,869	2,347	137			107		335	2,926
3,769	3,474	122	15			15	290	3,916
3,791	2,184	51	102				330	2,667

^acf. *Thoracosphaera albatrosiana* (see text for forms included)

^b*Calciadinellum operosum*

^c*Scrippsiella* cf. *S. trochoidea*

^dBicarbonate-type

^e?Calcareous cyst sp.

^fUnidentified calcareous cysts

^gUndifferentiated spherical brown protoperidinioid cysts

Dinoflagellate Thecae

Remains of motile dinoflagellates were of only passing interest in this study (as explained earlier). No unarmored dinoflagellates were observed, only the thecae (usually empty) of armored forms. Many were broken and partially decayed, but where possible these were identified at least to genus level. Most of these were robust types commonly recorded from open ocean plankton studies (e.g., *Blepharocystis*, *Ornithocercus*, *Cladopyxis*, *Dinophysis*, *Heteraulacus*, and *Protopteridinium*, illustrated in Plate 1.1, figures 1–6). However, small, seemingly fragile thecae were sometimes seen, and occasionally identified as species of either *Scrippsiella* (Plate 1.1, figure 9) with a distinctive plate pattern including 6 cingular plates or *Ensiculifera* with a prominent lance-like first cingular plate (Plate 1.1, figure 10).

It should be noted that *Cladopyxis* (Plate 1.1, figures 11–12) is included with the thecae since other workers have reported thecal plates in species of *Cladopyxis* (Taylor, 1976). However, no thecal plates were seen in the examples studied here, and the possibility that at least some of the specimens recorded here may be hitherto undescribed cysts is discussed later.

Organic-walled Cysts

Protopteridinium: Only a few types of organic-walled cysts were seen in sediment trap samples. Almost all of those encountered were spherical brown cysts of the type produced by many species of *Protopteridinium*. This group of cysts is one of the most difficult to identify at species level. Their simple body shape is indistinctive, and species are usually differentiated only by the diagnostic shape of the excystment aperture (the archeopyle). Often this feature is difficult to resolve in all but freshly excysted specimens, since either the cyst died before the archeopyle opened or the archeopyle shape becomes obscured by folding of the empty cyst wall. The sizes of specimens seen in the present study suggested the possibility of at least three distinct types with body diameters around 26 μm , 36 μm and 50 μm , respectively. However, archeopyle shape could not be resolved in most cases and as in many other reports they were simply recorded as undifferentiated spherical *Protopteridinium* cysts. One distinctive type was recognized, *Protopteridinium* sp. (Plate 1.1, figure 18), closely resembling *P. avellana* (Wall and Dale, 1968a) but smaller (26–30 μm diameter).

Impagidinium sphaericum (Wall) Harland, 1983 (Plate 1.1, figure 20) = *Leptodinium sphaericum* Wall, 1967, p. 108–109, Pl. 15, figs. 11, 12: This species shows diagnostic features of paraplates 1' and 4' used by Stover and Evitt (1978) to define the genus *Impagidinium*.

Dinoflagellate cyst; Form B Wall *et al.*, 1977, Pl. 1, fig. 2: A small cyst (cyst body around 36 μm diameter) with 8–10 μm long processes which are blade-like with clavate tips. First recorded from Recent shelf sediments near Pisco, Peru.

Other Organic-walled Cysts: Apart from the above types found in sediment trap samples, an assemblage composed entirely of organic-walled cysts was recovered from the bottom sediment at Station S. Percentages of the various cyst types counted are shown

Table 1.4: Dinoflagellate cyst assemblage in bottom sediment from Station S.

Dinoflagellate Cysts	Percentage Abundance
<i>Operculodinium centrocarpum</i> (Deflandre & Cookson) Wall, 1967	31
<i>Spiniferites bulloideus</i> (Deflandre & Cookson) <i>sensu</i> Wall, 1965	2
<i>S. membranaceus</i> (Rossignol) Sarjeant, 1970	<1
<i>S. elongatus</i> Reid, 1974	5
<i>S. spp.</i> (unidentified)	1
<i>Bitectatodinium tepikiense</i> Wilson, 1973	8
<i>Planinosphaeridium choanum</i> (Reid) Wall <i>et al.</i> , 1977	1
<i>Lingulodinium machaerophorum</i> (Deflandre & Cookson) Wall, 1967	<1
<i>Protoperidinium conicooides</i> (Paulsen) Balech, 1974	2
Undifferentiated spherical, brown protoperidinioid cysts)	31
<i>Peridinium faeroense</i> (Paulsen) Dale, 1977	18

in Table 1.4; additional rare specimens of *Impagidinium patulum* (Wall) Evitt and Stover, 1978, were seen in reference slides.

Calcareous Cysts

It is not always easy to identify a dinoflagellate cyst as such unless the direct link between cyst and motile stage has been established either by observing cyst formation in the motile stage or excystment producing a motile stage. Obviously, this will never be possible for most fossil cyst types, and these are defined morphologically. Occasionally, overall body shape is distinctive enough (*e.g.*, allowing recognition of fossil cysts of *Ceratium* or *Gymnodinium* affinities), but the main criteria used are evidence of paratabulation (see Evitt *et al.*, 1977, for definition) or an archeopyle. In practice, the archeopyle usually must show thecal-plate-like affinities for it to be used alone to define a dinoflagellate cyst as such.

Such morphologic definition has obvious weaknesses. For example, Lister (1970) pointed out its bias towards cysts of thecate dinoflagellates, since the cysts of forms lacking thecal plates in the motile stage may be expected to similarly lack paratabulation and distinctive archeopyles. But despite such limitations, the established morphologic definition remains the most practical approach to unknown forms. This is no less so for calcareous cysts encountered in the present study, and those recognized based on morphologic criteria are discussed below.

Calciodinellum operosum Deflandre, 1947 (Plate 1.1, figure 13; Plate 1.2, figures 1-20): This was the most easily identified calcareous cyst seen in the present study. Details of

paratabulation and archeopyle from light microscope observations agreed with those of Deflandre (1947, 1948) and Wall and Dale (1968b), while skeletal details (including the range of variability) seen in SEM agreed with the description of Fütterer (1977). The observations by Fütterer (1977, pl. 6, fig. 12) of an additional paraplate sometimes seen between paraplates 2', 4' and 3' on the operculum is confirmed here (Plate 1.2, figure 13). This is almost certainly equivalent to the apical pore characteristic for thecae of species belonging to the genera known to produce calcareous cysts, *Scrippsiella* and *Ensiculifera* (e.g., Plate 1.1, figure 9).

cf. Thoracosphaera albatrosiana Kamptner, 1963 (Plate 1.1, figures 14–15): Many cysts were seen in this study whose general morphologies agree with that of *T. albatrosiana*. Their overall appearance in light microscopy is shown in Plate 1.1, figures 14–15. Their size and archeopyle type are very similar to those of *Calciodinellum operosum*, but parasutural ridges are not developed. Details of ultrastructure from SEM observations suggest that several different types (not distinguishable in light microscopy) were probably included under this "taxon" in quantitative counts using the light microscope. These almost certainly included *T. albatrosiana* sensu Fütterer (1977) (Plate 1.3, figure 12) and the "granular form" of *T. albatrosiana* of Fütterer (1977) (Plate 1.1, figures 9–11). They may also have included *T. albatrosiana* Kamptner, 1963, sensu Fütterer (1977) (Plate 1.3, figures 1–8).

These obvious dinoflagellate cysts with distinctive archeopyles are not considered to be cogenetic with Thoracosphaeroideae. They should ultimately be removed from Thoracosphaeroideae, but formal transfer is not proposed here pending the results of culture work on this group.

Scrippsiella cf. Scrippsiella trochoidea (Stein) A.R. Loeblich III (Plate 1.4, figures 1–11): Spinose calcareous cysts generally resembling those described from *Peridinium trochoideum* by Wall and Dale (1968b) and Wall *et al.* (1970). Details of the forms encountered here seen in SEM were very similar to those described by Fütterer (1977) as *Peridinium cf. Peridinium trochoideum* (Stein) Lemmermann.

Bicarinate-type Wall and Dale, 1968b, p. 1405; text-fig. 3, 4–6; Pl. 172, figs. 14–15: A few specimens of this distinctive form were seen at one station. Size (40–50 μm) and characteristic parasutural ridge patterns agreed with the descriptions of Wall and Dale (1968b). Previously recorded from bottom sediments at Bermuda and various parts of the Caribbean region.

?Calcareous cyst sp. (Plate 1.3, figure 20; Plate 1.4, figures 12–13): A few distinctly elongate to oval calcareous tests were seen, around 25 μm in maximum width, with a skeletal ultrastructure resembling those of other dinoflagellate cysts recorded (Plate 1.4, figure 13). Though no definitive archeopyle was noted, Plate 1.3, figure 20 suggests a possible apical archeopyle.

