

SPECIES OF THE ACRITARCH GENUS *PALAEOSTOMOCYSTIS* DEFLANDRE 1937: POTENTIAL INDICATORS OF NERITIC SUBPOLAR TO POLAR ENVIRONMENTS IN ANTARCTICA DURING THE CENOZOIC

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Abstract

A palynological analysis was undertaken on 16 samples from seven piston cores collected along two offshore transects near Seymour and James Ross Islands. Diverse assemblages of reworked marine microplankton (including organic-walled dinoflagellate cysts, cymatiosphaerids, leiospheres, and other acritarchs) and terrestrial palynomorphs (including pollen and spores) were recovered from glacio-marine sediments of late Pleistocene age. Among the reworked taxa, four species belonging to the acritarch genus *Palaeostomocystis* Deflandre 1937 comprise up to 17% of all palynomorphs. Highest abundances were recorded from sites close to the coast. The potential use of *Palaeostomocystis* as a proxy for early ice-sheet development on the Antarctic margins is evaluated in light of earlier studies. This evaluation suggests that the high abundances of *Palaeostomocystis* on the Antarctic Peninsula reflect neritic-type environments (shallow waters, bay-like areas, or marginal seas) and sub-polar to polar conditions as exist in the Bering Sea, Greenland margins, and other sub-arctic to arctic areas today.

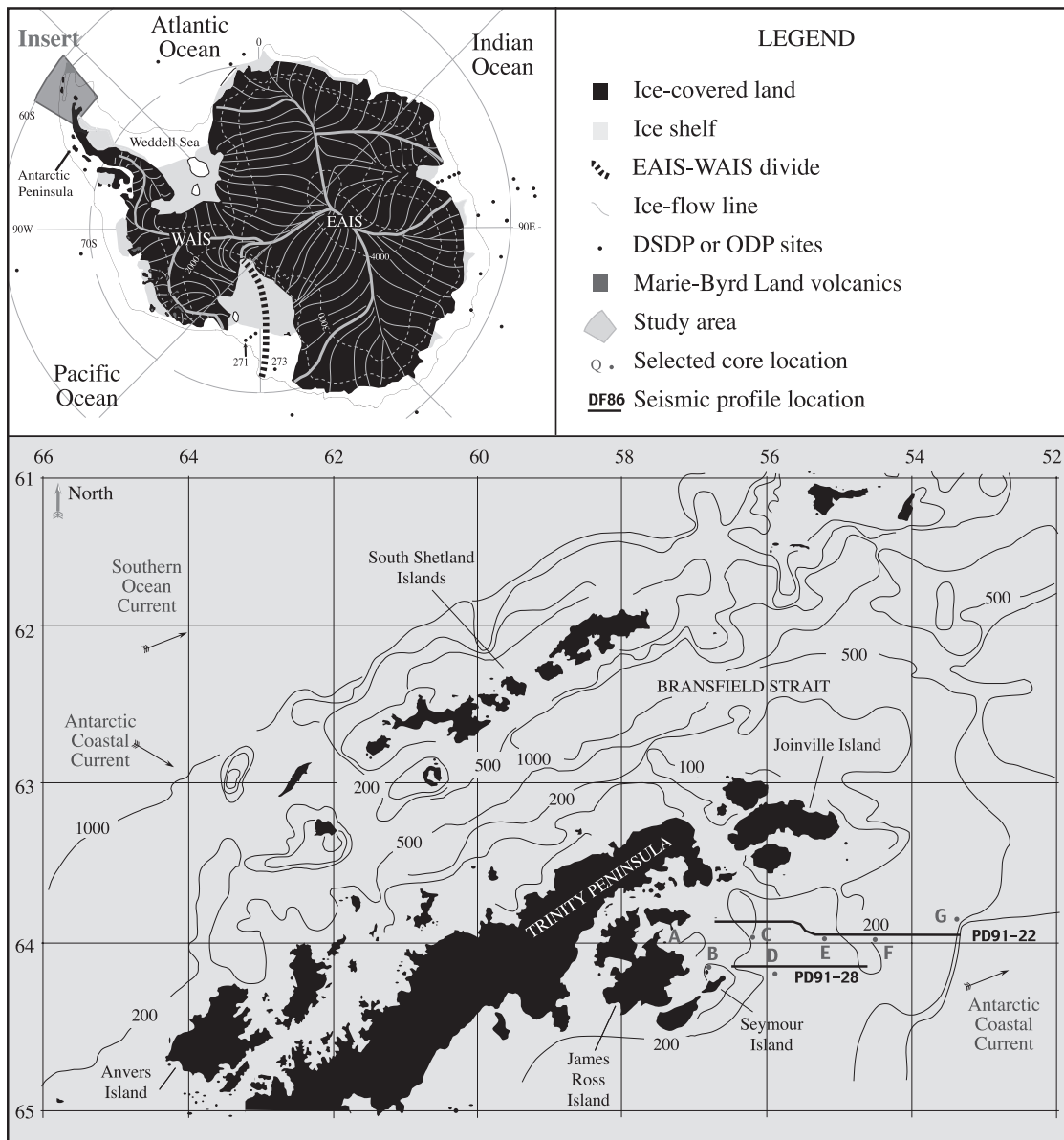
Key words: *Palaeostomocystis*; acritarch; palynomorph, Antarctica; glaciation; neritic.

INTRODUCTION

The Antarctic climate shifted from a temperate to polar climate through a series of steps in the Cenozoic, but there is still debate on the triggering mechanisms and precise timing of cryospheric development. Although few palynological studies are available from Antarctica, biostratigraphic and paleoenvironmental analysis based on palynomorphs recovered from offshore Antarctic sequences are yielding exciting results (Mohr, 1990; Mao and Mohr, 1994; Harland et al., 1998; Wrenn et al., 2001; Brinkhuis et al., 2003; MacPhail and Truswell, 2004; Warny et al., 2006). For instance, Eocene ecological changes have been registered in the marine and continental palynological records of sections studied on Seymour Island (Hall, 1977; Wrenn and Hart, 1988), King George Island (Birkenmajer and Zastawniak, 1989), and James Ross Island (Pirrie et al., 1997). In a recent study of a section dated by organic-

walled dinoflagellate cyst stratigraphy, Ivany et al. (2006) presented evidence of Eocene glacial marine deposits and a lodgment till on the Antarctic Peninsula, suggesting the controversial presence of an extensive West Antarctic ice sheet as early as the latest Eocene.

In the study presented here, late Pleistocene glacio-marine sediments recovered from piston cores collected along two transects off Seymour and James Ross islands were analyzed for their palynological content (see Text-Figures 1 and 2, and Table 1 for sample distribution). A diverse reworked association covering the Campanian to Miocene was identified and documented, and is summarized in Text-Figure 3. The association mainly comprises age-diagnostic dinoflagellate cysts similar to those found in formations outcropping on Seymour Island. Several species recovered are potentially of phylogenetic and environmental significance, and might have provided important information on sea-ice cover and other environmental

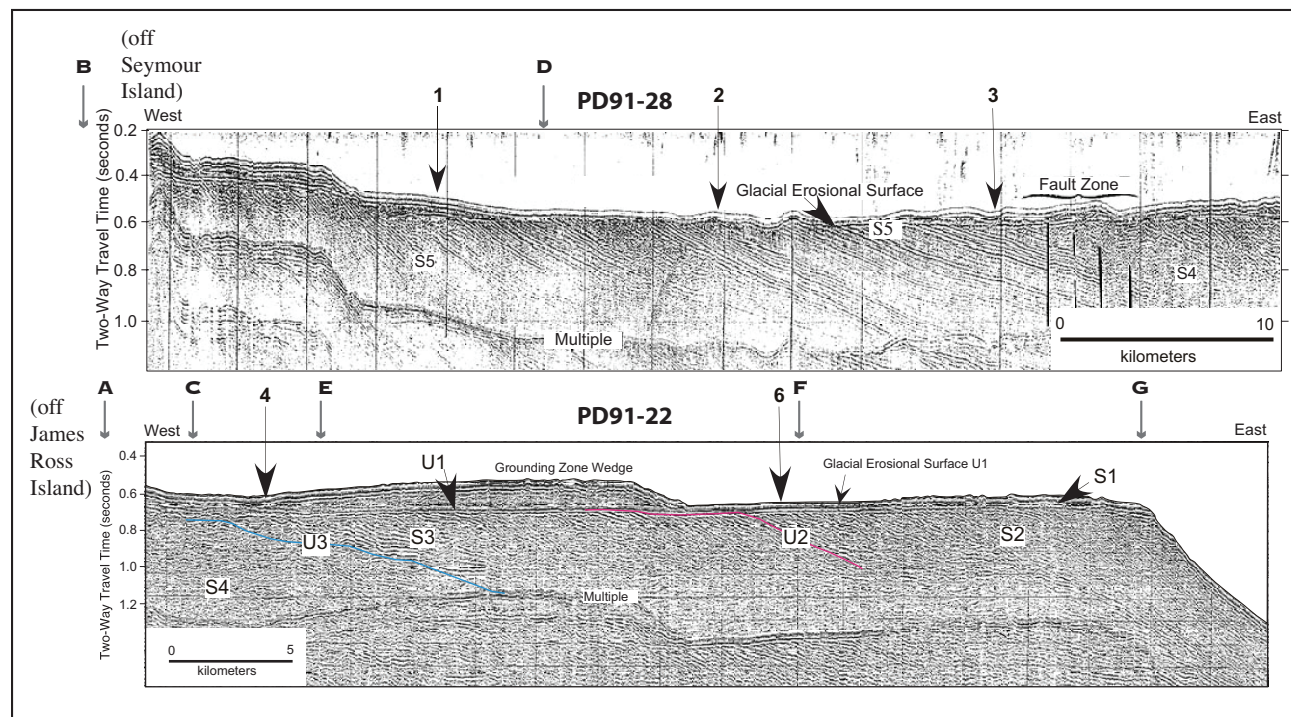


Text-Figure 1. Bathymetric map of the Antarctic Peninsula showing location of seismic profiles PD91-28, PD91-22 and DF86-11, and location of selected cores (see Text-Figure 2 for transect and Table 1 for details of sampling strategy). EAIS = East Antarctic ice sheet; WAIS = West Antarctic ice sheet.

parameters had they been found in situ. Nonetheless, because the association is fairly homogenous, it is believed that most species are reworked from a single area. Specimens of the acritarch genus *Palaeostomocystis* Deflandre 1937 are reported here in unusually high abundances. They are considered to have been reworked along with the dinoflagellate cysts. They therefore provide useful new data for future studies of older in-situ deposits, such as those recently drilled by the SHALDRIL campaign in the same geographical area (Anderson et al., 2006).

MATERIAL AND METHODS

Sixteen glacio-marine samples of late Pleistocene age were collected from piston cores acquired along two transects off Seymour and James Ross Islands. These piston cores sampled a thin glacio-marine layer that overlies an underlying basinward-tilted wedge of sedimentary deposits. The dip-oriented seismic profiles (PD91-28 and PD91-22 on Text-Figure 2) show this basinward-tilted wedge of sedimentary deposits truncated at, or near, the seafloor, and



Text-Figure 2. Interpreted seismic profiles PD91-28 and PD91-22 showing seismic units on the western Weddell Sea continental shelf (modified from Sloan et al., 1995). See Text-Figure 1 for profile locations. Numbers 1 through 6 are the proposed SHALDRIL Cruise 1 drill sites (after SHALDRIL Steering Committee, 2003). Locations A through G are the locations of the cores studied for this project.

reveal its subsurface geology (Anderson, 1999). This wedge is estimated to range from Late Eocene to Pliocene basinward (Anderson et al., 1992; Bart and Anderson, 1995; Anderson, 1999). Recent glacial erosion has 'exposed' virtually the entire stratigraphic section below a thin (a few meters) glacio-marine unit deposited on the seafloor. In selecting samples from this unit, it was assumed that the Upper Eocene through Pliocene sections under this thin glacial unit had been sampled by the ice sheet as it advanced across the shelf. Therefore, the glacio-marine sediments sampled by the piston cores should include palynomorphs originating from the underlying stratigraphic section. So, despite the fact that the sediment under study is glacio-marine, it gives us important clues as to what lays beneath in this Upper Eocene/Pliocene sequence. Samples studied are from the following piston cores: PC192 (3 samples), PC174 (3 samples), PC1 (3 samples), PC20 (2 samples), and PC28 (2 samples) from Glacier DF82; and PC3 (1 sample), and PC6 (2 samples) from Palmer NBP02-01.

The processing method used was based on Gray (1965) and Barss and Williams (1973). Approximately 10 g of dried sample was weighed and spiked with a known quantity of *Lycopodium* spores to permit computation of the

absolute abundance of palynomorphs in the sample; but in view of the reworked nature of the samples, relative abundances were used instead. Acid soluble minerals were digested in a Prolabo M-401 focused microwave digestion unit. Wet mounts of residues were examined with a microscope after each acid digestion step to determine the next appropriate procedure to follow. Palynomorphs were then concentrated by heavy liquid separation using sodium polytungstate (specific gravity 2.0) and/or filtration on a 10- μm sieve to remove fine debris. Oxidation, alkali, and ultrasound treatments were not performed on these samples. The residues were then mounted on microscope slides (at least two) using clear casting resin. Because of the low concentration of palynomorphs recovered (typical of post-Oligocene Antarctic or glacio-marine sediments), one hundred palynomorphs were counted where possible.

PALYNOLOGICAL RESULTS

An unusual feature of the recovered palynomorph association is the abundance of specimens belonging to *Palaeostomocystis* (Text-Figure 3) in most nearshore samples studied. Samples from the core located closest to

Table 1. Selected core description: All cores are archived at the Antarctic Research Facility, Florida State University. Water depth is in meters below sea level. Core length for all piston cores is in centimeters. Project core # relates to core location on Text-Figure 1. The last column summarizes the tentative age of the basinward-tilted seismic units underlying the sampled glacio-marine sediment. These ages are compiled from the literature.

Core #	Ship Name	Cruise ID	Core ID	Core Type	Latit.	Long.	Water Depth	Core Length	Depth (cm) of samples taken	Tentative age of seismic units
A	Glacier	DF82	192	PC	-63.91	-57.69	350	527	24	Eocene to Oligocene if section = S5
									39	
B	Glacier	DF82	174	PC	-64.17	-56.81	288	268	19	Paleogene (Wrenn and Hart, 1988)
									99	
									153	
C	Glacier	DF82	1	PC	-63.95	-56.36	430	271	9	Older than mid-Miocene if section = S4
D	Glacier	DF82	20	PC	-64.24	-55.91	381	290	144	Eocene to Oligocene if section = S5
									201	
									289	
E	Palmer	NBP02-01	3	PC	-63.98	-55.28	378	44.5	barren	Older than mid-Miocene if section = S4
F	Palmer	NBPO2-01	6	PC	-63.98	-54.57	410	166	37	Pliocene if section = S2
									89	
									164	
G	Glacier	DF82	28	PC	-63.88	-53.31	703	225	145	Pliocene if section = S2
									223	

the continent (Site A, Glacier DF 82-192) contain 17%, followed by 5% in Site B (Glacier DF 82-174), 6% in Site C (Glacier DF 82-01), and up to 3% percent in Site D (Glacier DF 82-20). Specimens were absent from the most distal sites studied, Sites F and G. Several species were identified: *Palaeostomocystis sphaerica* Deflandre 1937, *Palaeostomocystis fritilla* (Bujak 1984) Roncaglia 2004, *Palaeostomocystis reticulata* Deflandre 1937, and an undescribed species herein referred to as *Palaeostomocystis* sp. 1 (Text-Figure 4, Plate 1). These species are described below, and discussed particularly to clarify the ecological significance of *Palaeostomocystis*.

SYSTEMATIC PALEONTOLOGY

Group ACRTARCHA Evitt 1963

Genus *Palaeostomocystis* Deflandre 1937

Palaeostomocystis reticulata Deflandre 1937

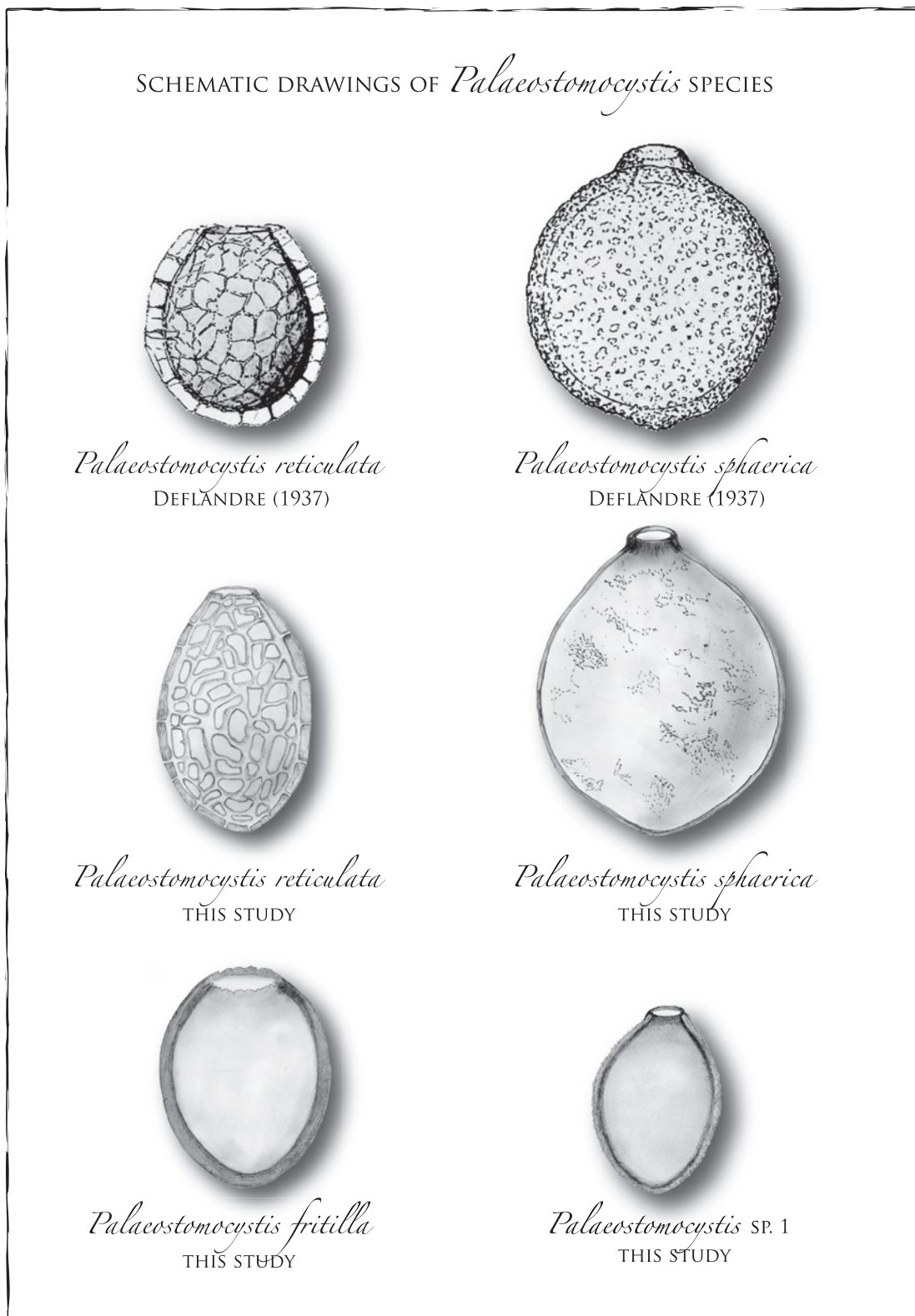
(Plate 1, figs. 1–2; Text-Figure 4)

Discussion. The genus *Palaeostomocystis* was first established by Deflandre in 1937 from Cretaceous sediments

of France (Text-Figure 4, top two drawings from the original protologue of Deflandre, 1937). The type species *Palaeostomocystis reticulata* Deflandre 1937 was defined as having a small organic-walled vesicle, always characterized by the presence of a pore of more-or-less large opening that sometimes exhibits a variably developed collar. The general shape of the vesicle described by Deflandre varies from spheroidal to ellipsoidal or ovoidal, with dimensions of about 10 to 40 μ m, and a psilate to ornamented wall surface.

Palaeostomocystis fritilla (Bujak 1984) Roncaglia 2004
(Plate 1, figs. 6–8; Text-Figure 4)

Discussion. Bujak (1984) described *Palaeostomocystis fritilla* (as *Beringiella fritilla*) from Deep Sea Drilling Project (DSDP) Leg 19, Sites 184, 185, and 186 in the Aleutian Basin, Bering Sea and northern North Pacific, the holotype being selected from DSDP Hole 191B in the Aleutian Basin. This species is characterized by an undulating pylome margin, a thick vesicle wall, and a foveolate wall resulting in a reticulate network of muri. Bujak observed that one of the poles is lost by the development of a



Text-Figure 4. Drawings of some of the main *Palaeostomocystis* species discussed. The two drawings at the top are reproduced from Deflandre (1937).

large pylome. He reported dimensions ranging from 57 to 63 μm . The sediments Bujak (1984) analyzed were Eocene to Pleistocene in age, but because the species was present only in Pleistocene sections, he noted a late Pleistocene occurrence for this species.

Bujak (1984) erected the genus *Beringiella* with *Beringiella fritilla* as its type. He noted that *Beringiella fritilla* differs from species of *Palaeostomocystis* by lacking 'narrow, relatively high muri which form a reticulate network' (Bujak, 1984, p. 195). However, as stated by Roncaglia (2004), the original diagnosis of *Palaeostomocystis* allows for smooth or variably ornamented walls; thus, the diagnosis of *Beringiella fritilla* is circumscribed by that of *Palaeostomocystis*. Roncaglia (2004) emended *Beringiella fritilla* and transferred the species to *Palaeostomocystis*, making *Beringiella* a taxonomic junior synonym of *Palaeostomocystis*. This emendation and transfer are followed here, based on the belief that all *Palaeostomocystis* species should include small, single-layered, organic-walled vesicles characterized by the presence of a large pylome, and the absence of a cingulum. Based on the original diagnosis, the shape of the vesicle is highly variable, the wall surface is psilate to ornamented and a collar may occur around the pylome. However, it is acknowledged that the large aperture of *Palaeostomocystis fritilla*, with its frilled edge, is different from the collared pylomes of the other members of the genus.

Palaeostomocystis subtilithea Roncaglia 2004

Discussion. This species was not recovered in the present study but is discussed as an example of a *Palaeostomocystis* species, albeit younger than the study material, occurring in association with sea-ice conditions – in this case, Greenland (Roncaglia, 2004).

This species was described from Holocene muddy silt from the upper 267 cm of core DA00-03, Egedesminde Dyb, central West Greenland. It has a circular, rimmed macro-pylome and an ovoidal to obtuse-coniform, unilayered, thin-walled vesicle with circular to oval equatorial outline. The wall surface is psilate to microgranulate. A partly detached macro-operculum usually occurs in the interior of the vesicle (Roncaglia, 2004). According to Roncaglia (2004), *Palaeostomocystis subtilithea* differs from *Palaeostomocystis pachytheca* (Cookson & Eisenack 1971) Jansonius 1989 and *Palaeostomocystis ovata* (Wilson 1967) Eisenack et al. 1973 by having a very thin, transparent wall. It differs from *Palaeostomocystis pachytheca* also by being larger, and differs from *Palaeostomocystis ovata* by having a psilate to microgranulate wall surface and detached operculum.

Roncaglia also noted that *Palaeostomocystis subtilithea* differs from *Palaeostomocystis fritilla* by lacking the readily discernible foveolate wall structure that characterizes the latter species. *Palaeostomocystis subtilithea* also resembles species of the genus *Fromea* Cookson & Eisenack 1958 in overall size and shape, but it is readily distinguished by lacking indications of a cingulum and by having occasional wall surface ornamentation.

Palaeostomocystis sphaerica Deflandre 1937 (Plate 1, fig. 9; Text-Figure 4)

Discussion. *Palaeostomocystis sphaerica* was first established by Deflandre in 1937 from a chalk pebble of Cretaceous age, collected from the Paris Basin, France. It was defined as having an organic-walled vesicle somewhat larger than *Palaeostomocystis reticulata*, and bearing a conic pore of medium size surrounded by a collar. The vesicle is generally spheroidal in shape, with a noted dimension of 20 μm , and has an irregularly granulated surface covering a relatively thick wall (Deflandre, 1937). Specimens found in the present study are morphologically identical but vary in size, with dimensions ranging from 30 to 120 μm .

Palaeostomocystis sp. 1 (Plate 1, figs. 3–5; Text-Figure 4)

Description. Small organic-walled vesicle bearing sharply defined opening at one pole that always exhibits small collar. General shape of vesicle ovoidal, with dimensions ca. 10 to 20 μm ; wall thick, smooth to psilate surface.

Discussion. Specimens are about two-thirds the size of most other *Palaeostomocystis* species. Although specimens are all reworked, their morphology is very consistent. *Palaeostomocystis* sp. 1 occurs in most samples studied.

BIOLOGICAL AFFINITY OF *PALAEOSTOMOCYSTIS*

Palaeostomocystis subtilithea shares features with species of the genus *Leiosphaeridia* Eisenack 1958 in its non-sculptured outline and thin wall. However, it clearly differs from *Leiosphaeridia* by having an ovoidal to obtuse-coniform outline in lateral view and a macro-pylome. Bujak (1984) classified the genus *Beringiella*, here treated as a taxonomic junior synonym of *Palaeostomocystis*, as having unknown affinity but possibly representing an egg capsule or an algal cyst. Overall, *Palaeostomocystis* also resembles some palynomorphs described by van Waveren (1994) as tintinnids from recent marine sediments of Indonesia. *Palaeostomocystis* may also have biological affini-

ties with heterotrophic ciliates such as those that are abundant in the waters of central Greenland (Munk et al., 2003). Roncaglia (2004) classified it as an acritarch, i.e. without clear biological affinity. Ichinomiya et al. (2004) reported cysts of the marine planktonic ciliate *Strombidium conicum* from modern marine sediments in Onagawa Bay near the subarctic area of the western North Pacific. These cysts closely resemble *Palaeostomocystis* sp. 1 of the present study. Nonetheless, it is clear that the affinity of *Palaeostomocystis* remains poorly understood, for which reason it is here treated as an acritarch following Fensome and Williams (2004).

(PALEO)ENVIRONMENTAL SIGNIFICANCE OF *PALAEOSTOMOCYSTIS*

The most intriguing and paleoenvironmentally significant observation made during this study is the high relative abundance (up to 17%) of *Palaeostomocystis* species in samples close to the coast. The genus *Palaeostomocystis* has seldom been discussed in depth in the literature, presumably because of its low representation in the fossil record and uncertainty about its affinity. A consequence is that few data exist on this genus, although a trend is discernible from that published so far. Other non-sculptured palynomorphs such as species of *Leiosphaeridia* have been known as excellent indicators of cold, polar waters for more than a decade (Mudie, 1992). Such non-sculptured palynomorphs might reflect polar environments. Hypotheses on 'ecomorphology' postulating the morphological convergence of palynomorphs in response to specific water characteristics (e.g. sea-surface temperature, salinity and sea-ice cover) are relatively new, but worth investigating further. In addition to the overall morphology of *Palaeostomocystis* species, most occurrences tend to confirm its affinity for both neritic and polar to subpolar environments. *Palaeostomocystis fritilla* was described from Pleistocene sediments recovered in the Bering Sea and northern North Pacific at DSDP Sites 184, 185, 186, and 191 by Bujak (1984). The land surrounding the drilling

locations ranges from vast alluvial plains in western Alaska to the high mountains of Siberia. The southern limit of drilling was the Aleutian Island volcanic arc, including a gap in the arc facilitating water exchange with the Pacific Ocean. To the north of these islands, restricted water exchange occurs with the Arctic Ocean through the shallow Bering Strait (Bujak, 1984). In Bujak's study, all species were found in sites drilled in proximity to the island arc, either on the Bering Sea side or just south in the Pacific Ocean. *Palaeostomocystis fritilla* has also been reported in samples where *Brigantedinium* sp. is common to frequent. The dominance in the sample of protoperidiniacean cysts such as *Brigantedinium* is often characteristic of zone of high diatom productivity (Radi and de Vernal, 2004). Because most protoperidiniaceans are heterotrophic organisms and utilize dissolved and particulate organic matter for nutrition, it is expected to find them in waters with high nutrient content, such as upwelling regions, where they are associated with high diatom productivity. The area off Seymour and James Ross Islands, in the Weddell Sea, is similar to the Bering Sea in being a high-latitude area with high diatom productivity. Large numbers of *Protoperidinium* cysts have been reported in the Weddell Sea in association with high diatom productivity (Balech and El-Sayed, 1965).

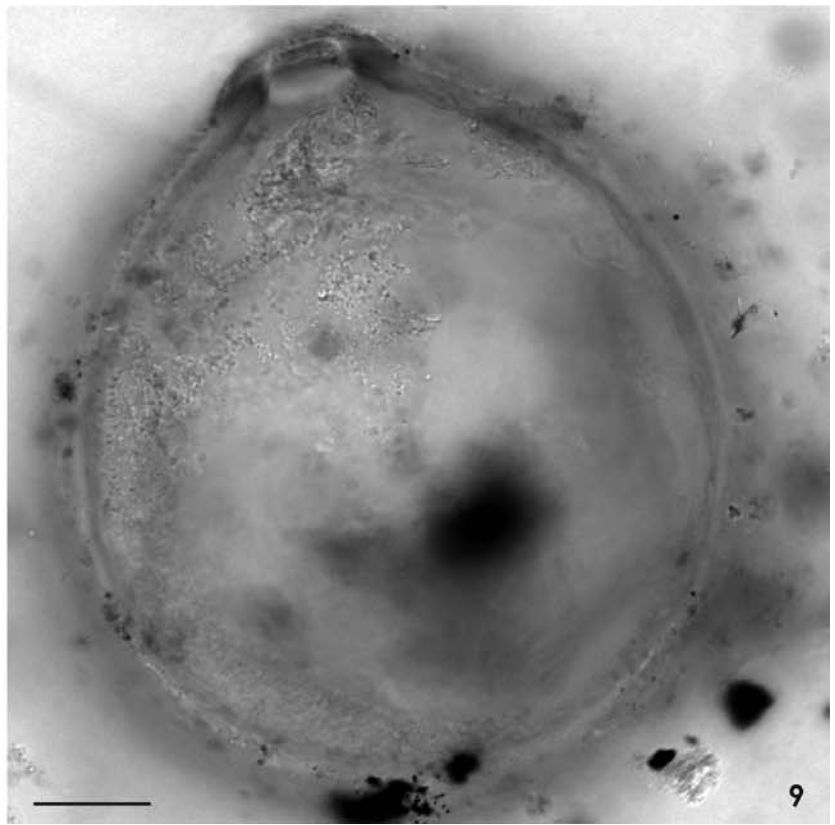
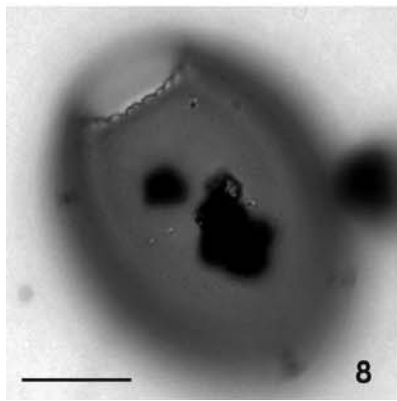
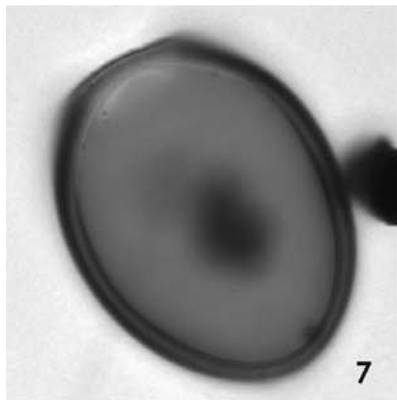
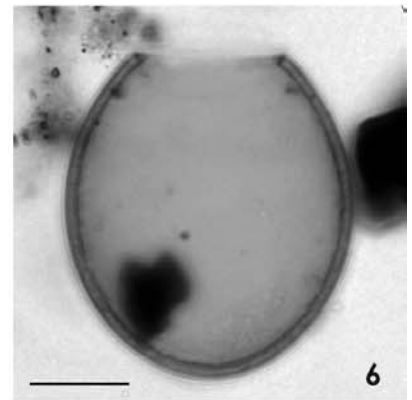
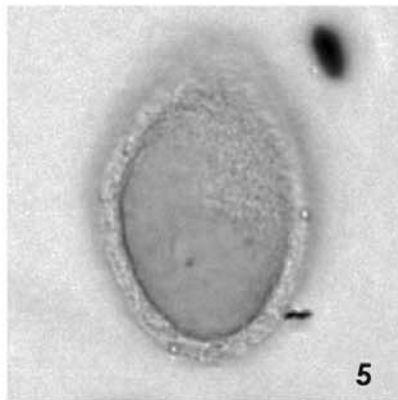
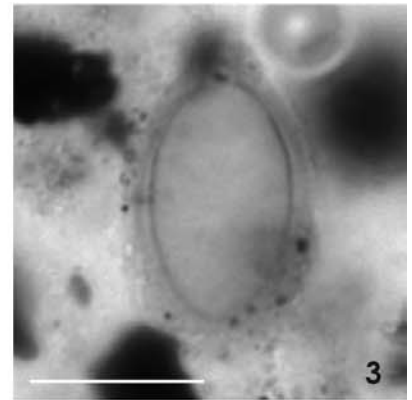
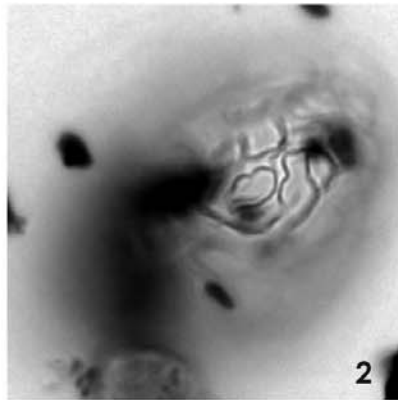
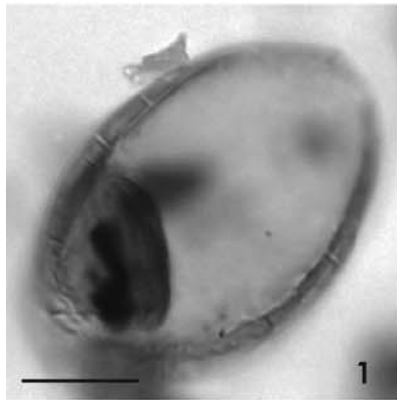
There are no prior reports of the palynomorph here referred to as *Palaeostomocystis* sp.1, but its morphology closely resembles cysts of the ciliate *Strombidium conicum* as reported from modern marine sediments in Onagawa Bay (Ichinomiya et al., 2004). This species was found near the sub-arctic area of the western North Pacific at a shallow depth of 22 meters.

Palaeostomocystis subtilithecica was reported by Roncaglia (2004) from Holocene sediments in Egedesminde Dyb and Kangarsuneq Fjord, Disko Bugt, central West Greenland, and from the Faeroe Islands. The highest abundance was recorded in sediments deposited under stratified waters during the summer months, and characterized by a mean summer sea-surface temperature of 4°C and salinity of ≤ 33.25 . Roncaglia (2004) thus

PLATE 1

Photomicrographs of selected *Palaeostomocystis* species all taken using plain transmitted light. All specimens are at the same magnification. Scale bar = 20 μ m.

- | | | | |
|------|--|------|--|
| 1, 2 | <i>Palaeostomocystis reticulata</i> Deflandre 1937, core DF82/PC20/144cm, coordinate 7.7 \times 147.7. | 6 | <i>Palaeostomocystis fritilla</i> (Bujak 1984) Roncaglia 2004, core DF82/PC20/201cm, coordinate 14 \times 139.3. |
| 3 | <i>Palaeostomocystis</i> sp.1, core DF82/PC174/153cm, coordinate 22 \times 120. | 7, 8 | <i>Palaeostomocystis fritilla</i> (Bujak 1984) Roncaglia 2004, core DF82/PC01/9cm, coordinate 14 \times 143.4. |
| 4, 5 | <i>Palaeostomocystis</i> sp.1, core DF82/PC01/9cm, coordinate 14 \times 152. | 9 | <i>Palaeostomocystis sphaerica</i> Deflandre 1937, core DF82/PC192/39cm, coordinate 21 \times 136.8. |



inferred that *Palaeostomocystis subtilithec*a is an indicator of polar to subpolar environments. The paleoecological significance of *Palaeostomocystis reticulata* is the most uncertain as this species ranges from Maastrichtian to Danian (Foucher, 1971). In the Maastrichtian, *Palaeostomocystis reticulata* is found in association with species typical of marginal seas, in water depth of approximately 200 m, with high plankton productivity and nutrient content.

Conversely, it is instructive to examine where *Palaeostomocystis* species have not been found. For example, Mao and Mohr (1994) described warm-water Eocene dinoflagellate cyst assemblages from somewhat lower latitudes, off Bruce Bank, Antarctica. The lack of *Palaeostomocystis* species in these warmer Eocene Antarctic localities (latitude 60°33.6'S as compared with 63–64°S of the present study) is consistent with the affinity of this genus for colder, higher-latitude waters.

In summary, a review of the literature shows that most species of *Palaeostomocystis* identified in this study are known from coastal areas, and in regions where subpolar to polar conditions prevail. It is proposed that *Palaeostomocystis* can be used in Antarctica as a neritic, polar to subpolar indicator. Therefore, the abundance of this acritarch, although found only as reworked specimens in the present study, probably reflects a time of deposition (of the original strata) when subpolar conditions were first being established in the Antarctic Peninsula, possibly in the Eocene–Oligocene interval, if we consider the similarity between palynomorph species found in the reworked association and the Eocene La Meseta formation on Seymour Island. The study of underlying in-situ sequences is needed to confirm the sediment source of the reworked *Palaeostomocystis* species in order to firmly establish the age of these species and the precise timing of the development of subpolar/polar conditions off the Peninsula.

CONCLUSIONS

Although few data have been published on the spatial and stratigraphic distributions of the genus *Palaeostomocystis*, some general trends are observed for this genus that point to its utility as a paleoenvironmental indicator from Maastrichtian to Holocene times.

The species discussed in this paper have been found (1) in the present study as reworked specimens in sediments from an area close to Seymour Island and James Ross Island, in water depths less than 200 m for four of the sites, (2) close to the Aleutian Islands, being reported on both the Bering Sea and Pacific Ocean sides, (3) in bay-like areas, and (4) in marginal seas off Greenland, in water depths of approximately 200 m, with high planktonic productivity

and nutrient content. It is therefore hypothesized that occurrences of *Palaeostomocystis* can be used to indicate neritic environments (e.g. marginal seas, bays, island margins) in water depths possibly not exceeding 200 m, and where planktonic productivity and nutrient content are high.

The second characteristic is that the Oligocene to Pleistocene species discussed have all been found (1) around the Antarctic Peninsula, (2) in the Bering Sea, (3) in Greenland, and (4) other Subarctic areas. It is concluded that these species all indicate polar to subpolar environments. The older species *Palaeostomocystis reticulata* and *Palaeostomocystis sphaerica* might have been tolerant of sea-surface temperature fluctuations. This tolerance to fluctuations in water temperatures and to colder water episodes in the Maastrichtian and the Danian might have set an evolutionary trend towards affinity for polar climates in the genus *Palaeostomocystis*.

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