

# RECENT DINOFLAGELLATE CYSTS IN A TRANSECT FROM THE FALKLAND TROUGH TO THE WEDDELL SEA, ANTARCTICA

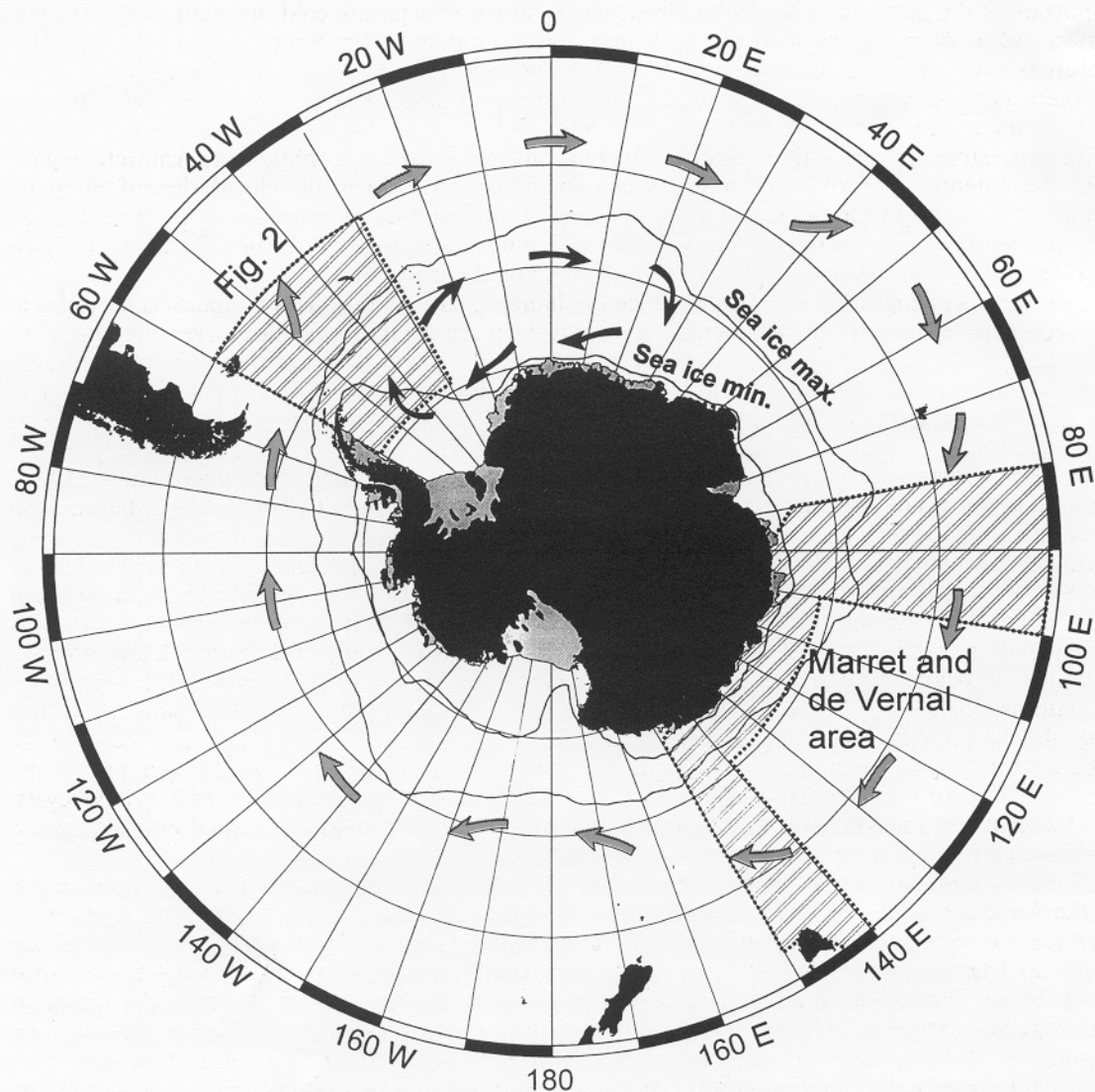
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**ABSTRACT.** Dinoflagellate cyst analysis has been completed on core-top samples that form a transect from the area of the Falkland Islands to the Weddell Sea, Antarctica. This study is the first to document the distribution of the Recent dinoflagellate cyst thanatocoenosis in the area. All the dinoflagellate cysts recovered are described and at least two species, *Dalella chathamense* and *Selenopemphix antarctica*, are recognized as endemic to the southern hemisphere from the results of this study and from previous research. Data presented here reveal a clear latitudinal trend in the cyst distribution such that subdivision into two domains is possible. The first, to the south of 60° S, is characterized by low numbers of cysts, low diversity and the presence of *Impagidinium pallidum*, *Algidasphaeridium?* *minutum*, *Pentapharsodinium dalei?*, round brown *Protoperidinium* cysts and *Selenopemphix antarctica*. The second, to the north of 60° S, is characterized by richer assemblages, higher species diversity and the presence of *Dalella chathamense*, *Impagidinium sphaericum*, *Nematosphaeropsis labyrinthus* and high numbers of *Selenopemphix antarctica*. This division of the cyst assemblages coincides approximately with the northern winter limit of sea-ice and demonstrates the potential of dinoflagellate cyst analysis in the elucidation of the palaeoceanography of the area using this criterion.

The seas around the continent of Antarctica play a major rôle in the production of the cold, dense bottom water which is largely responsible for driving the global thermohaline circulation system. Most of the world's bottom water is formed in the large embayments of Antarctica, namely the Weddell and Ross seas, with a minor secondary component deriving from the Nordic seas of the northern hemisphere. The Weddell Sea, under present interglacial conditions, is the source for about 80 per cent. of Antarctic Bottom Water (AABW), which in itself forms a major component of the thermohaline circulation (Foldvik and Gammelsrod 1988). AABW fills all of the deepest parts of the ocean basins bringing its properties of temperature, salinity and carbon isotope composition through the western Atlantic basins as far as 40° N (Kroopnick 1985).

The global thermohaline circulation system is now thought to be a major factor in driving general ocean circulation and its activity is also implicated in the fluctuations of climate that characterize the Quaternary (Broecker *et al.* 1985, 1990). Indeed, the relative stability and long residence time of water within the thermohaline circulation may well act as a buffer in preventing sudden reversals in the climate system. The production of AABW over time is an essential component to understanding of variation in the global thermohaline circulation and its response to changes in solar insolation throughout the Pleistocene. A factor in the production of this cold, dense bottom water is the seasonally variable extent and volume of Antarctic sea-ice. The greater the rate of ice growth the greater the potential formation and flux of AABW. Concern has been expressed recently over the amount of ice retreat in the Antarctic, thought to be as a result of global warming, and the possible consequences to the global circulation pattern.

The Antarctic region is also a well known and important area of upwelling and primary production, with the enhancement of diatom production being a particularly notable feature. Upwelling is caused by northward Ekman transport associated with the strong and persistent West Wind Drift or the Antarctic Circumpolar Current (ACC). This is reinforced by the action of



TEXT-FIG. 1. Map of the Antarctic continent and Southern Ocean showing the areas of the present study (Text-fig. 2) and that of Marret and de Vernal (1997). Also depicted are the maximum and minimum sea-ice limits as illustrated in the Sea Ice Climatic Atlas (1985) and the surface water circulation pattern from Nowlin and Klinck (1986). Black arrows, Weddell Gyre; grey arrows, Antarctic Circumpolar Current.

katabatic winds off the ice sheet, forcing surface water in an offshore direction and allowing the upwelling of nutrient-rich water from below the thermocline. This upwelling phenomenon occurs to the south of the Antarctic Convergence or Polar Front within the ACC in the area under discussion herein.

This unique juxtaposition of the production of cold, dense water to drive the global thermohaline circulation system and the upwelling of nutrient-rich water from depth to enhance primary production provides a potential wealth of important information to assist in detailing the changing oceanography of the area through time. In particular the enhanced primary production provides increased carbon fixing and production of a  $C_{ORG}$  flux to the accumulating bottom sediments. Also

important is the position of the Polar Front which serves to separate cold, nutrient-rich Antarctic surface water from the warmer, nutrient-poor surface waters of the South Atlantic Ocean. This feature is known to occur between about 55° S and 60° S in this area and, like its counterpart in the northern hemisphere, may have changed its geographical position over time with fluctuations in global climate.

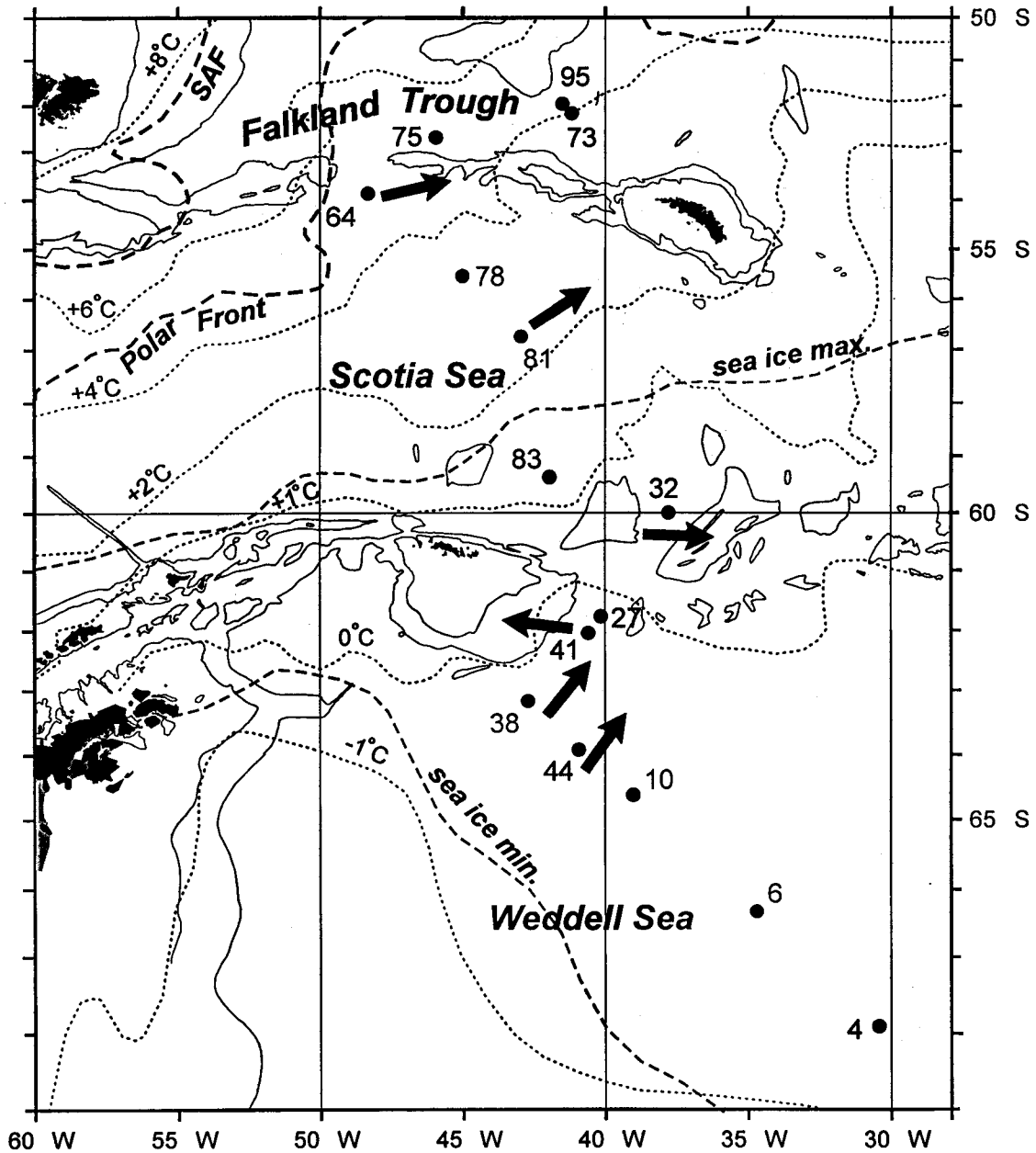
It is, therefore, apparent that temporal fluctuations in the oceanography of the Antarctic region have the potential to provide clear proxy climate signals to assist in the elucidation of changing global climate and the construction of global climate models. In addition, such time series data on the production of oceanic deep water together with data on the fixing of carbon from nutrient rich surface waters will enhance our knowledge of the global carbon budget.

Changing oceanography as a consequence of changing climate produces temporal differences in the sediment record on the continental shelf and deep sea floor, particularly over the glacial to interglacial time scale. Deep sea sediment cores which preserve a complete depositional record are of particular interest. In the Weddell Sea, Scotia Sea and Falkland Trough (Text-figs 1–2) there are extensive areas of Quaternary deposition, mainly of hemipelagic and muddy contourite facies with some sandy contourites in the Falkland Trough. The sediments have been mapped and described by Pudsey *et al.* (1988), Pudsey (1992), Howe *et al.* (1997) and Pudsey and Howe (1998). The cores were dated by magnetostratigraphy (Pudsey *et al.* 1988; O'Brien 1989), diatom and radiolarian abundance stratigraphy (Jordan and Pudsey 1992; Pudsey and Howe 1998) and by chemostratigraphy (Shimmield *et al.* 1994). Sedimentation rates are generally low (4 mm/ky) in the central Weddell Sea and increase northwards to 30–40 mm/ky near 60° S (Grunig 1991) and 70–100 mm/ky in the northern Scotia Sea and Falkland Trough. Lithofacies include muddy diatom ooze and diatom-bearing mud, with a diatom content decreasing southwards and with foraminifera present only near the Polar Front. The high primary productivity of the area and the abundance of diatoms, particularly in the Scotia Sea, pointed to the possibility that a dinoflagellate cyst record may also be present. This is especially true for the heterotrophic dinoflagellates that may well be taking advantage of the high diatom crop (diatoms are known to be one of the prey groups of some of the heterotrophic dinoflagellates). A knowledge of the population of dinoflagellate cysts, produced by both autotrophic and heterotrophic motile forms, provides potential information on both the first and second tiers of the trophic web.

This study aims to establish the occurrence of Recent dinoflagellate cysts in the surface sediments of the Antarctic region and to examine their distribution. In order to fulfil this aim a transect of core-top samples has been examined from the Falkland Trough, to the south and east of the Falkland Islands, to the Weddell Sea, east of the Antarctic Peninsula, south of the Polar Front (Text-fig. 2). This information is essential before any attempt is made to look at the temporal dinoflagellate cyst record. This study establishes a Recent dinoflagellate cyst distribution baseline in relation to the present oceanography. In this context it is important to note that very little information is available on the occurrence of modern dinoflagellate cysts in Antarctica despite the seminal work of Balech (1973, 1976) and Balech and El-Sayed (1965) on the taxonomy and distribution of motile dinoflagellates in the plankton from the area.

Recently, Marret and de Vernal (1997) published a detailed and comprehensive account of the modern distribution of dinoflagellate cysts in the southern Indian Ocean (Text-fig. 1). They recognized the presence of a latitudinal distribution trend that is similar to the distribution patterns described for the Arctic and North Atlantic oceans in the northern hemisphere. Their latitudinal distribution of dinoflagellate cysts in bottom sediments includes circum-Antarctic, Subantarctic and Antarctic domains. McMinn (1995) suggested that there are no dinoflagellate cysts in the bottom sediments of the Antarctic region, an assumption that both Marret and de Vernal (1997) and we refute.

Before the work of Marret and de Vernal (1997), no information was available for the presence or distribution of modern and Recent dinoflagellate cysts in the Southern Ocean. This situation is in marked contrast to that for the North Atlantic Ocean and Nordic Seas where considerable data are now available (see de Vernal *et al.* 1994; Matthiessen 1995; Dale 1996). Some of the more



TEXT-FIG. 2. Location map showing the area of study including the Weddell Sea, Scotia Sea and the Falkland Trough with the sites of the core-top samples and various oceanographic parameters including bottom water circulation. Bathymetry (500 m and 2000 m contours) from Tectonic Map of the Scotia Arc (1985). Summer sea surface temperature isotherms from Olbers *et al.* (1992) and maximum and minimum sea-ice limits from Sea Ice Climatic Atlas (1985). SAF is the Subantarctic Front, the northern boundary of subantarctic surface water.

reliable data-sets have been reviewed by Edwards and Andrle (1992) and plotted against known winter and summer sea surface temperature, together with depth of recovery; this has produced the best summation of dinoflagellate cyst ecology to date from the study of bottom sediments. However, bottom sediment assemblages may not, in themselves, provide all the potential information on the modern ecology of dinoflagellate cysts as the data are always severely constrained by a number of factors. Not least is that bottom sediments are often not truly modern but are an integration of the record over hundreds of years due to bioturbation within the mixed layer.

This paper describes the occurrence of Recent dinoflagellate cysts along a transect from the Falkland Trough to the Weddell Sea (Text-fig. 2). This is a preliminary attempt at providing some ecological information, from the recognition of dinoflagellate cyst assemblages in core-top samples and their relationship to the oceanography of the area. A specific aim of this study was to identify any biogeographical signal that would prove useful in elucidating changing oceanographic and climatic conditions through the Pleistocene in the Antarctic region. This is an essential precursor to the analysis of dinoflagellate cysts through time and before any further detailed ecological work is available or attempted. We believe that the study of dinoflagellate cysts in the Antarctic realm will add to the understanding of the global dynamics of oceanographic and climatic change. In particular the extent of sea-ice, and any fluctuations in the nature and strength of the ACC will have an effect on the thermohaline circulation system and the primary production in the area respectively. Using the occurrence of dinoflagellate cysts as proxies for primary production and as a tool for reconstructing the oceanography of the area over time will add to our knowledge of the Antarctic region. The use of dinoflagellate cysts as proxies for climate and oceanographic change in the Quaternary of the Atlantic Ocean is now well established; this study is a first step in using dinoflagellate cysts in the Southern Ocean to this same end.

#### OCEANOGRAPHY

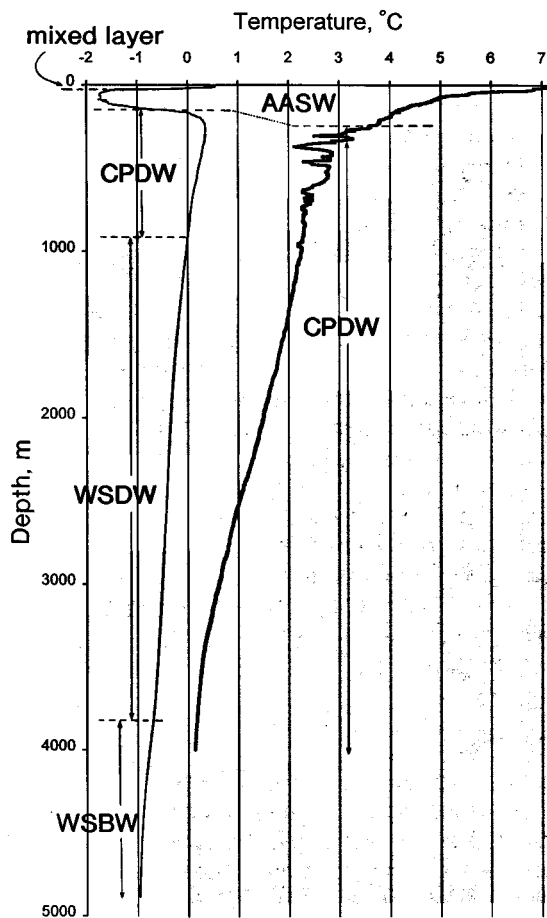
Comprehensive reviews of the oceanography of the area were given by Orsi *et al.* (1993, 1995). The Scotia Sea and Weddell Sea are dominated by two major current systems and their associated surface-water fronts. The eastward flowing ACC is wind driven, although the flow extends to the sea bed in many areas. The axis of strongest flow coincides with the position of the Polar Front. The Weddell Gyre extends from the western margin of the Weddell Sea (Text-fig. 2) to about 30° E. Flow is clockwise and mainly driven by thermohaline density contrasts in the deep water masses, although there is some wind forcing of surface waters near the coast.

##### *Water masses*

At the eastern end of the Weddell Gyre, Circumpolar Deep Water (CPDW) (Text-fig. 3) flows south and then west along the Antarctic continental margin. In the southern and western Weddell Sea, the relatively warm and saline CPDW mixes with very cold and dense shelf water. The resulting mixture is denser than the CPDW and sinks beneath it, flowing downslope as Weddell Sea Bottom Water (WSBW). Newly formed WSBW is the deepest water mass in the northern Weddell Sea; it is colder than  $-0.7$  °C and has an oxygen content of 5.75–6.00 ml/l (Text-fig. 3; Carmack and Foster 1975; Foster and Middleton 1979). It is corrosive to siliceous and calcareous microfossil tests and this, combined with low productivity consequent on the short annual ice-free period, is the reason for the low organic content of Weddell Sea sediments (Pudsey and King 1998).

Between WSBW and the warm core of CPDW at 300–400 m depth is Weddell Sea Deep Water (WSDW) with temperatures of 0 to  $-0.7$  °C. This water mass spreads through deep gaps in the topography into the southern Scotia Sea (Locarnini *et al.* 1993) and via the South Sandwich Trench into the south-western Atlantic where it is termed AABW.

In the northern Weddell Sea, CPDW has a temperature maximum of about  $0.4$  °C and its upper boundary with AASW is sharp (Text-fig. 3). In winter, the upper 150 m of the water column is close to freezing (Winter Water of Mosby 1934), but in summer a mixed layer develops, 20–30 m thick



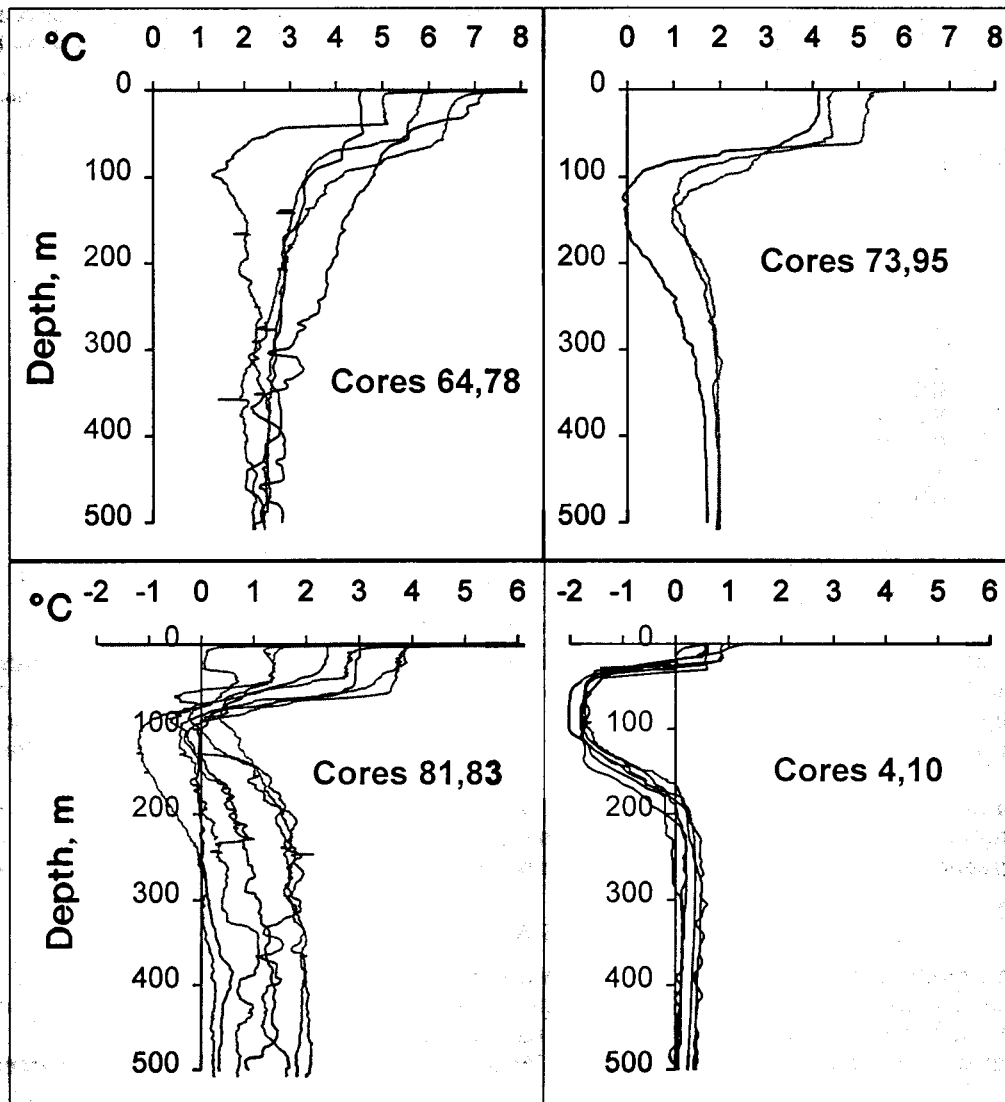
TEXT-FIG. 3. Full depth temperature profile compiled from CTD (conductivity-temperature-depth) and XBT (expendable bathythermograph) casts near the site of core-top 10 in the Weddell Sea (thin line) and near site of core-top sample 64 in the northern Scotia Sea just south-east of the Polar Front (thick line). AASW, Antarctic Surface Water; CPDW, Circumpolar Deep Water; WSBW, Weddell Sea Bottom Water; WSDW, Weddell Sea Deep Water.

and reaching 1 °C. Farther north, the summer mixed layer is deeper (to 80 m) and the AASW is warmer and merges more gradually with CPDW. Near the Polar Front, summer SST is 6–8 °C and temperature decreases downwards through the CPDW to sea bed values of 0–1 °C at 4000 m (Text-fig. 3). CPDW, being warmer and less oxygenated than WSBW, is less corrosive to siliceous and calcareous microfossil tests.

In Text-figure 4 we show temperature profiles at selected core sites, collected during several seasons from 1984–85 to 1992–93. The Weddell Sea sites (4 and 10) are characterized by low and stable temperatures. In the southern Scotia Sea (sites 81 and 83) there is considerable interannual variability, as well as spatial mixing of water masses shown by the small-scale irregularities in the profiles. Farther north at sites 64 and 78 the SST is 4–7 °C and the Winter Water from the south is scarcely discernible. North of the Polar Front at site 62, not included in this study, the region is more stable with less mixing. Interestingly, at sites 73 and 95 there is a Weddell-type temperature structure although these sites are a long way north.

#### Currents

From Drake Passage to 0° W, near surface velocities of 200–600 mm/s have been measured using current meters and drifting buoys (Nowlin and Clifford 1982; Hofmann 1985; Grose *et al.* 1995). There are few direct measurements of bottom water flow except in Drake Passage, where Bryden and Pillsbury (1977) and Whitworth *et al.* (1982) reported unsteady flow with speeds of up to



TEXT-FIG. 4. CTD and XBT profiles for the upper 500 m of the water column from areas close to the sites of the core-top samples used in this study. Cores 4 and 10 are typical of all sites from 41 southwards.

100 mm/s at *c.* 2700 m depth. Deep currents have been measured by several 1–2 year deployments of moored current meters within the area of Text-figure 2. The first results were reported by Barber and Crane (1995); bottom water flow was to the north-east at sites 44 and 38 (mean speeds of 28 and 97 mm/s respectively), to the west at site 41 (68 mm/s) and to the east near site 32 (76 mm/s). Two more moorings at the sites of cores 64 and 81 recorded mean speeds of 116 and 125 mm/s, with eastward flow (Pudsey and Howe 1998). These results are all from areas of Quaternary sediment deposition; considerably higher current speeds have been reported from rocky, non-depositional areas (Zenk 1981).

TABLE 1. Location and water depth for each of the core-top samples. All samples were taken from 0–1 mm except GC 027 which was taken from 0–2 mm. GC = gravity core; KC = Kasten core; PC = piston core; TC = trigger core.

Core	Latitude	Longitude	Water Depth (m)	Sea Area
TC 004	67° 55·7' S	30° 25·50' W	4546	Weddell Sea
TC 006	66° 20·3' S	34° 42·99' W	4694	Weddell Sea
TC 010	64° 37·9' S	39° 01·20' W	4802	Weddell Sea
TC 044	63° 56·8' S	40° 55·90' W	4548	Weddell Sea
PC 038	63° 10·1' S	42° 43·40' W	3802	Weddell Sea
TC 041	62° 03·9' S	40° 35·20' W	3310	Weddell Sea
GC 027	61° 47·3' S	40° 08·30' W	3470	Weddell Sea
TC 032	60° 00·1' S	37° 47·20' W	2915	Scotia Sea
KC 083	59° 22·2' S	41° 57·90' W	3900	Scotia Sea
KC 081	56° 44·3' S	42° 58·10' W	3662	Scotia Sea
PC 078	55° 33·0' S	45° 00·90' W	3840	Scotia Sea
KC 064	53° 52·1' S	48° 20·30' W	4304	Scotia Sea
KC 075	52° 40·7' S	45° 57·60' W	3388	Falkland Trough
KC 073	52° 09·2' S	41° 10·70' W	3760	Falkland Trough
KC 095	51° 56·5' S	41° 30·40' W	3402	Falkland Trough

#### Sea ice

The extent of sea ice varies from a minimum in early March when ice normally occupies only the western Weddell Sea, to a September maximum with the ice edge near 58° S (Sea Ice Climatic Atlas 1985, fig. 1). The pattern of melt-back is north to south in the Scotia Sea and north-west to south-east in the Weddell Sea, because of the continuous clockwise drift of the Weddell Gyre (Pudsey 1992). Cores from sites 4, 6, 10, 44 and 38 are covered by sea ice for eight to nine months of the year, sites 27, 32, 41 and 83 for three to seven months and sites 81 northwards have open water all year around. This is reflected in the diatom flora recovered in cores from the sites with the ice-related form *Fragilariopsis curta* (Van Heurck) Hustedt being rare north of 57° S (Jordan and Pudsey 1992).

#### MATERIALS AND METHODS

Fifteen core-top samples were used in this study and were taken from various types of core (Table 1) in a transect from the Falkland Trough, to the east of the Falkland Islands, through the Scotia Sea and into the Weddell Sea, to the east of the Antarctic Peninsula (Text-fig. 2; Table 1). The material was recovered as part of the British Antarctic Survey's deep-water coring programme, developed to study climate change and deep-ocean interaction across the area. Cores were taken during cruises onboard the *RRS Discovery* (1984–85 and 1987–88), and the *RRS James Clark Ross* (1993 and 1995). The core-top samples include the top 10 mm of material and, therefore, are an unavoidable integration of the dinoflagellate cyst record over the time span required to deposit that thickness of sediment. The samples were taken from the upper part of the mixed layer and their lithology and the interpreted environments of deposition are detailed in Table 2. All the samples are derived from hemipelagic and contourite areas avoiding any turbiditic sedimentation and are consistent with the known modern sedimentology.

Since we do not have unequivocal proof, from radiometric control, that this core-top material is modern we have, at this stage, made the assumption that the samples are, at least, Holocene in age. However, recent work in the north-east Atlantic Ocean has demonstrated the dynamism of the Holocene dinoflagellate cyst record through the Holocene (Harland and Howe 1995) and ongoing sedimentological research also points to the complexity of Holocene oceanography. For this preliminary study we believe that the data acquired is as close an approximation to a Recent age as can reasonably be expected, given the nature of the samples and their sedimentological regimen.



TABLE 2. Lithology, environment of deposition and mean bottom water current speed from the sampled localities.

Core	Lithology	Area	Process/Environment	Mean Current Speed	Comments
4	Clayey mud	Weddell Sea	Hemipelagic	?	Weddell abyssal plain
6	Clayey mud	Weddell Sea	Hemipelagic	16 mm/s	Weddell abyssal plain
10	Clayey mud	Weddell Sea	Hemipelagic	?	—
44	Clayey mud	Weddell Sea	Hemipelagic	32 mm/s	—
38	Clayey mud	Weddell Sea	Muddy contourite	97 mm/s	—
41	Clayey mud with diatoms	Weddell Sea	Hemipelagic	68 mm/s	—
27	Clayey mud with diatoms	Weddell Sea	Hemipelagic	?	—
32	Muddy diatom ooze	Scotia Sea	Muddy contourite	78 mm/s	—
83	Muddy diatom ooze	Scotia Sea	Pelagic biogenic	?	—
81	Diatom ooze	Scotia Sea	Muddy contourite	125 mm/s	On sediment drifts
78	Muddy diatom ooze	Scotia Sea	Muddy contourite	?	On sediment drifts
64	Diatomaceous mud with foraminifera	Scotia Sea	Muddy contourite	116 mm/s	On sediment drifts
75	Muddy diatom ooze with foraminifera	Falkland Trough	Muddy contourite	?	On sediment drifts
73	Diatom ooze	Falkland Trough	Pelagic biogenic	?	—
95	Muddy diatom ooze	Falkland Trough	Muddy/sandy contourite	?	—

TABLE 3. Raw counts of the dinoflagellate cysts in each of the core-top samples including trophic information where known or surmised. [A] = autotrophic species; [H] = heterotrophic species.

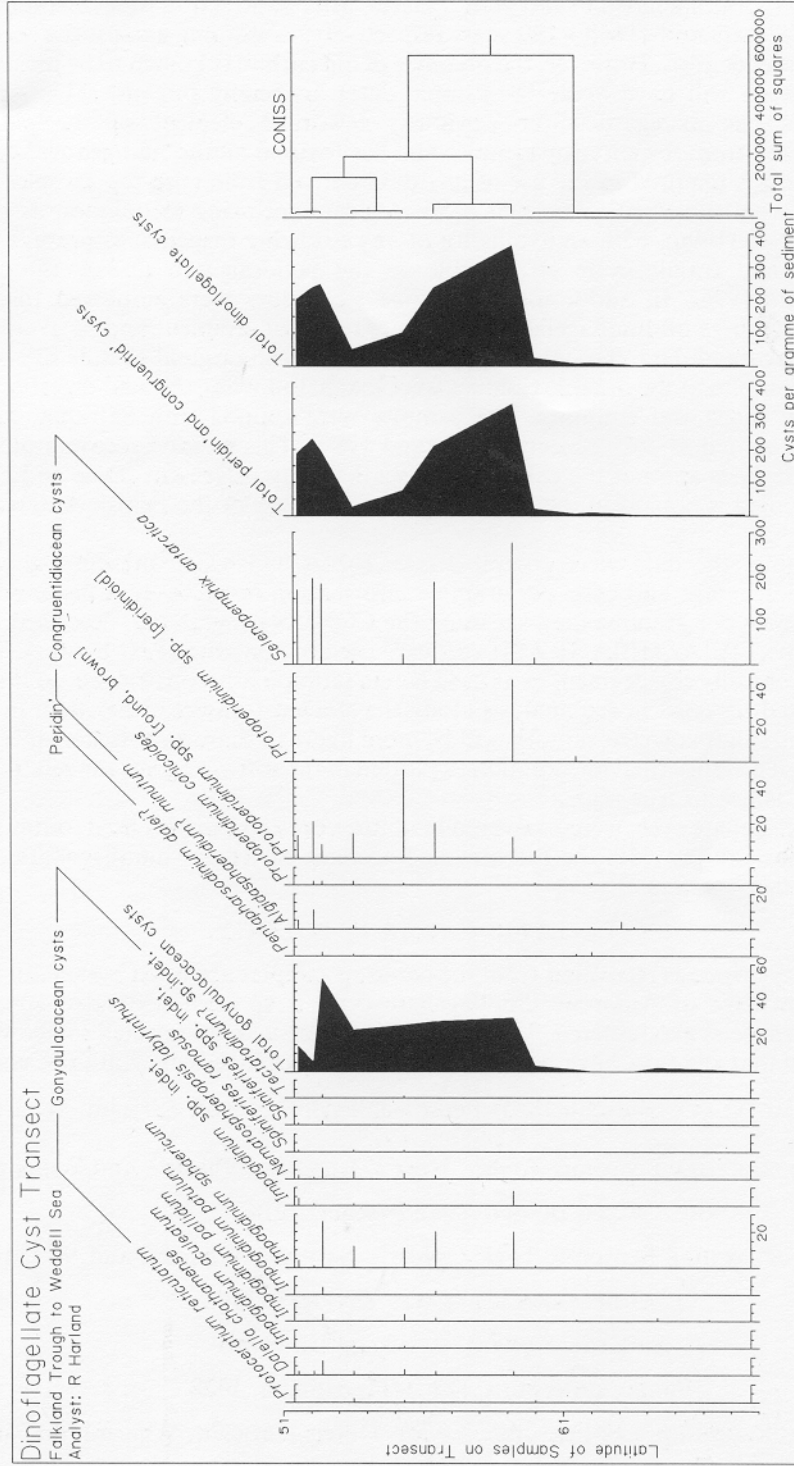
Sample Number	TC 004	TC 006	TC 010	TC 044	PC 038	TC 041	GC 027	TC 032	KC 083	KC 081	PC 078	KC 064	KC 075	KC 073	KC 095
Gonyaulacacean cysts															
<i>Protoceratium reticulatum</i> [A]	/	/	/	/	/	/	/	4	/	/	2	6	/	/	/
<i>Dalella chathamense</i> [A]	/	/	/	/	/	/	/	/	1	3	9	7	8	2	2
<i>Impagidinium aculeatum</i> [A]	/	/	/	/	/	/	/	/	/	/	2	1	/	/	/
<i>Impagidinium pallidum</i> [A]	/	3	6	/	/	/	1	/	/	2	12	/	4	/	/
<i>Impagidinium patulum</i> [A]	/	/	/	/	/	/	/	/	/	1	/	/	3	/	/
<i>Impagidinium sphaericum</i> [A]	/	/	/	/	/	/	/	1	16	31	34	42	23	1	5
<i>Impagidinium</i> spp. indet. [A]	/	/	/	/	/	/	/	2	6	/	4	1	/	1	4
<i>Nematosphaeropsis labyrinthus</i> [A]	/	/	/	/	/	/	/	/	/	2	8	13	5	1	2
<i>Spiniferites ramosus</i> [A]	/	/	/	/	/	/	/	/	/	/	2	4	/	/	1
<i>Spiniferites</i> spp. indet. [A]	/	/	/	/	/	/	/	/	/	/	/	/	1	/	1
<i>Tectatodinium?</i> sp. indet. [A]	/	/	/	/	/	/	/	/	/	/	2	/	1	/	/
Peridiniacean cysts															
<i>Pentapharsodinium dalei?</i> [A]	/	/	/	/	/	6	2	/	/	/	/	1	1	/	/
Congruentiacean cysts															
<i>Algidasphaeridium?</i> minutum [H]	4	/	/	1	11	3	/	/	/	1	/	5	/	9	6
<i>Protoperidinium conicoides</i> [H]	/	/	/	/	/	1	/	3	/	/	3	8	2	2	/
<i>Protoperidinium</i> spp. indet. [round, brown] [H]	8	1	1	/	/	/	5	12	9	32	150	47	7	18	15
<i>Protoperidinium</i> spp. indet. [peridimoid] [H]	/	2	2	/	/	1	/	/	36	/	/	/	/	1	/
<i>Selenopemphix antarctica</i> [H]	5	/	/	/	3	12	11	47	220	289	70	24	163	166	194
Total (n)	17	6	9	1	14	23	19	69	288	361	298	159	218	201	230

TABLE 4. Percentage data of the dinoflagellate cysts in each of the core-top samples.

Sample Number	TC 004	TC 006	TC 010	TC 044	PC 038	TC 041	GC 027	TC 032	KC 083	KC 081	PC 078	KC 064	KC 075	KC 073	KC 095
Gonyaulacacean															
cysts	/	/	/	/	/	/	/	5.8	/	/	0.7	3.8	/	/	/
<i>Protoceratium reticulatum</i>	/	/	/	/	/	/	/	/	0.4	0.8	3	4.4	3.7	1	0.9
<i>Dalella chathamense</i>	/	/	/	/	/	/	/	/	/	/	0.7	0.6	/	/	/
<i>Impagidinium aculeatum</i>	/	/	/	/	/	/	/	/	/	0.6	4	/	1.8	/	/
<i>Impagidinium pallidum</i>	50	66.7	/	/	/	/	5.3	/	/	0.6	/	/	1.4	/	/
<i>Impagidinium patulum</i>	/	/	/	/	/	/	/	/	0.3	/	/	/	/	/	/
<i>Impagidinium sphaericum</i>	/	/	/	/	/	/	1.5	5.6	8.6	8.6	11.4	26.4	10.6	0.5	2.2
<i>Impagidinium</i> spp. indet.	/	/	/	/	/	/	/	2.9	2.1	/	1.3	0.6	/	0.5	1.7
<i>Nematosphaeropsis labyrinthus</i>	/	/	/	/	/	/	/	/	/	0.6	2.7	8.2	2.3	0.5	0.9
<i>Spiniferites ramosus</i>	/	/	/	/	/	/	/	/	/	/	0.7	2.5	/	/	0.4
<i>Spiniferites</i> spp. indet.	/	/	/	/	/	/	/	/	/	/	/	/	0.5	/	0.4
<i>Tectatodinium?</i> spp. indet.	/	/	/	/	/	/	/	/	/	/	0.7	/	0.5	/	/
Peridiniacean cysts															
<i>Pentaparsodinium dalei?</i>	/	/	/	/	/	26.1	10.5	/	/	/	/	0.6	0.5	/	/
Congruentiacean cysts															
<i>Algidasphaeridium?</i> minutum	23.5	/	/	100	78.5	13	/	/	/	0.3	/	3.2	/	4.5	2.6
<i>Protoperidinium conicoides</i>	/	/	/	/	/	4.4	/	4.4	/	/	1	5	0.9	1	/
<i>Protoperidinium</i> spp. indet. [round, brown]	47.1	16.7	11.1	/	/	/	26.3	/	3.1	8.9	50.3	29.6	3.2	9	6.5
<i>Protoperidinium</i> spp. indet. [peridinioid]	/	33.4	22.2	/	/	4.4	/	17.4	12.5	/	/	/	/	0.5	/
<i>Selenopemphix antarctica</i>	29.1	/	/	/	21.4	52.2	57.9	68.1	76.4	80.1	23.5	15.1	74.8	92.6	84.4
Total (n)	17	6	9	1	14	23	19	69	288	361	298	159	218	201	230

TABLE 5. Cysts per gramme of sediment information of the dinoflagellate cysts in each of the core-top samples.

Sample Number	TC 004	TC 006	TC 010	TC 044	PC 038	TC 041	GC 027	TC 032	KC 083	KC 081	PC 078	KC 064	KC 075	KC 073	KC 095
Gonyaulacacean cysts															
<i>Protoceratium reticulatum</i>	/	/	/	/	/	/	/	1	/	/	1	2	/	/	/
<i>Dalella chathamense</i>	/	/	/	/	/	/	/	/	2	2	3	2	8	2	2
<i>Impagidinium aculeatum</i>	/	/	/	/	/	/	/	/	/	/	1	1	/	/	/
<i>Impagidinium pallidum</i>	/	1	2	/	/	/	1	/	/	2	4	/	4	/	/
<i>Impagidinium patulum</i>	/	/	/	/	/	/	/	/	/	2	/	/	4	/	/
<i>Impagidinium sphaericum</i>	/	/	/	/	/	/	1	20	20	20	11	12	26	1	4
<i>Impagidinium</i> spp. indet.	/	/	/	/	/	/	1	8	/	/	1	1	/	1	4
<i>Nematosphaeropsis labyrinthus</i>	/	/	/	/	/	/	/	/	2	3	4	6	1	1	2
<i>Spiniferites ramosus</i>	/	/	/	/	/	/	/	/	/	/	1	1	/	/	1
<i>Spiniferites</i> spp. indet.	/	/	/	/	/	/	/	/	/	/	/	/	2	/	1
<i>Tectatodinium?</i> spp. indet.	/	/	/	/	/	/	/	/	/	/	1	/	2	/	/
Peridiniacean cysts															
<i>Pentapaharsodinium dalei?</i>	/	/	/	/	/	2	1	/	/	/	/	1	2	/	/
Congruentiacean cysts															
<i>Algidasphaeridium? minutum</i>	1	/	/	1	4	1	/	/	/	2	/	2	/	11	5
<i>Protoperidinium conicoides</i>	/	/	/	/	/	1	/	/	/	/	1	2	2	2	/
<i>Protoperidinium</i> spp. indet. [round, brown]	1	1	1	/	/	2	4	12	20	20	50	14	8	21	13
<i>Protoperidinium</i> spp. indet. [peridinioid]	/	1	1	/	/	1	/	46	/	/	/	/	/	1	/
<i>Selenopemphix antarctica</i>	1	/	/	/	1	4	3	15	276	186	23	7	182	195	169
Total (n)	3	4	4	1	5	9	7	23	364	236	100	49	246	235	201



TEXT-FIG. 5. Cyst per gramme data from the core-top samples plotted along the transect against the latitude of the samples. Not to scale. Also plotted is the latitudinally constrained cluster analysis illustrating the division of the data into two distinct domains.

Most recently Pudsey and King (1998) have published AMS  $^{14}\text{C}$  dates for the core-top samples from core 41 and 44, both included in this study. Dates, after subtraction of a reservoir age (1430 years), are  $9560 \pm 75$  years and  $11150 \pm 190$  years respectively, cautioning against the acceptance of a fully Recent thanatocoenosis. However, the presence of old carbon is known to be present (Pudsey and King 1998) which will have made the sample dates artificially too old. This study of the dinoflagellate cysts has disregarded the obviously reworked element of the palynological assemblages recovered from the core-top samples and has focused on the 'indigenous' component. Clearly some caution is required in the use of any data derived from core-top samples.

All the samples were subjected to normal palynological processing techniques, as outlined in general by Wood *et al.* (1996), with an avoidance of any oxidizing reagents, to prevent the loss of the more delicate and fragile cysts attributable to the peridiniacean and congruentiacean dinoflagellates (Dale 1976). In addition, quantitative techniques were employed to enable the calculation of the numbers of dinoflagellate cysts per gramme of sediment and to avoid a reliance on the use of proportional data. To obtain quantitative data the original sample dry weight was noted and aliquot samples of the organic residues were taken, following the acid digestion stage, for mounting on strew slides and counting. The samples were stained with Safranin, mounted in Elvacite and were counted at  $\times 10$  objective (Harland 1989). This method recovers only organic-walled dinoflagellate cysts and not the calcareous cysts that may be present (Dale and Dale 1992). All the material studied is housed in the palynological collections of the British Antarctic Survey, Cambridge.

Following counting, the data were compiled into Tables 3–5 which present the raw counts together with the percentage and cysts per gramme information respectively. Cluster analysis was performed on the cysts per gramme data-set using the CONISS programme, described by Grimm (1987), as part of the TILIA/TILIAGRAPH software used to construct Text-figure 5. The cluster analysis is stratigraphically constrained, or as used herein latitudinally constrained, so that adjacent samples are weighted to assist in the analysis along the studied transect rather than in a random fashion. This assumes that adjacent samples will be more likely to share a characteristic than others within the transect. The latitudinal information as plotted in the software gives the relative positions of the samples but is not to true scale.

Indigenous dinoflagellate cysts were recovered in all the core-top samples used in this study. The systematic palaeontology provides the first detailed account of Recent dinoflagellate cysts to be found in these southern waters.

#### SYSTEMATIC PALAEOLOGY

The dinoflagellate cyst species recovered from the core-top samples are listed systematically below. Since existing knowledge of Antarctic dinoflagellate cysts is so poor, extended comments are included for all the species encountered. The synonymies presented are selected to show the major taxonomic changes that the taxa have undergone since first published; they are not complete.

Division DINOFLAGELLATA (Bütschli 1885) Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993

Subdivision DINOKARYOTA Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993

Order GONYAULACALES Taylor, 1980

Suborder GONYAULACINEAE (Autonym)

Family GONYAULACACEAE Lindemann, 1928

Subfamily CRIBROPERIDINIOIDEAE Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993

*Remarks.* Although the subfamily is known mostly from the fossil cyst record the modern cyst-forming genus *Protoceratium* has a recognizable cribroperidinoidean tabulation (see Dodge 1989).

#### Genus PROTOCERATIUM Bergh, 1882

*Type species.* *Protoceratium aceros* Bergh, 1882, original designation by monotypy.

*Remarks.* This genus was erected by Bergh (1882) to accommodate the type species only. Later it was accepted that *P. aceros* was a junior synonym of the previously described *Peridinium reticulatum* Claparède and Lachmann, 1859 and Bütschli (1885) effected the new combination.

#### *Protoceratium reticulatum* (Claparède and Lachmann 1859) Bütschli, 1885

##### Plate 1, figure 1

- 1859 *Peridinium reticulatum* Claparède and Lachmann, p. 405, pl. 20, fig. 3.  
 1882 *Protoceratium aceros* Bergh, p. 242, pl. 14, fig. 36.  
 1885 *Protoceratium reticulatum* (Claparède and Lachmann 1859) Bütschli, p. 1007, pl. 52, fig. 2.  
 1967 *Operculodinium centrocarpum* (Deflandre and Cookson 1955) Wall, p. 111 (*pars*), pl. 16, figs 1–2, 5.  
 1967 *Gonyaulax grindleyi* Reinecke, p. 157, pl. 1, figs A–C, text-fig. 1.  
 1997 *Operculodinium centrocarpum sensu* Wall and Dale, 1968; Marret and de Vernal, p. 387.

*Remarks.* Incubation experiments have firmly linked the cyst and motile stages of this species (Wall and Dale 1968). In the past, the cyst stage has been identified, in palynological literature, as *Operculodinium centrocarpum* (Deflandre and Cookson 1955) Wall, 1967. However, with the incubation evidence and the revision of the part of the family Gonyaulacaceae by Dodge (1989) it is now more appropriate to use the designation *Protoceratium reticulatum* (Claparède and Lachmann 1859) Bütschli, 1885 for modern cysts of this taxon and to reserve *O. centrocarpum* for those cysts clearly attributable to the separate and recognizably different Miocene taxon. Undoubtedly, there are many specimens in modern and fossil assemblages that will be difficult to assign definitively to either taxon until further information is available. In this study we agree with the views of Head (1996) and Harland and Long (1996) and use the modern extant taxon designation for our specimens.

*Discussion.* The specimens observed herein accord with the descriptions and size of material more commonly associated with the northern hemisphere and the North Atlantic Ocean (see Harland 1977). However, there was insufficient material available in this study to facilitate a full description and comparison of this southern hemisphere occurrence, let alone a full population analysis.

*Occurrence.* *Protoceratium reticulatum* occurs only in low numbers; never more than two cysts per gramme of sediment or more than 5.8 per cent. of the assemblages, and is confined to samples around and to the north of 61° S. Significantly, higher numbers of the cyst have not been seen by the authors until north of the Antarctic Convergence or Polar Front in the South Atlantic Ocean at about 48° S where we have recorded them at over 90 cysts per gramme of sediment. Marret and de Vernal (1997) recorded this species, as *Operculodinium centrocarpum*, north of the Subtropical Convergence in the southern Indian Ocean, where it dominates their Assemblage V in waters with a SST<sub>w</sub> of 13–14 °C and a SST<sub>s</sub> of 16–17 °C.

*Ecology.* This species is well known to possess an ubiquitous distribution pattern which has been summarized by Edwards and Andrieu (1992) as estuarine to oceanic and of broad thermal tolerance.

There is evidence of some ecophenotypic variation (de Vernal *et al.* 1989) but the case has yet to be fully demonstrated. Interestingly Wall *et al.* (1977, p. 146) reported that the species failed to develop distribution centres in environments with extensive coastal upwelling. It was also suggested that it may not be tolerant of non-stratified waters.

Subfamily GONYAULACOIDEAE Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993

*Remarks.* Most extant gonyaulacacean dinoflagellate cysts belong to this subfamily.

Genus DALELLA McMinn and Sun, 1994

*Type species.* *Dalella chathamense* McMinn and Sun, 1994, by original designation.

*Dalella chathamense* McMinn and Sun, 1994

Plate 1, figures 2–4

1994 *Dalella chathamense* McMinn and Sun, pp. 43, 45, pl. 1, figs 1–12.

1997 *Dalella chathamense* McMinn and Sun, 1994; Marret and de Vernal, p. 382, pl. 1, figs 1–4.

*Remarks.* This species is characterized, in particular, by its possession of a trabeculum which connects to the autocyst at the parasulcus, archeopyle margin and apex. The trabeculum consists of ribbon-like threads with a central thickened ridge. The paratabulation, as detailed by McMinn and Sun (1994) and Marret and de Vernal (1997), appears to be gonyaulacacean, sexiform with an S-type ventral organization. Specimens observed in the present study appear to conform with previous descriptions. This cyst has never undergone incubation experiments so the motile stage is unknown; the nature of the paratabulation suggests, however, an attribution to the modern genus *Gonyaulax* Diesing, 1866.

*Occurrence.* The present data show this cyst species to occur only to the north of 60° S in fairly low numbers never exceeding eight cysts per gramme of sediment or 4.4 per cent. of the assemblage. The occurrence of this species agrees well with the distribution pattern established by Marret and de Vernal (1997) and discussed below.

*Ecology.* Recent research from Marret and de Vernal (1997), using principal component analysis on a dataset of dinoflagellate cyst occurrences throughout the southern Indian Ocean, suggests that *Dalella chathamense* might be a Subantarctic endemic species, possibly oceanic in its preference, with its highest relative abundance in their Subantarctic domain (4.7 per cent.).

Genus IMPAGIDINIUM Stover and Evitt, 1978

*Type species.* *Impagidinium dispertitum* (Cookson and Eisenack 1965) Stover and Evitt, 1978, by original designation.

*Impagidinium aculeatum* (Wall 1967) Lentin and Williams, 1981

Plate 1, figure 5

1967 *Leptodinium aculeatum* Wall, p. 105, pl. 14, figs 18–19, text-fig. 3C–D.

1981 *Impagidinium aculeatum* Wall, 1967; Lentin and Williams, p. 153.



*Remarks and occurrence.* This species was identified in the present study in very minor amounts, about one cyst per gramme of sediment and less than 1 per cent of the assemblages, from two samples north of 56° S. It is probably attributable to an unidentified *Gonyaulax* species and until incubation data are available it is described under its palynological name.

*Ecology.* Edwards and Andrie (1992) summarized its ecology as outer neritic to oceanic and cool-temperate to tropical. Its occurrence in this study in such low numbers may have more to do with redeposition than with an autochthonous origin; however, it does occur in that part of the transect closest to the cool-temperate waters of the South Atlantic. Marret and de Vernal (1997) recognized *Impagidinium aculeatum* in their Subantarctic and Subtropical domains.

*Impagidinium pallidum* Bujak, 1984

Plate 1, figures 6–7

1984 *Impagidinium pallidum* Bujak, p. 187, pl. 2, figs 9–12.

1986 *Impagidinium(?) pallidum* Bujak, 1984; Mudie, p. 803, pl. 3, fig. 2.

*Remarks.* This species was attributed originally to the genus *Impagidinium* despite the absence of a clearly demonstrable paratabulation, because of the difficulty in deciphering the pale and thin-walled cysts. This led Mudie (1986) to question its affinity to the genus but without offering any extra information. Subsequent workers (Dale and Dale 1992; Matthiessen 1995) have accepted this species within *Impagidinium* and Dale and Dale (1992, pl. 3.1, figs 1–4), in particular, have published photomicrographs that are a convincing demonstration of some of the paratabulation and archeopyle formation, leading to the attribution as accepted herein. However, there remains the lack of published morphological description that adequately describes the paratabulation in detail. The material recovered in this study is not sufficiently well presented for the present authors to offer any further morphological information. This cyst is probably attributable to an unidentified *Gonyaulax* species and until incubation data are available it is described herein under its palynological name.

*Occurrence.* *Impagidinium pallidum* occurs in many of the samples analysed and was present in samples from both the Weddell Sea and the Scotia Sea together with the Falkland Trough. However, it never exceeds more than four cysts per gramme of sediment but may exceed 50 per cent. of the assemblages where the numbers of cysts recovered is very low. It was one of the few species of dinoflagellate cyst recovered in the Weddell Sea.

*Ecology.* Research to date suggests that this species is prevalent in high latitude regions and is particularly noted from the Greenland and Iceland seas (Matthiessen 1995). Marret and de Vernal (1997) recorded its most abundant distribution within the Antarctic domain where the SST<sub>w</sub> is –1–0 °C and the SST<sub>s</sub> is 3–5 °C. The occurrence of *I. pallidum* in this study is compatible with its known ecological preferences.

*Impagidinium patulum* (Wall 1967) Stover and Evitt, 1978

Plate 1, figure 8

1967 *Leptodinium patulum* Wall p. 105, pl. 14, fig. 20; pl. 15, figs 1–4; text-fig. 4.

1978 *Impagidinium patulum* (Wall 1967) Stover and Evitt, p. 166.

*Remarks.* This well-known dinoflagellate cyst has long been recognized from the northern hemisphere. Undoubtedly it has affinities to an unknown *Gonyaulax* species, but until incubation data are available the palynological name is preferred herein.

*Occurrence.* This *Impagidinium* species forms a minor component of two samples from the Scotia Sea and Falkland Trough, never exceeding more than four cysts per gramme of sediment or greater than 1.4 per cent. of the assemblages. It does not occur south of 57° S and probably has more affinity with waters to the north of the Antarctic Convergence.

*Ecology* Edwards and Andrlé (1992) summarized the ecology of this species as being outer neritic to oceanic and with a broad thermal tolerance. This study is consistent with this information.

*Impagidinium sphaericum* (Wall 1967) Lentin and Williams, 1981

Plate 1, figures 9–12

- 1967 *Leptodinium sphaericum* Wall, p. 108, pl. 15, figs 11–15, text-fig. 2a–c.  
1981 *Impagidinium sphaericum* (Wall 1967); Lentin and Williams, p. 154.

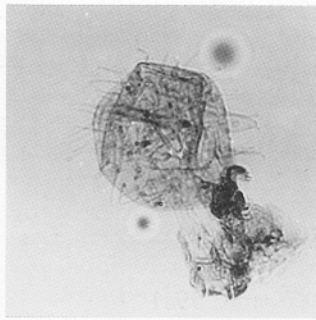
*Remarks.* This species has been identified often from bottom sediments in the northern hemisphere. As with other species of this genus, its affinities are with a species of *Gonyaulax*, but until incubation evidence is available the palynological designation is preferred.

*Occurrence.* In this study *Impagidinium sphaericum* forms an important part of the assemblages recovered in the core-top samples of both the Scotia Sea and the Falkland Trough. It does not occur south of 60° S but appears to be a major constituent in the northern part of the transect in contrast with other members of the genus. Numbers of cysts reach 26 cysts per gramme of sediment and up to 26.4 per cent. of the assemblages.

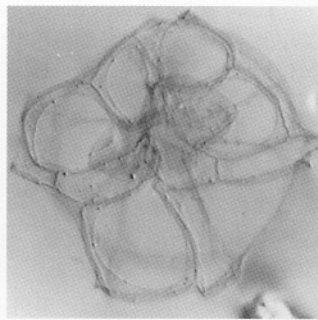
*Ecology.* Like other constituent species of the genus Edwards and Andrlé (1992) summarized this species as having outer neritic to oceanic preferences in cool temperate to tropical environments.

EXPLANATION OF PLATE 1

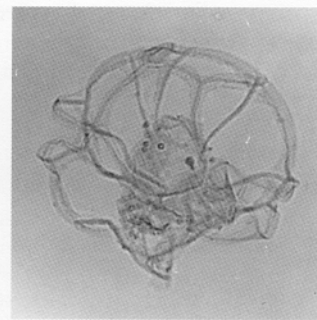
- Fig. 1. *Protoceratium reticulatum* (Claparède and Lachmann 1859) Bütschli, 1885; JR04/KC064/0.0-0.01/A2; Falkland Trough; orientation unknown, high focus showing the overall morphology.
- Figs 2–4. *Dalella chathamense* McMinn and Sun, 1994. 2, JR04/KC064/0.0-0.01/B2; Falkland Trough; dorsal view, high focus showing the paratabulation outlined by the trabeculae. 3, JR04/PC078/0.0-0.01/B1; Scotia Sea; slightly oblique dorsal view, high focus showing the paratabulation and faint 3" archeopyle. 4, JR04/KC075/0.0-0.01/A1; Falkland Trough; orientation unknown, high focus showing the overall appearance.
- Fig. 5. *Impagidinium aculeatum* (Wall 1967) Lentin and Williams, 1981. JR04/PC078/0.0-0.01/A3; Scotia Sea; oblique dorsal view, high focus showing the overall morphology and the 3" archeopyle.
- Figs 6–7. *Impagidinium pallidum* Bujak, 1984. 6, JR04/KC081/0.0-0.01/A2; Scotia Sea; orientation unknown, possibly antapical, low focus, showing the enigmatic morphology of this cyst species. 7, JR04/PC078/0.0-0.01/A1; Scotia Sea; orientation unknown, low focus showing the general nature of the morphology.
- Fig. 8. *Impagidinium patulum* (Wall 1967) Stover and Evitt, 1978. JR04/KC075/0.0-0.01/A7; Falkland Trough; oblique right lateral view, high focus showing the paratabulation on the hypocyst and the 3" archeopyle at the top left of the photomicrograph.
- Figs 9–12. *Impagidinium sphaericum* (Wall 1967) Lentin and Williams, 1981. 9–10, JR04/KC064/0.0-0.01/B1; Falkland Trough. 9, slightly oblique dorsal view, low focus showing the paratabulation and 3" archeopyle. 10, ventral view, high focus showing the detail of the ventral paratabulation. 11–12, JR04/KC064/0.0-0.01/A1; Falkland Trough. 11, dorsal view, low focus showing the paratabulation and 3" archeopyle. 12, ventral view, high focus showing the detailed paratabulation of the parasulcus and the prominent apical boss.
- All photomicrographs taken under plane polarized light, except fig. 2 taken with Nomarski interference contrast; all  $\times 500$ .



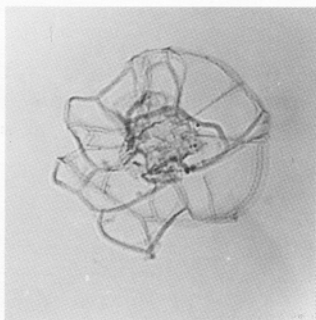
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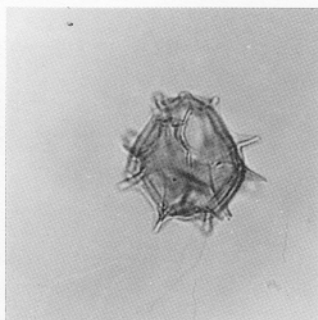
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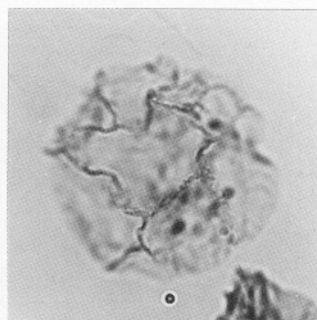
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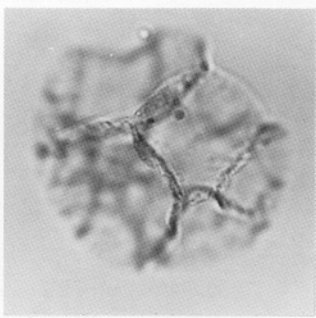
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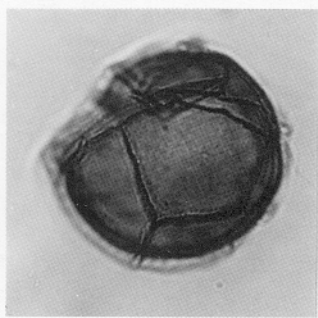
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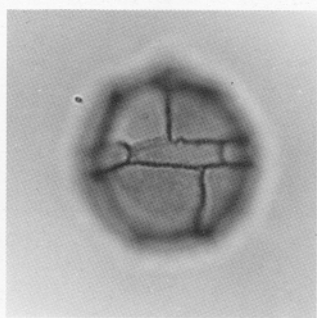
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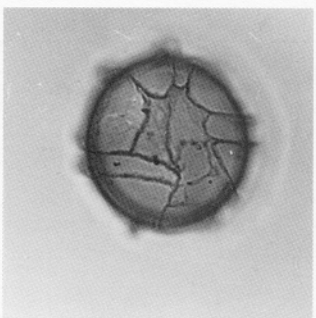
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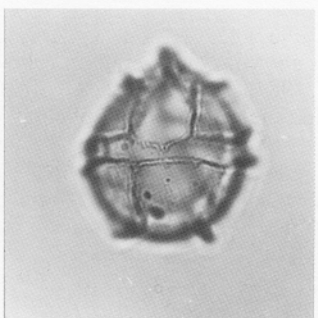
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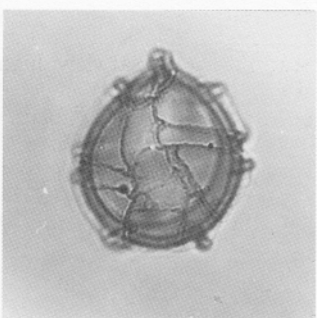
9



10



11



12

The prominence of *I. sphaericum* in this study may suggest a potential indicator of particular ecological circumstances. Marret and de Vernal (1997) noted its presence in bottom sediments within their Subantarctic to Subtropical domains.

*Impagidinium* spp. indet.

*Remarks.* This category includes all those forms that are broken, crushed or in an unadvantageous orientation to preclude definitive identification to species level. This category forms a minor part of the assemblages north of about 60° S and so is consistent with the record of occurrence for most of the *Impagidinium* spp. described above except for *I. pallidum*.

Genus NEMATOSPHAEROPSIS Deflandre and Cookson, 1955 emend. Wrenn, 1988

*Type species.* *Nematosphaeropsis balcombiana* Deflandre and Cookson, 1955, by original designation.

*Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid, 1974

Plate 2, figures 1–2

1903 *Pterosperma labyrinthus* Ostenfeld, p. 578, fig. 127.

1974 *Nematosphaeropsis labyrinthea* (Ostenfeld 1903); Reid, p. 592, pl. 1, figs 8–9.

*Remarks.* Despite this species being a well known component of modern dinoflagellate cyst assemblages its taxonomy is controversial (see Head and Wrenn 1992). Originally described as a prasinophyte from plankton collected in the Faeroes area, the species was recombined into the dinoflagellate cyst genus *Nematosphaeropsis* by Reid (1974). However, Wrenn (1988) argued that the species concept was untenable for a number of reasons: the original descriptions and line drawings could not be compared with Reid's (1974) material; there was no type material; and the morphology as described by Ostenfeld (1903) did not allow an unequivocal assignment to the Dinoflagellata. Wrenn (1988) suggested that the name *Nematosphaeropsis lemniscata* Bujak, 1984 emend. Wrenn, 1988 be applied to the species described by Reid (1974) with the original epithet remaining solely for the original discovery. For the moment, however, and until a comprehensive study of modern material from the type area has been achieved, the original epithet is preferred to maintain nomenclatural stability; to accept that Ostenfeld's *P. labyrinthus* is really a dinoflagellate cyst; and that Reid (1974) was correct in his recombination. Unfortunately the specimens recovered in the present study do not add any new useful information to support either case within the argument. This species is known to have affinities with *Gonyaulax spinifera* (Claparède and Lachmann 1859) Diesing, 1866 by incubation experiments (Wall and Dale 1968).

*Occurrence.* This species occurs only in the northern end of the transect to the north of 57° S always in small numbers, never exceeding six cysts per gramme of sediment or 8.2 per cent. of the assemblages.

*Ecology.* According to the summary published by Edwards and Andrie (1992) *Nematosphaeropsis labyrinthus* occurs in inner neritic to oceanic environments and has a broad thermal tolerance. However, Marret and de Vernal (1997) noted from their observations and those of McMinn and Sun (1994) that the species is most abundant where the SST<sub>w</sub> are 6–13 °C and the SST<sub>s</sub> are 8–17 °C. Baumann and Matthiessen (1992) suggested that the species prefers colder oceanic environments.

Recent research on high resolution samples of Holocene sediments from the North Atlantic (Harland and Howe 1995) suggested that the ecology of *N. labyrinthus* is perhaps rather more complex than it at first appears and is in need of further study.

Genus SPINIFERITES Mantell, 1850 emend. Sarjeant, 1970

*Type species.* *Spiniferites ramosus* (Ehrenberg 1838) Mantell, 1854, by subsequent designation.

*Spiniferites ramosus* (Ehrenberg 1838) Mantell, 1854

Plate 2, figure 3

1838 *Xanthidium ramosus* Ehrenberg, pl. 1, figs 1–2, 5.

1854 *Spiniferites ramosus* (Ehrenberg 1838) Mantell, p. 239.

*Remarks.* This species has a long history that dates back to the first discovery of dinoflagellate cysts. The holotype was not designated originally, but a lectotype was established by Davey and Williams (1966). Specimens of the species clearly belonging to the genus *Spiniferites* have long been recovered from modern sediments and many of them have been attributed to this species and also to *Spiniferites bulloideus* (Deflandre and Cookson 1955) Sarjeant, 1970. Harland (1977) discussed some of the difficulties in reconciling the identifications of specimens to either *S. ramosus* or to *S. bulloideus* and, after a review of the current literature, regarded *S. bulloideus* as a subjective junior synonym of *S. ramosus*. Subsequent to this, various research workers have used both names for cysts with essentially identical morphologies (see Harland 1977, pl. 1, figs 5–6). The difficulty remains and is intrinsic in the use of a name established in the fossil literature for a modern cyst that is assumed to have an affinity to the thecate dinoflagellate *Gonyaulax spinifera* (Claparède and Lachmann 1859) Diesing, 1866; despite some references in the literature, *Spiniferites ramosus sensu stricto* has never been incubated whereas *Spiniferites bulloideus sensu* Wall and Dale 1968 has successfully hatched to produce *Gonyaulax scrippsae* Kofoid, 1911. Until further incubation work is completed, this taxon will remain the focus of much controversy. We follow the argument of Harland (1977) and maintain this species within the taxon *Spiniferites ramosus* until further evidence becomes available.

*Occurrence.* This species is a very minor component of the assemblages and is to be found at the northern end of the transect to the north of 56° S. It does not occur in numbers greater than one cyst per gramme of sediment or more than 2.5 per cent. of the assemblages.

*Ecology.* This well known if somewhat controversial species is regarded by Edwards and Andrieu (1992) as estuarine to outer neritic in habit with a broad thermal tolerance. Marret and de Vernal (1997) do not record this cyst type in their Antarctic or Subantarctic domains. The extremely low numbers observed in this study are not inconsistent with the findings of Marret and de Vernal (1997).

*Spiniferites* spp. indet.

*Remarks.* This informal grouping includes all the dinoflagellate cyst specimens that show an affinity to the genus but cannot be identified to species level. It includes specimens that do not show clear morphological detail because of either poor orientation, being obscured by debris or by being broken. It is assumed that this informal grouping has affinities with the modern genus *Gonyaulax* Diesing, 1866.

*Occurrence.* These cysts form a minor component in samples that are found north of 53° S and never make up more than 0.5 per cent. of the assemblages.

*Ecology.* *Spiniferites* spp. are regarded as neritic in their habitat from the arctic to the tropics. Further comment is unwarranted on these indeterminate specimens.

#### Genus TECTATODINIUM Wall, 1967 emend. Head, 1994

*Type species.* *Tectatodinium pellitum* Wall, 1967 emend. Head, 1994, by original designation.

*Tectatodinium?* sp. indet.

Plate 2, figure 4

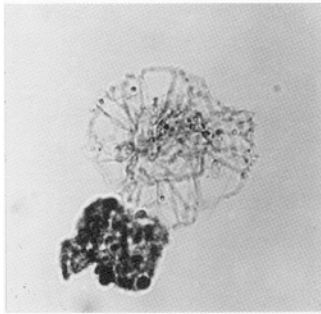
*Remarks.* Specimens attributed to this informal category are ovoidal and possess an indeterminate archeopyle. The wall structure has not been determined in detail, and this, with the indeterminate nature of the archeopyle, precludes firm assignment to the genus. It might prove to be the case that the specimens in question are the internal endocysts of reworked cavate cysts; the low numbers and sporadic occurrence preclude further comment.

*Occurrence.* These specimens occur only in two samples situated north of 56° S in the transect and never exceed 0.7 per cent. of the assemblages.

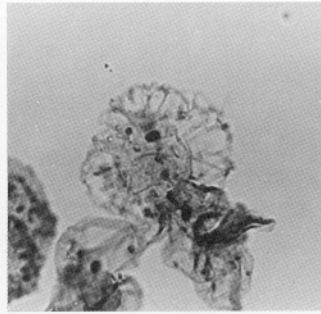
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#### EXPLANATION OF PLATE 2

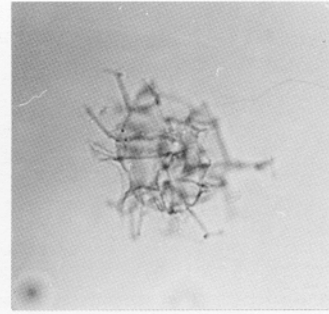
- Figs 1–2. *Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid, 1974. 1, JR04/KC064/0.0-0.01/A3; Falkland Trough; orientation unknown, high focus showing the overall trabeculate morphology. 2, JR04/KC073/0.0-0.01; Falkland Trough; orientation unknown, high focus showing the general morphology.
- Fig. 3. *Spiniferites ramosus* (Ehrenberg 1838) Mantell, 1854; JR096/KC095/0.0-0.01; Falkland Trough; oblique ventral view, low focus showing the typical spiniferate morphology.
- Fig. 4. *Tectatodinium?* sp. indet.; JR04/KC075/0.0-0.01/A8; Falkland Trough; possible dorsal view, low focus showing the precingular archeopyle and overall morphology.
- Fig. 5. *Pentapharsodinium dalei* Indelicato and Loeblich III, 1986?; D172/TC041/0.0-0.01; Weddell Sea; orientation unknown, high focus showing the overall nature and the bifurcations at the distal tips of the processes.
- Figs 6–7. *Algidasphaeridium?* *minutum* (Harland and Reid 1980) Matsuoka and Bujak, 1988. 6, D154/TC004/0.0-0.01; Weddell Sea; orientation unknown, high focus showing the overall nature of the morphology. 7, D154/PC038/0.0-0.01; Weddell Sea; orientation unknown, high focus showing the general morphology.
- Figs 8–9. *Protoperidinium conicoides* (Paulsen 1905) Balech, 1974. 8, D172/TC032/0.0-0.01; Scotia Sea; dorsal view, high focus showing the 2a archeopyle and nature of the overall morphology. 9, JR04/KC073/0.0-0.01/B1; Falkland Trough; dorsal view, high focus showing the intercalary 2a archeopyle with the operculum within the cyst.
- Figs 10–12. *Selenopemphix antarctica* Marret and de Vernal, 1997. 10, JR04/KC075/0.0-0.01/A5; Falkland Trough; apical view, high focus showing the intercalary 2a archeopyle and the nature of the granulations on the surface of the cyst. 11, JR04/KC073/0.0-0.01/B3; Falkland Trough; apical view, high focus showing the archeopyle and surface ornamentation. 12, JR04/KC073/0.0-0.01/B2; Falkland Trough; apical view, high focus showing the overall morphology of the cyst.
- All photomicrographs taken in plane polarized light; all  $\times 500$ .



1



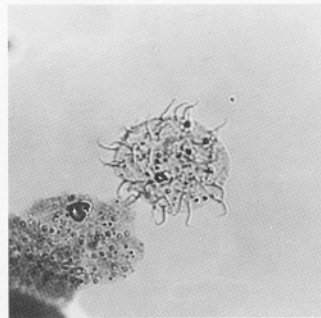
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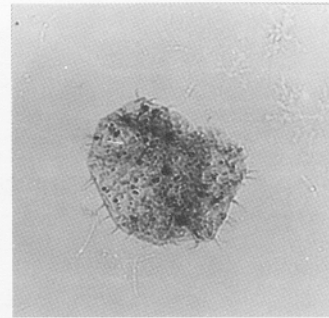
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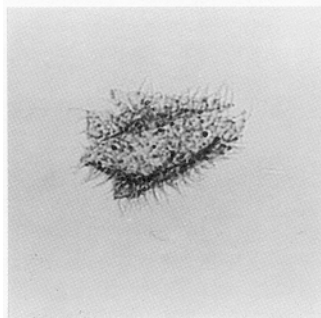
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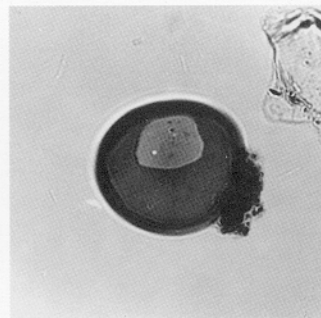
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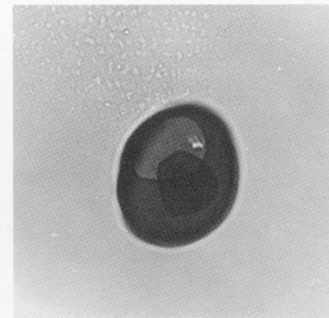
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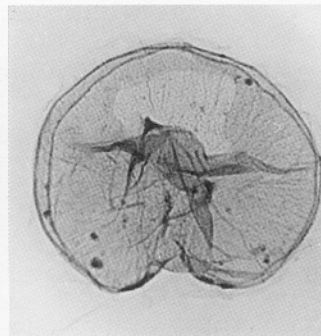
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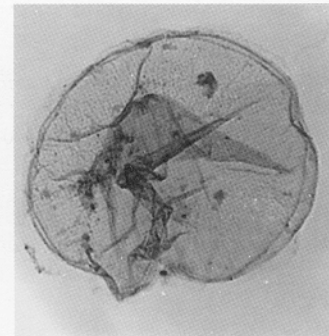
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11



12

Order PERIDINIALES Haeckel, 1894  
 Suborder PERIDININEAE (Autonym)  
 Family PERIDINIACEAE Ehrenberg, 1831  
 Subfamily uncertain

Genus PENTAPHARSODINIUM Indelicato and Loeblich III, 1986

*Type species.* *Pentapharsodinium dalei* Indelicato and Loeblich III, 1986, by original designation.

*Remarks.* This genus was erected as part of an attempt to clarify some of the taxonomic difficulties surrounding the scrippsielloid dinoflagellates. The genus is in part characterized by the possession of five cingular plates (4+t) and a wholly organic cyst.

*Pentapharsodinium dalei?* Indelicato and Loeblich III, 1986

Plate 2, figure 5

- 1977 *Peridinium faeroense* Paulsen, 1905; Dale, p. 243, figs 1-5, 7-8, 10-11, 14-19, 21, 23-25, 27-30.  
 1986 *Pentapharsodinium dalei* Indelicato and Loeblich III, p. 158.

*Remarks.* Cysts of this dinoflagellate were first incubated by Dale (1977) and identified as *Peridinium faeroense*. It is often a difficult cyst to identify in palynological preparations because of its small size and its propensity for attracting adhering organic material. Later Indelicato and Loeblich III (1986) described this taxon as a new species within their new genus *Pentapharsodinium*. The present authors have followed this taxonomic assignment. However we have questionably assigned some of our material to this taxon for the moment and until fuller comparisons with the northern hemisphere specimens are achieved. Recent work by Buck *et al.* (1992) on a dinoflagellate cyst morphotype from the Antarctic sea-ice opens the possibility that further cyst types might be present and that particular care should be exercised in the identification of small, inconspicuous cyst morphotypes.

*Occurrence.* This species occurs in small numbers, never more than two cysts per gramme of sediment but up to 26.1 per cent of assemblages with a low number total, at both the southern and northern ends of the transect. It is one of the few cyst species that occurs in some of the Weddell Sea core-top samples.

*Ecology.* Dale (1977) recorded this species from fjörds and embayments in the north temperate regions of the North Atlantic and north-eastern Pacific Ocean. Matthiessen (1995) noted its presence in the neritic, cold temperate regions of the Norwegian-Greenland seas. It is perhaps not inconsistent to record its presence in this study. It was observed by Marret and de Vernal (1997) only in surface samples from south-western Australia and, except for a single record, not from their Antarctic or Subantarctic domains.

Family CONGRUENTIDIACEAE Schiller, 1935  
 Subfamily CONGRUENTIDIOIDEAE (Autonym)

Genus ALGIDASPHAERIDIUM Matsuoka and Bujak, 1988

*Type species.* *Algidasphaeridium capillatum* Matsuoka and Bujak, 1988, by original designation.

*Remarks.* This genus was erected to accommodate small, spiny cysts with a chasmic archeopyle. Matsuoka and Bujak (1988) assigned the genus to the order Gymnodiniales Lemmermann, 1910 on



the basis that chasmic archeopyles had previously been observed on modern gymnodinialean cysts of the genera *Pheopolykrikos* Chatton, 1933 and *Cochlodinium* Schütt, 1896. However, there are no incubation data available to support their claim. For the moment, we prefer the more conservative assignment to the Peridiniales, on their general morphology and similarity to cysts described in the literature under the cyst genus *Multispinula* Bradford, 1975, which is attributable by incubation to the modern genus *Protoperidinium*. Incubation research will eventually provide unequivocal information on the assignment of this cyst taxon to its parental thecate dinoflagellate.

*Algidasphaeridium?* *minutum* (Harland and Reid 1980) Matsuoka and Bujak, 1988

Plate 2, figures 6–7

1980 ?*Multispinula minuta* Harland and Reid, p. 216, fig. 2M–O.

1988 *Algidasphaeridium?* *minuta* (Harland and Reid 1980) Matsuoka and Bujak, p. 36.

*Remarks.* In the present controversy over the correct assignment of this taxon, we are satisfied that the polygonal archeopyle as observed by Matthiessen (1995) and the similarity of the taxon to some forms previously attributed to *Multispinula* justify its inclusion within the Peridiniales. However, the general uncertainty over the detailed morphology and archeopyle type together with the lack of incubation data argues for its conservative interim retention in *Algidasphaeridium*, rather than any attempt to recombine the taxon into *Protoperidinium*. Incubation experiments will undoubtedly provide the necessary definitive information to allow the correct taxonomic and systematic assignment in the future.

*Occurrence.* This species occurs throughout the transect and is one of the few species that is present in the southern part within the Weddell Sea. However its most prominent occurrence, at 11 cysts per gramme of sediment and 4.5 per cent. of the assemblage, occurs at core-top KC 073. Higher percentages are recorded at other sites but based upon poor cyst recovery of only one or two specimens in total.

*Ecology.* *Algidasphaeridium?* *minutum* was noted in low percentages in the Subantarctic and Subtropical domains of Marret and de Vernal (1997). It is a species associated with polar and subpolar waters in the North Atlantic Ocean and Nordic Seas (Dale 1996). Its presence in this study lends support to its characterization as a high latitude cold water indicator.

GENUS PROTOPERIDINIUM Bergh, 1881 emend. Balech, 1974

*Type species.* *Protoperidinium pellucidum* Bergh, 1881, by subsequent designation by Loeblich Jr and Loeblich III (1966).

*Remarks.* This genus accommodates, for the most part, the marine species formerly belonging to the genus *Peridinium* Ehrenberg, 1830. The diagnosis of the genus was emended by Balech (1974) who also provided a taxonomic framework at the subgeneric level on the detailed tabulation of the thecae. The consequence of this action on the systematics of various cyst taxa was explored by Harland (1982) but is not adopted by the present authors as insufficient taxa were available in the present study to warrant use of this further hierarchy. It should be noted that many species within this taxonomic grouping have a heterotrophic habit and therefore occupy quite a different position in the trophic web from the gonyaulacacean autotrophic dinoflagellates described above.

*Protoperidinium conicoides* (Paulsen 1905) Balech, 1974

Plate 2, figures 8–9

1905 *Peridinium conicoides* Paulsen, 1905, p. 3, fig. 2.

1974 *Protoperidinium conicoides* (Paulsen 1905) Balech, 1974, p. 58.

*Remarks.* Although a successful incubation experiment was not achieved by Wall and Dale (1968) acetolysis of thecae with enclosed cysts almost certainly established the relationship between the parent theca and cyst which, in palynological literature, has long been known as *Brigantedinium simplex* Wall, 1965 *ex* Lentin and Williams, 1993. This species is one of several that is often grouped within the so called 'round, brown' cysts whose morphology of a simple, brown spheroidal body can lead to confusion when the specimens are orientated unfavourably or are crushed so as to obscure the nature of the archeopyle. The archeopyle is virtually the only distinguishing morphological feature of this group of cysts.

*Occurrence.* *Protoperidinium conicoides* occurs in small numbers throughout the transect, never more than eight cysts per gramme of sediment were recorded or 5 per cent. of the assemblages, but it is more than likely that poorly orientated and crushed specimens have also been included in the counts for the unidentified, round, brown *Protoperidinium* cysts.

*Ecology.* Edwards and Andrie (1992) characterize the ecology of this cyst as inner neritic to oceanic and arctic to warm temperate. Dale (1996) also regards this taxon as having a polar to temperate distribution. The occurrence of this cyst species in the present study is, therefore, consistent with our present knowledge. Indeed Dale (1996) also noted its occurrence in the coastal regions of Antarctica and southern Chile. Marret and de Vernal (1997) described its presence as part of their *Brigantedinium* spp. grouping where it is especially dominant in the Subantarctic domain. They also noted that much of its distribution may be the result of its dependence on the distribution of diatoms, as it is a heterotrophic species and diatoms are often used as a food source. Its position in the trophic web is quite different from that of the autotrophic dinoflagellate species. Undoubtedly the heterotrophic nature of this taxon affects its distribution pattern as its survival strategy is different to that of autotrophs and it may not be so dependent on the intrinsic SST and SSS except inasmuch as it affects the distribution of its preferred food.

*Protoperidinium* spp. indet. [round, brown]

*Remarks.* This taxonomic category includes all the round, brown *Protoperidinium* cysts that could not be speciated because of their orientation or compression. Many such cysts probably belong to the taxon *Protoperidinium conicoides* described above, but unless a clearly defined archeopyle is present a definitive identification cannot be made. It may also include other species of *Protoperidinium* that possess this conservative round, brown morphology.

*Occurrence.* These cysts were recovered throughout the transect but occurred in higher numbers to the north of 60° S where up to 50 cysts per gramme of sediment were recovered with percentages of up to 50.3 per cent.

*Ecology.* It is impossible to give any detailed ecological information for this taxon as it may include several species with different ecological requirements. However, it is likely that most if not all of this group are heterotrophic and are therefore largely controlled by the distribution and numbers of their preferred prey. It is not surprising that in this area of upwelling and high productivity that large numbers of this group, including *Protoperidinium conicoides*, should be strongly represented.

*Protoperidinium* spp. indet. [peridinioid]

*Remarks.* A second group of undifferentiated *Protoperidinium* cysts is included in this study and these have a recognizable pentagonal peridinioid morphology. Unfortunately, insufficient morphological detail was available to identify them to species level because of poor orientation,

compression or the obscuring of detail by organic debris. It is possible that a new species may be present in sample KC 083, but insufficient specimens were available for a detailed taxonomic study.

*Occurrence.* This group of cysts occurs in very low numbers and sporadically through the transect. High numbers, up to 46 cysts per gramme of sediment, occur in one sample only and may represent a new species. Further work is expected to clarify this observation.

*Ecology.* It is impossible to outline any meaningful ecology for this group of dinoflagellate cysts except to reiterate the possibility that, with their affinities to the genus *Protooperidinium*, they are also probably heterotrophic in their nutritional habits.

#### Genus *Selenopemphix* Benedek, 1972 emend. Head, 1993

*Type species.* *Selenopemphix nephroides* Benedek, 1972, by original designation.

*Remarks.* The emended definition published by Head (1993) recognizes polar compression as a key feature in its characterization and to separate it from *Lejeunecysta* Artzner and Dörhöfer, 1978 emend. Bujak, 1980. However, incubation evidence has for some considerable time linked cysts with a *Selenopemphix* morphology to the dinoflagellate genus *Protooperidinium*. Undoubtedly, cysts of this genus should be subsumed into *Protooperidinium*, as attempted by Harland (1982), but not largely recognized. For the moment we prefer the use of the newly published cyst taxonomy for the species until other definitive evidence is available.

#### *Selenopemphix antarctica* Marret and de Vernal, 1997

Plate 2, figures 10–12

1997 *Selenopemphix antarctica* Marret and de Vernal, p. 389, pl. 5, figs 1–5.

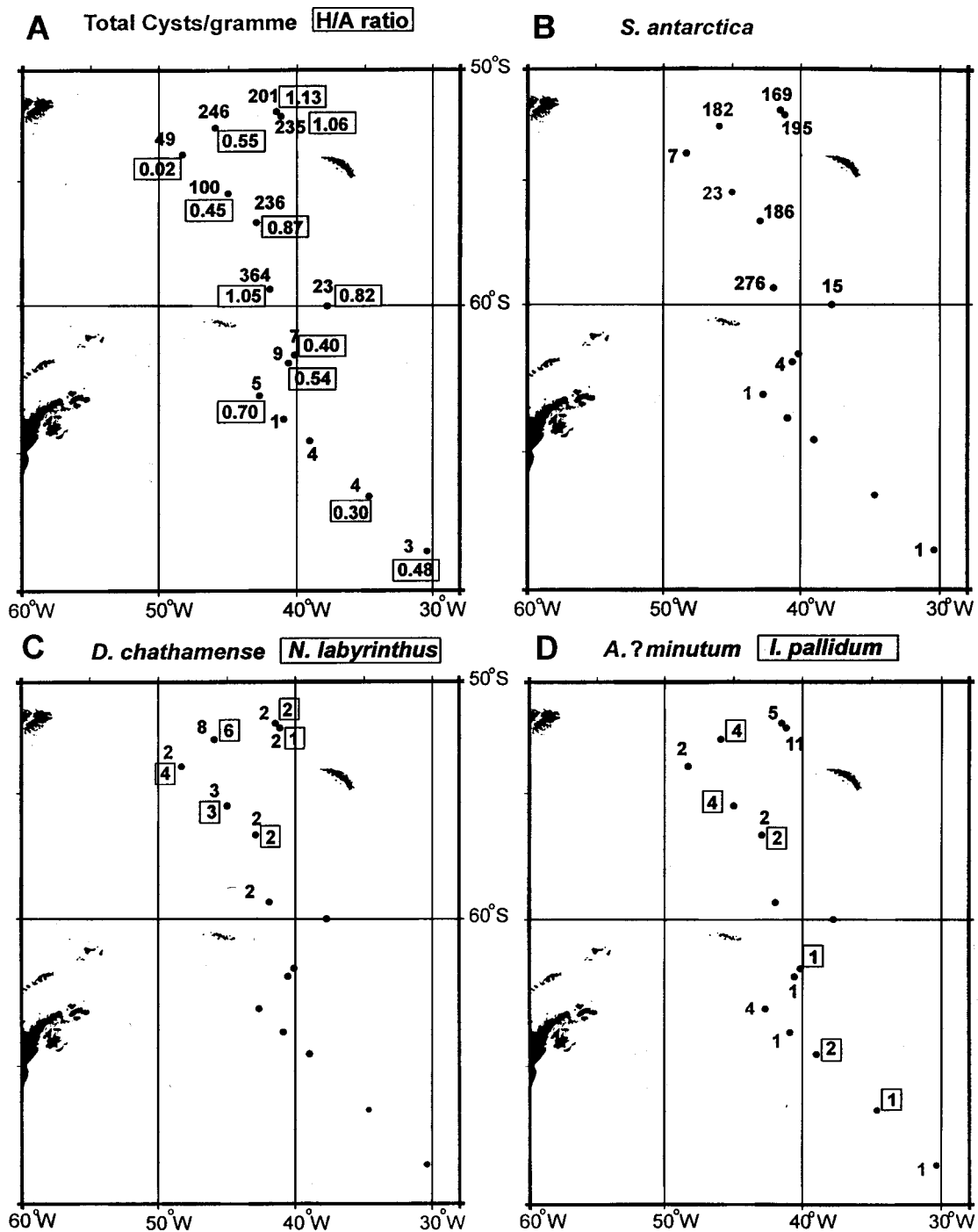
*Remarks.* This species is a conspicuous and characteristic component of dinoflagellate cyst assemblages in the present study. It is identifiable from its possession of two antapical horns and the granulations on the cyst surface that are concentrated around and on top of the apical and antapical horns. To date it has only been described by Marret and de Vernal (1997) and ourselves, but its prominence in southern hemisphere high latitude assemblages will undoubtedly lead to its recognition in other material. It is anticipated that this cyst species is derived from the genus *Protooperidinium* but confirmation of this must await incubation work.

*Occurrence.* *Selenopemphix antarctica* is a prominent component of the dinoflagellate cyst assemblages from the northern half of the transect to the north of 60° S where it forms the dominant species in the assemblages. Up to 276 cysts per gramme of sediment have been recorded and percentages as high as 92.6 per cent. It has also been observed in low numbers in the more southerly samples from the Weddell Sea.

*Ecology.* Marret and de Vernal (1997) recorded this species from the southern Indian Ocean to the south of 40° S dominating assemblages of their Antarctic and Subantarctic domains. In these areas the SST averages –1.8–0 °C in summer and freezes in the winter. They believed that *Selenopemphix antarctica* can be associated with cold waters and seasonal ice cover and that the species is endemic to high latitudes in the southern hemisphere.

## RESULTS

Dinoflagellate cyst analysis of core-top samples has been completed on a transect from the Falkland Trough to the Weddell Sea (Text-fig. 6). The basic numerical data are shown in Tables 3 to 5 and include the raw counts, the percentages and the numbers of cysts per gramme of sediment. Rather than attempt to draw a whole series of distribution maps along the transect, one or two examples



TEXT-FIG. 6. Maps of the distribution of dinoflagellate cysts along the studied transect. A, total cysts per gramme of sediment and H/A ratio. B, *Selenopemphix antarctica*. C, *Dalella chathamense* and *Nematosphaeropsis labyrinthus*. D, *Impagidinium pallidum* and *Algidasphaeridium? minutum*.

are illustrated (Text-fig. 7) only, the data are arranged in a dinoflagellate cyst spectrum that is ordered according to latitude. The resulting cyst spectrum is illustrated in Text-figure 5. In order to aid the interpretation of results, a cluster analysis was performed on the data using CONISS (Grimm 1987) as part of the TILIA/TILIAGRAPH software package.

One of the first facts to emerge is that the number of cysts per gramme of sediment recovered in all the samples studied is much lower than from Recent and late Holocene sediments from the north-eastern Atlantic (Harland and Howe 1995). In that study some samples contained over 10000 cysts per gramme of sediment and certainly figures in excess of 1000 cysts per gramme of sediment were the norm. In this study none of the samples contained more than 364 cysts per gramme and many contained fewer than 20 cysts per gramme (see Text-fig. 6A). These figures are, however, not unlike the low numbers counted by Marret and de Vernal (1997) for material in the Southern Ocean where low dinoflagellate cyst concentrations typify their Antarctic and subAntarctic domains.

Second, it is immediately apparent from an inspection of the data, from the dinoflagellate cyst spectrum and from the cluster analysis, that there is a distinctive change in the data-set which is portrayed in the diagram between sites 032 and 083; that is between 60° 00.10' S and 59° 22.20' S. This change is manifested in the total numbers of dinoflagellate cysts per gramme of sediment and in the diversity of the assemblage, together with the species composition of the assemblages. The maps presented in Text-figure 6 of the cysts per gramme of sediment along the transect together with the occurrence of selected cyst species clearly show the influence of the 60° S line of latitude.

To the south of 60° S the assemblages are low in numbers of cysts per gramme, never exceeding 23 cysts per gramme of sediment. The assemblages are of low diversity and contain a maximum of six species with the common components including taxa such as *Impagidinium pallidum* (Pl. 1, figs 6–7; Text-fig. 7D) amongst the gonyaulacacean cysts and *Algidasphaeridium? minutum* (Pl. 2, figs 6–7; Text-fig. 7D), *Pentapharsodinium dalei?* (Pl. 2, fig. 5), round brown *Protoperidinium* cysts including *Protoperidinium conicoides* (Pl. 2, figs 8–9) and *Selenopemphix antarctica* (Pl. 2, figs 10–12; Text-fig. 7B) amongst the peridiniacean and congruentidiacean cysts. This sparse and low diversity assemblage has also been observed in additional assemblages at similar latitudes in the area. Indeed Marret and de Vernal (1997) recovered fewer than ten taxa in their Antarctic and subAntarctic domains. The cluster analysis clearly differentiates this assemblage from the data-set.

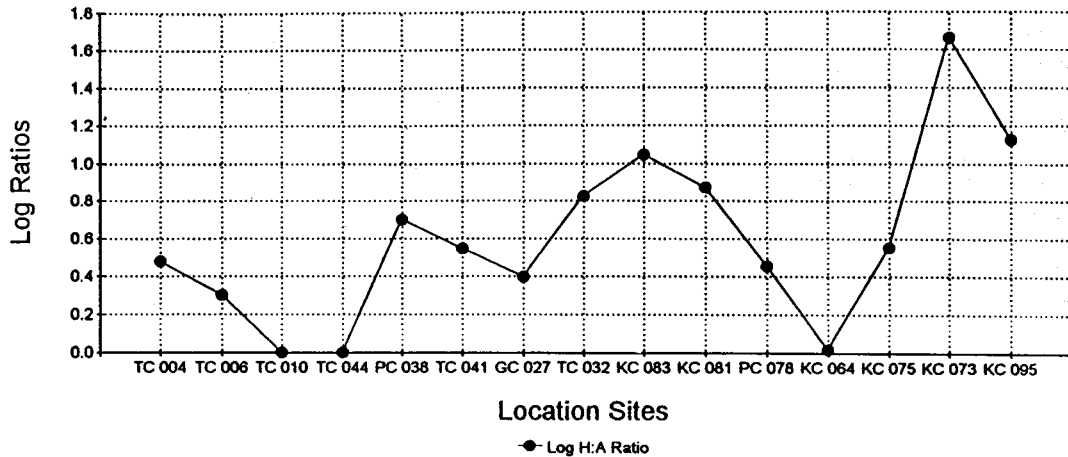
In contrast, the assemblages to the north of about 60° S are characterized by relatively rich dinoflagellate cyst assemblages with a high diversity cyst content. Cyst numbers can reach 364 cysts per gramme of sediment (Text-fig. 7A) with a diversity of 12 species. The assemblages are typically dominated by *Impagidinium sphaericum* (Pl. 1, figs 10–12), with subsidiary *Dalella chathamense* (Pl. 1, figs 2–4; Text-fig. 7C) and *Nematosphaeropsis labyrinthus* (Pl. 2, figs 1–2; Text-fig. 7C) amongst the gonyaulacacean cysts and *Selenopemphix antarctica* (Pl. 2, figs 10–12; Text-fig. 7B) amongst the congruentidiacean cysts, with subsidiary round brown *Protoperidinium* species. The cluster analysis is suggestive of a possible subdivision of this more northern assemblage. This subdivision is manifested in the higher numbers of the round, brown *Protoperidinium* species together with greater numbers of *Impagidinium sphaericum* and *Selenopemphix antarctica* in the more southerly part of this assemblage, and higher numbers of *Dalella chathamense*, *Nematosphaeropsis labyrinthus*, *Protoceratium reticulatum*, *Spiniferites* spp. and *Algidasphaeridium? minutum* in the more northerly part. We have insufficient evidence, at the moment, to substantiate this subdivision and certainly it is not as clearly defined as that at the 60° S line of latitude.

The latitude of 60° S appears to be clearly influential on the distribution of dinoflagellate cysts in the core-top samples from the studied samples of the transect and can be demonstrated clearly in terms of the numbers of cysts, in the cyst species diversity and in the composition of the recovered assemblages given all the constraints outlined previously.

## COMPARISONS

We have already noted that few dinoflagellate cyst data are available from this part of the ocean. Indeed the lack of cyst information and the obvious importance of the Antarctic in the genesis of

### Heterotrophic Ratio along Transect



TEXT-FIG. 7. Graph of the heterotrophic ratio along the transect from the Weddell Sea (left) to Falkland Trough (right). Note the general increasing trend away from the Weddell Sea.

the global circulation pattern and providing a site of upwelling adds to the significance of this the first study of dinoflagellate cysts in the area of remit of the British Antarctic Survey.

However, it is pertinent to compare our results with those of Marret and de Vernal (1997) from the southern part of the Indian Ocean in the immediate vicinity of Antarctica. Using Principal Component Analysis on a data-set of 44 samples, Marret and de Vernal (1977) recognized two main groupings each of which contains three identified assemblages. Their most southerly group, a circum-Antarctic domain, contains identified dinoflagellate cyst assemblages to which the data presented herein can be compared. This circum-Antarctic domain is characterized by the high proportions of the cyst species *Selenopemphix antarctica*, *Impagidinium pallidum*, and round, brown *Protoperidinium* cysts referred to as *Brigantedinium* spp. It is immediately apparent from our data that our assemblages are also characterized by the same cyst taxa.

Within the circum-Antarctic domain Marret and de Vernal (1997) defined three separate assemblages: a proximal Antarctic assemblage (Assemblage I), an Antarctic assemblage (Assemblage II), and a Subantarctic assemblage (Assemblage III). Assemblage I contains *Selenopemphix antarctica* (> 70 per cent.), with *Impagidinium pallidum* (1–35 per cent.) and *Brigantedinium* spp. (2–15 per cent.); Assemblage II consists of *S. antarctica* (19–74 per cent.), with *Brigantedinium* spp. (8–56 per cent.) and *I. pallidum* (2–35 per cent.); Assemblage III is dominated by *Brigantedinium* spp. (16–72 per cent.), with *Nematosphaeropsis labyrinthus* (2–48 per cent.) and *S. antarctica* (0.6–20 per cent.).

We believe that our data are comparable to those of Marret and de Vernal (1997) and that our assemblages south of 60° S are similar to their Assemblage I, with high percentages of *S. antarctica* (0–68.1 per cent.), *I. pallidum* (0–66.7 per cent.) and round, brown *Protoperidinium* cysts (0–47.1 per cent.) and with significant proportions of *Algidasphaeridium? minutum* (0–78.5 per cent.). To the north of 60° S we believe that our assemblages are similar to Assemblage II of Marret and de Vernal (1997), with *S. antarctica* (15.1–92.6 per cent.), round, brown cysts (3.1–51.3 per cent.) and *I. pallidum* (0–4.0 per cent.). The possible subdivision of our data to the north of 60° S as intimated on the cluster analysis may be associated with Assemblage III of Marret and de Vernal (1997) especially on the increased presence of *Nematosphaeropsis labrinthus*, an important element of their

Assemblage III. However, we feel that there is insufficient evidence available at the moment to identify, with confidence, a subdivision of the dinoflagellate cyst assemblages north of 60° S. We are confident in identifying the two assemblages divided by the 60° S line of latitude and the clear similarity with Assemblages I and II of Marret and de Vernal (1997) which occur in the south Indian Ocean to the north and south of 65° S.

In addition to describing various dinoflagellate cyst assemblages from the area as a result of the Principal Component Analysis, Marret and de Vernal (1997) developed a transfer function relating the assemblages to SST and SSS. The best analogue methodology was used and all the procedures (described in de Vernal *et al.* 1994) yielded comparable reconstructions. Testing against the known modern environmental parameters of temperature and salinity yielded excellent coefficients of correlation. Since that time Drs Marret and de Vernal have included our data and have found it to be fully compatible with theirs and have utilized it in further refinements of their transfer function. This makes us confident that our data are meaningful within the constraints that we identified earlier.

#### DISCUSSION

To date, few data are available on Recent dinoflagellate cyst distributions in the southern hemisphere except for around Australia and New Zealand, e.g. Baldwin (1987), Bint (1988), Bolch and Hallaegraff (1990), McMinn (1990, 1991, 1992), McMinn and Sun (1994), Sun and McMinn (1994) and from the southern Indian Ocean (Marret and de Vernal 1997). In most cases the dinoflagellate cysts recovered can be assigned to species already known from the northern hemisphere. There are very few species that can be said to be endemic to the southern hemisphere. This is perhaps not surprising given the planktonic nature of the thecate dinoflagellate life stage, but it may also reflect the lack of a detailed systematic study of the taxonomy of the southern forms. However, two species are sufficiently taxonomically unique to be identified confidently as endemic to the southern hemisphere: *Dalella chathamense* and *Selenopemphix antarctica*. The increased interest in the dinoflagellate cyst flora of the southern oceans, as revealed in bottom sediments, may well lead to the description of other endemic species and *Impagidinium variaseptum* Marret and de Vernal, 1997 may prove to be one of these. However, the presence of the two species mentioned above in any palynological assemblage is, for the moment, a clear indication of deposition in the southern hemisphere and in the case of *Selenopemphix antarctica* to deposition in a circum-Antarctic domain.

In contrast with this rather limited evidence of endemism in dinoflagellate cyst distributions is the reinforcement that the major sea surface factor in controlling dinoflagellate cyst distributions is temperature. This is usually expressed in the latitudinal or climatic distribution trend and the biogeography of dinoflagellate cysts as first recognized by Wall *et al.* (1977) and later clearly demonstrated by Dale (1983). The results of the present study also show evidence of this latitudinal trend. As Dale (1996) pointed out, in coastal and neritic environments the distribution of dinoflagellate cysts follows a standard biogeographical zonation and appears to be bipolar on the global scale. The recognition of any of these biogeographical boundaries within Recent cyst distribution patterns provides a signal which can then be utilized in the sediment record to chart oceanographic and climatic changes.

The latitudinal distribution of the core-top dinoflagellate assemblages and the clear differentiation of dinoflagellate cyst assemblages at 60° S appears to provide such a biogeographical boundary. It remains to be proven as to whether this boundary can be utilized in the Quaternary fossil record. This 60° S boundary appears to coincide approximately with the limit of maximum sea-ice, and is the approximate position of the 1 °C summer SST isotherm (Text-fig. 2). To the north of 60° S there are about eight months of open water from mid October to mid June (Sea Ice Climatic Atlas 1985). The limit of sea-ice is important in its rôle in the suppression of light energy and therefore as a limiting factor for photosynthesis and primary production from phytoplankton including the autotrophic dinoflagellates. Indeed, it is interesting to note that Hasle (1969) observed a major decline in dinoflagellate numbers south of 60° S along transects at 90° W and 150° W. However, to

TABLE 6. Log ratio of heterotrophic dinoflagellates to autotrophic dinoflagellates. Total cyst numbers are given as cysts per gramme of sediment. A minimum value of 1 (shown in italics) was assigned to those assemblages without autotrophic forms to facilitate the calculation.

Core	Log H:A Ratio	Total Heterotroph Cysts	Total Autotroph Cysts
TC 004	0.4771	3	<i>1</i>
TC 006	0.301	2	1
TC 010	0	2	2
TC 044	0	1	<i>1</i>
PC 038	0.69897	5	<i>1</i>
TC 041	0.5441	7	2
GC 027	0.39794	5	2
TC 032	0.8239	20	3
KC 083	1.04663	334	30
KC 081	0.87091	208	28
PC 078	0.45426	74	26
KC 064	0.01773	25	24
KC 075	0.55091	192	54
KC 073	1.66276	230	5
KC 095	1.12571	187	14

the north of this line of latitude and beyond the winter sea-ice limit, numbers of dinoflagellates in the surface waters are controlled largely by nutrient availability.

The dinoflagellate cyst floras that have been recovered in the present study reveal that north of 60° S the diversity and recovery of dinoflagellate cysts increases markedly. Most of this increase derives from congruentiacean cysts belonging, by inference or from incubation experiments, to the modern dinoflagellate genus *Protoperidinium*. Indeed Holm-Hansen *et al.* (1977) noted that this genus was the most important dinoflagellate genus to be found south of the Antarctic Convergence or Polar Front. *Protoperidinium* is heterotrophic in its nutritional strategy, often feeding upon diatoms which are the most predominant constituent of the phytoplankton in Antarctic waters (Jacques *et al.* 1979). These heterotrophic dinoflagellates are *r*-strategists and take advantage of the high nutrient content which encourages the increased diatom populations upon which the heterotrophic dinoflagellates feed. The diatoms, whilst autotrophic, are also *r*-strategists.

The area north of 60° S is a well-known area of upwelling from the effect of Ekman transport and katabatic winds off the Antarctic continent and it is to be expected that the effect of upwelling will be seen in the phytoplankton populations. We have already alluded to this in the increased numbers of *Protoperidinium* dinoflagellates and their cysts as seen in the core-top samples. An area of upwelling is also unstable and unpredictable and favours *r*-strategists. It is important, therefore, in this context to examine the numbers of autotrophic dinoflagellates and their cyst record in comparison with the heterotrophic dinoflagellates and their cysts. One of the ways of making this comparison is to look at the ratios between the two groups of dinoflagellate cysts. A simple intuitive approach was first described by Harland (1973) as the gonyaulacacean ratio although at the time it was not associated with nutritional strategies. Later it became more obvious that it was a measure of the numbers of peridiniacean cysts and hence of the importance of nutrient input into an environment encouraging heterotrophic nutrition. Recently, Powell *et al.* (1990) used the ratio of P-cysts to G-cysts as an indicator of nutrient enhancement and a guide to the history of coastal upwelling off the coast of Peru. They calculated a logarithmic ratio between peridiniacean and chorate cysts as a substitute for the peridiniacean/gonyaulacacean ratio. Dale (1996) argued the case to identify clearly the trophic categories, avoiding confusion with taxonomy or morphology.

In this study we have identified autotrophs and heterotrophs within our assemblages and have indicated the same on Table 3. Table 6 shows the numbers of cysts per gramme of sediment



assignable to each category and the calculated log ratios of heterotrophs to autotrophs (the 'H-cysts' and 'A-cysts' of Dale 1996). The results of plotting this ratio against the core-top samples along the transect (Text-fig. 6) reveals a general rising value from south to north with one of the major steps in the ratio occurring at about 60° S. This reinforces the other results presented in this paper and underscores the importance of the upwelling phenomenon in enhancing the numbers of the congruentiacean dinoflagellate cysts and the position of the maximum limit of sea-ice. However, there is sufficient variation within the data for it to be treated with some caution. There is some potential, however, in using this methodology as a useful tool within the temporal record.

Relationships to productivity are less easy to disentangle, not least because of the possible allochthonous nature of the record and the difficulties in identifying modern sedimentation, as the congruentiacean dinoflagellate cysts are representatives of the second tier within the trophic web feeding upon the dominant primary producers, the diatoms. A general assumption is that increased numbers of diatoms will inevitably lead to increased numbers of congruentiacean dinoflagellate cysts; this also assumes that there is a simple relationship between the numbers of thecate forms, feeding upon diatoms, and the number of cysts produced as a result of sexual reproduction. This is perhaps rather too many assumptions to make at the moment and certainly none of these relationships is as yet proven nor has any quantitative model been established. Indeed, we have little information, for instance, on the competition faced by heterotrophic dinoflagellates from foraminifera and other planktonic organisms for food. We believe this will prove to be an extremely fruitful and exciting area for dinoflagellate research in the future. The importance of these relationships is becoming more and more apparent such that the link between dinoflagellate productivity, cyst production and positions in the first or second tier of the trophic web becomes paramount if ever the dinoflagellate cyst record is to be used as a proxy for productivity. It is to be welcomed that new data are becoming available on the numbers of cysts falling through the water column and being sampled in sediment trap arrays (Dale and Dale 1992). These data will assist in our understanding of cyst production and their final incorporation as a thanatocoenosis in bottom sediments.

In contrast to the discussion above on the role of the heterotrophic dinoflagellates, there is an increase in the absolute numbers of cysts derived from autotrophic dinoflagellates to the north along the studied transect (Text-fig. 6A). This trend increases toward the edge of the ACC and across the Antarctic Convergence as these *K*-strategists gain prominence in the more stable, predictable and nutrient-poor environments of the South Atlantic. Nonetheless, these autotrophic dinoflagellate cysts remain a minor component of the assemblages dominated by the congruentiacean heterotrophs described herein. Further confirmation of this trend across the Antarctic Convergence must await further study on a more extensive dataset.

Finally, the relationship between the contained dinoflagellate cysts and the core-top sample lithologies also requires some comment. The poor recovery of dinoflagellate cysts south of 60° S also corresponds with an increase in the percentage of terrigenous sediment, low percentages of biogenic carbonate and silica and the presence of highly corrosive and oxygenated WSBW (Pudsey and Howe 1998). North of 60° S the increased numbers of dinoflagellate cysts is accompanied by increased percentages of biogenic material and a lower percentage of terrigenous sediment. This is further evidence to substantiate the effect of increased nutrient supply within the system leading to increased productivity and the importance of the sea-ice limit together with the nature of the bottom water masses. The relationships of biogenic material within core-top material is, however, also impossible to interpret without a clear understanding of the detailed sedimentation across the benthic boundary layer and the nature of the sedimentary record held in the uppermost millimetres of any sediment core and included in our core-top samples. Indeed, in Core 32 the Holocene in its entirety may be only 0.1 m thick. The different methods of core recovery may also be an important factor. However, the overall scale of this study and the comparisons with the work of Marret and de Vernal (1997) lead us to be confident in our identification of a biogeographical boundary for use within the palaeoceanographic history of the area. The biogeographical boundary identified herein is coincident with the maximum limit of sea-ice and, as a consequence, the length of time open sea

conditions prevail, as well as the availability of nutrients from upwelling. The detailed ecology of dinoflagellates within this particular environment is complex and will need further research before an adequate paradigm becomes available.

### CONCLUSIONS

Our study is the first to describe in detail an indigenous dinoflagellate cyst thanatocoenosis from Recent bottom sediments in the Antarctic region. It provides distribution data and taxonomy of 17 taxa along a transect from the Falkland Trough to the Weddell Sea and it demonstrates a latitudinal trend in the cyst distributions. In comparison with the regional oceanography of the area the maximum limit of sea-ice appears to be the defining parameter in the cyst distributions. Hence the analysis of temporal (downcore) dinoflagellate cyst data should provide a proxy to recognize fluctuations in the limit of winter sea-ice through the more recent geological record. The recognition of this biogeographical and oceanographic boundary has implications for the extent and volume of sea-ice around the continent of Antarctica, the production of cold, dense bottom water and the dynamics of the thermohaline circulation system. The recognition of this and other biogeographical boundaries in the geological record also allows the detailing of climatic change in the region. Finally, the potential of using the dinoflagellate cyst record of autotrophic and heterotrophic dinoflagellates for investigating the trophic web, productivity, nutrient availability and upwelling histories has been discussed and identified as an area of future fundamental research.

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