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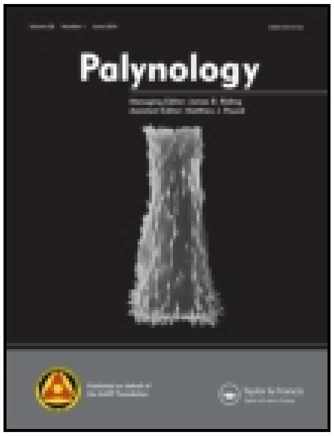

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Small Antarctic Late Cretaceous chorate dinoflagellate cysts: biological and palaeoenvironmental affinities

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Small spiny marine palynomorphs have been the focus of recent palynological studies since their high proportions in Antarctic Late Cretaceous and Cenozoic assemblages were noted. These palynomorphs were assigned to the dinoflagellate cyst *Impletosphaeridium clavus* and they were believed to have had an affinity with some modern round brown spiny cysts (RBSCs). Our study aims to analyse there together with potential modern analogues by comparing Late Cretaceous and Cenozoic Antarctic specimens with some RBSCs recorded from the Holocene of southern Argentina. We confirm several features in common between these specimens, although differences in processes and the cyst wall are observed. The species could have been produced by dinoflagellates similar to those that generate some RBSCs. Their abundance in the Late Cretaceous may have occurred in response to short term cooling pulses without development of sea-ice cover. Cenozoic records are considered to be reworked, restricting the stratigraphical range of *Impletosphaeridium clavus*.

Keywords: dinoflagellate cysts; modern analogues; palaeoenvironment; Late Cretaceous–Holocene; Antarctica; Argentina

1. Introduction

Small spiny palynomorphs (~20 microns) have been recognised in Upper Cretaceous and Cenozoic marine sediments from different localities in Antarctica. These forms have been identified by several authors as the acritarch *Micrhystridium* or as an extinct organic-walled dinoflagellate cyst belonging to the genus *Impletosphaeridium*. This duality in the assignment is based on the position of the processes (non-tabular) and the doubtful existence of an archaeopyle. Depending on whether it is considered to be an acritarch or a dinoflagellate cyst, the palaeoenvironmental interpretation varies. In this sense, some authors (Smith 1992; Askin 1999; Schrank 2003) proposed that the abundance of small acritarchs (the *Micrhystridium* group) may depend on the depositional environment. The *Micrhystridium* group reaches greater abundances and diversity in shallow marine sandstones (i.e. in relatively coarse sediments), while it is much less frequent in open marine facies (finer-grained sediments), characterised by diverse dinoflagellate cyst assemblages (Schrank 2003). However, Warny et al. (2007) and Bowman et al. (2013a) identified these small forms as dinoflagellate cysts assigned to the genus *Impletosphaeridium*. Additionally, based on the morphology of these small spiny cysts, the previous authors hypothesised the affinity of *Impletosphaeridium* being with some cysts of extant dinoflagellates such as *Echinidinium* spp., *Islandinium cezare*, *Islandinium minutum* and *Pentapharsodinium dalei.* Since these extant species have a strong relationship with sea-ice cover and are considered morphologically similar to *Impletosphaeridium* species, Warny et al. (2007) proposed that the presence of *Impletosphaeridium* in Cenozoic Antarctic deposits could indicate the development of ephemeral sea-ice in the areas where these small spiny dinoflagellate cysts were abundant. According to these authors, the dominance of *Impletosphaeridium* could be the first major dinoflagellate cyst event marking the onset of Antarctic sea-ice development off Seymour Island, possibly at the end of the Eocene.

Traditionally, previous palynological studies from Antarctica have focused on the analysis of dinoflagellate cysts, which are useful for providing biostratigraphical and palaeoenvironmental interpretator. Small marine palynomorphs, though, have not been the principal subject of study. Often, large palynomorphs are usually so common that the smaller forms tend to be overlooked during routine light microscopy study (Schrank 2003). In this work, we focus on small

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*Corresponding author. Email: amenabar@gl.fcen.uba.ar spiny palynomorphs, which were assigned either to *Micrhystridium* or *Impletosphaeridium*. Despite their apparent simple morphology, visible under optical microscopy, these extinct forms are poorly-known, and current understanding of their affinity with living dinoflagellates is not well understood.

Upon discovering that these forms were present in high proportions in some samples, their study has gained relevance. Warny et al. (2007) observed that these forms (assigned to *Impletosphaeridium*) were abundant in marine cores drilled offshore from the eastern Antarctic Peninsula, ranging from Upper Eocene to Upper Neogene. The authors indicated that such small dinoflagellate cysts were reworked from the Eocene through the Miocene and they represented 32 to 100% (average of 63%) of the reworked marine assemblage. Later, Thorn et al. (2009) analysed the uppermost ~318 m (Late Maastrichtian) of the López de Bertodano Formation on Seymour Island, northern Antarctic Peninsula. They noted that a great abundance of these forms (assigned to *Micrhystridium* spp.) occurred together with an acme of *Manumiella seymourensis* at ~257 m below the Cretaceous/Paleogene (K/Pg) boundary. Warny and Askin (2011a) also noted high amounts of small palynomorphs (as *Micrhystridium*) in the Middle Miocene of the Joinville Plateau, Weddell Sea, northern Antarctic Peninsula. Bowman et al. (2013a) stated that both intervals (the Late Maastrichtian and the middle Miocene) were characterised by an acme of *Impletosphaeridium* in Antarctic sediments. Recently, Bowman et al. (2013b) demonstrated two more acmes of *Impletosphaeridium clavus* in the lowermost 700 m (Early Maastrichtian) of the López de Bertodano Formation on Seymour Island.

One of the most important topics emerging from the investigations above is the need to separate the *in situ* palynomorphs (not necessarily in place but coeval with the deposition of the Cenozoic diamictite) from those that are reworked (material from rocks of one age that have been eroded, transported and redeposited in sediments of a younger age), in order to avoid reaching erroneous or doubtful palaeoenvironmental and age interpretations. Recycling is a very frequent process in Antarctic Cenozoic (Neogene) diamictites. These deposits have large amounts of reworked material (including palynomorphs), as would be expected in glacial environments, where glaciers transport huge volumes of sediment. Reworked palynomorphs, together with an expected scarcity of *in situ* palynomorphs in the Neogene rocks of Antarctica, make these deposits very difficult to study. Salzmann et al. (2011) proposed the separation of *in situ* and reworked palynomorphs based on five different criteria: fluorescence microscopy to identify taphonomic histories, colour and preservation of palynomorphs to identify thermal maturation, age-diagnostic dinoflagellate cysts, potentially age-indicative acritarchs and ratio of pollen types such as *Nothofagidites lachlaniae* and *N. flemingii* to infer the presence of *in-situ Nothofagidites* pollen. However, they concluded that with some palynomorphs, identification as *in situ* or reworked forms was still problematical.

In addition, Salzmann et al. (2011) analysed Cretaceous and Late Neogene diamictite samples from James Ross Island, Antarctic Peninsula. They detected an abundance of these small spiny cysts (identified as *Impletosphaeridium* spp.) in Cretaceous samples underlying the Lower Pliocene diamictites. Therefore, they concluded that it was highly unlikely that these small spiny dinoflagellate cysts, which are now extinct and have no evident modern analogue, could indicate proximate sea-ice cover, as suggested by Warny et al. (2007).

Recently, Bowman et al. (2013a), in their emendation of *Impletosphaeridium clavus*, revised all the publications where these small spiny cysts had been mentioned either as *Micrhystridium* or *Impletosphaeridium*, transferring them to *Impletosphaeridium clavus*. Thus, these problematic palynomorphs with a questionable origin are now considered to be cysts of dinoflagellates, although the authors still believed that the specimens with similar morphology to *Impletosphaeridium clavus* but with solid and hollow processes, with mostly simple process terminations and flared bases, should be considered acritarchs.

Therefore, the detailed morphological analyses of *Impletosphaeridium clavus* carried out by Bowman et al. (2013a) show that it has not been possible to find an unequivocal modern analogue of *Impletosphaeridium*, although the authors indicate that these spiny dinoflagellate cysts were comparable, in gross morphology, to extant dinoflagellate cysts from Quaternary and modern sediments typical of cold high-latitude oceans.

Considering that the gross morphology of *Impletosphaeridium* resembles modern analogues (round brown spiny cysts or RBSCs), as previously observed by different authors, this work is a detailed morphological comparison between the Late Cretaceous and Cenozoic specimens obtained from James Ross, Vega and Snow Hill Islands, with RBSCs and other modern similar small spiny dinoflagellate cysts recorded in recent marine sediments from the Beagle Channel. If it is possible to define an affinity, and if the ecological preferences of the modern organisms are related to the Late Cretaceous *Impletosphaeridium* assemblages, we will be able to inter a palaeoenvironmental significance for the *Impletosphaeridium* acmes recorded in the Upper Cretaceous.

2. Materials and methods

2.1. Localities sampled

2.1.1. Cretaceous of Antarctica

2.1.1.1. Ekelöf Point, James Ross Island. Ekelöf Point (64° 13′ 26.0″ S; 57° 12′ 14.0″ W) is located in the Southeast of James Ross Island (Figure 1A). It constitutes a 300-metre-high plateau, composed of Upper Cretaceous marine sediments, which are unconformably overlain by Cenozoic diamictites and volcanic rocks from the James Ross Island Volcanic Group (JRIVG). Upper Cretaceous deposits belong to the Rabot (lower section) and Snow Hill Island (upper section) formations of the Marambio Group, separated by an unconformity (Robles Hurtado et al. 1997; Olivero 2012). These units are dated as Late Campanian–Early Maastrichtian, based on ammonites (Olivero 2012 and references therein) and dinoflagellate cysts from the lower section (Sumner 1992). The detailed study of the complete outcrop (lower, middle and upper parts) comprises an integrated stratigraphical section 325 m thick, consisting of dark grey siltstones and ochreous clay alternating with very thin indurated tuff levels and yellow claystones. The whole section was studied palynologically based on 40 samples (Amenábar et al. 2012, 2013a, 2013b). All produced abundant dinoflagellate cysts, pollen and spores in variable percentages. Sparse algae, organic foraminiferal linings, scolecodonts and fungi were also recognised in the assemblage. The most representative dinoflagellate cyst species are *Chatangiella tripartita, C. victoriensis, Exochosphaeridium bifidum, Isabelidinium cretaceum, I. korojonense, I. pellucidum, Manumiella seelandica, M. seymourensis, Odontochitina porifera, Phelodinium exilicornutum, Trichodinium castanea* and *Xenikoon australis.* Peridiniacean dinoflagellate cysts dominate the section with percentages of *Impletosphaeridum* lower than 25%. In only one sample this taxon reaches up to 73.5% of the marine palynomorph assemblage.

Continental palynomorphs are represented by the pollen species *Nothofagidites dorotensis*, *Peninsulapollis gillii* and *Phyllocladidites mawsonii*, and the spores *Retitriletes austroclavatidites*, *Cyathidites minor*, *Baculatisporites comaumensis*, *Perotrilites majus* and *Evansispora senonica*. Algae include *Paralecaniella indentata*, *Botryococcus braunii* and *Palambages* sp. The results of the palynological study corroborated the age on the basis of other fossil groups.

2.1.1.2. Sanctuary Cliffs, Snow Hill Island. Sanctuary Cliffs is the name of the nunatak located in the centre of Snow Hill Island (S 64° 26′ 44.7″ S; 57° 11′ 13.1″ W), southeast of James Ross Island (Figure 1A). The Upper Cretaceous deposits outcropping in the

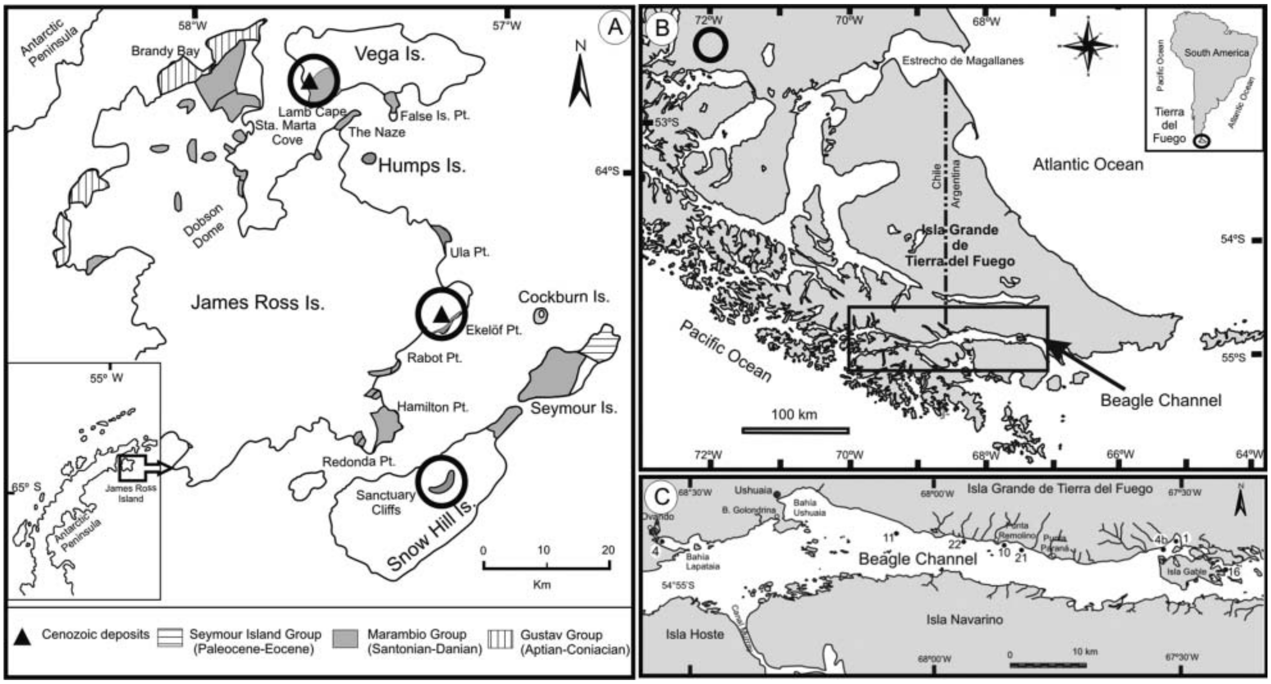


Figure 1. Location map of the areas studied. **A.** James Ross and Vega Islands, Antarctica (modified from Olivero 2012). **B.** Santa Cruz and Isla Grande de Tierra del Fuego Provinces, Patagonia, southern Argentina. The circle represents the location of cores drilled by Yacimientos Carboníferos Fiscales. **C.** Beagle Channel and sediment sample locations with reworked dinoflagellate cysts content (modified from Candel et al. 2012).

nunatak correspond to the Sanctuary Cliff Member of the Snow Hill Island Formation (Pirrie et al. 1997a). Neither the base nor the top of the unit is exposed at this locality. A Late Campanian–Early Maastrichtian age is attributed to the Cretaceous section, based on the ammonite fauna (Olivero & Medina 2000), calcareous nannofossils (Robles Hurtado & Concheyro 1995) and palynomorphs (Pirrie et al. 1997a). The section is 240 m thick and consists of poorly lithified calcareous sandstones, dark grey mudstones and thin limestones. The complete outcropping section was later studied on the basis of 27 samples (di Pasquo et al. 2006; Amenábar & di Pasquo 2008) and yielded abundant dinoflagellate cysts, spores and pollen in variable percentages, as well as some other palynomorphs (algae, organic foraminiferal linings and fungi) as subordinate elements. The species *Isabelidinium pellucidum*, *Odontochitina indigena*, *Operculodinium radiculatum* and *Phelodinium exilicornutum* are the taxa with the highest representation, while *Isabelidinium korojonense*, *Odontochitina porifera*, *Palaeocystodinium lidiae* and *Spiniferites ramosus* are less frequent species. Abundant small spiny cysts (assigned to *Micrhystridium piliferum* by di Pasquo et al. 2006; Amenábar & di Pasquo 2008) are present in several levels, representing from 7 to 31% of the marine assemblage.

The continental assemblage is composed of pollen grains of *Nothofagidites* spp., *Peninsulapollis gillii* and *Phyllocladidites mawsonii* and the spores *Ceratosporites equalis*, *Leptolepidites verrucatus* and *Perotrilites majus*, among others (di Pasquo et al. 2006; Amenábar & di Pasquo 2008). The results of the palynological study corroborated the age based on other fossil groups.

2.1.2. *Cenozoic of Antarctica*

Cenozoic samples come from diamictites situated at different localities of James Ross and Vega Islands.

2.1.2.1. Ekelöf Point, James Ross Island. Six scattered diamictites were recognised in southeast James Ross Island at Ekelöf Point (64° 13′ 26.0″ S; 57° 12′ 14.0″ W) (Figure 1A). These deposits overlie Upper Cretaceous sediments (see *Section 2.1.1.1*) and they usually underlie the JRIVG or may even be intercalated between different levels of the Cenozoic volcanic rocks. The argon-40/argon-39 (^{40}Ar/^{39}Ar) isotopic ages of JRIVG lavas at Ekelöf Point were dated as 3.52 Ma, which is Late Pliocene (Smellie et al. 2008). Ekelöf point diamictites probably belong to more than one stratigraphical unit but they are currently assigned to the Hobbs Glacier Formation (Pirrie et al. 1997b).

Ekelöf point diamictites have a lenticular geometry and consist of a matrix-supported conglomerate, with the exception of some clast-supported levels containing abundant invertebrate fossils. Up to 12 levels from each diamictite deposit have been sampled. The most fossiliferous one contains a well-preserved macrofauna that includes articulated bivalves, pectinids, brachiopods, serpulids, balanids, gastropods and bryozoans, together with microfossils such as foraminifera, ostracods and palynomorphs (Concheyro et al. 2010). The foraminiferal fauna is characterised by benthic calcareous and agglutinated specimens and includes both Cenozoic and Late Cretaceous reworked species. It was also possible to recover somewhat rare ostracod specimens, and the taxa identified indicate cold Antarctic and subantarctic waters. The palynological assemblage consists mainly of Late Cretaceous reworked species (e.g., *Isabelidinium* spp., *Odontochitina porifera*), which came from the underlying Upper Cretaceous rocks, and also rare Cenozoic palynomorphs where some of them (e.g. *Spiniferites ramosus*, *Lejeunecysta* sp.) could be considered as penecontemporaneous with the deposition of the diamictite. Small spiny palynomorphs are present in all the samples with variable percentages as a conspicuous element of the palynological assemblages (67–86% of the marine assemblage).

2.1.2.2. Cape Lamb, Vega Island. A diamictite deposit outcrops at Cape Lamb (63° 54′03″ S; 57° 37′ 22″ W), southern Vega Island, overlying Upper Cretaceous sediments and underlying the JRIVG. Smellie et al. (2008) dated the JRIVG at Cape Lamb with a ^{40}Ar/^{39}Ar age of 2.07 Ma (Early Pleistocene). The Cape Lamb diamictite consists of a 7-metre-thick fossiliferous marine deposit containing foraminifera, bryozoans and palynomorphs. Two of the diamictite levels yielded a foraminiferal fauna characterised by benthic calcareous species, thus suggesting a post-Late Oligocene age, but the absence of planktonic and benthic diagnostic foraminifera species and other microfossils with high temporal resolution, such as calcareous nannofossils, prevents a more precise age assessment (Caramés & Concheyro 2013). Well-preserved bryozoan colonies with encrusting habits are developed on scallop bivalve fragments in the upper parts of the diamictite (Adamonis 2007). Six palynological samples of the deposit have been analysed. They contain well-preserved dinoflagellate cysts, pollen and spores, and remains of algae. As part of the palynological assemblage, small spiny palynomorphs were also recorded. They were attributed to *Micrhystridium piliferum* (Caramés et al. 2008) and they represent 4 to 25% of the marine assemblage. Some of the palynomorphs are characteristic of the Late Cretaceous and

Paleogene, and a single pollen grain which is exclusive to the Miocene has also been recorded. All of them are interpreted as reworked material. The palynological assemblages also contain striate bisaccate pollen reworked from the Permian and only a few specimens can be considered *in situ* palynomorphs: *Spiniferites ramosus*; *Franseria meyeniana*; *Haloragacidites trioratus*; and *Ceratosporites equalis* (Caramés et al. 2008).

2.1.3. Holocene of Argentina

2.1.3.1. Beagle Channel, Tierra del Fuego. The Beagle Channel (54° 53′ S; 67° 00′–68° 40′ W) connects the Atlantic and Pacific oceans in the southernmost part of South America, and is located in the subantarctic environment (Figure 1B–C). The Beagle Channel is a former tectonic valley which was completely covered by ice during the last glaciation (Rabassa et al. 2000). After the ice melt, the channel opened before 8200 carbon-14 (^{14}C) years before present (BP) and the marine environment was fully established at least by 7900 ^{14}C years BP (Rabassa et al. 1986). The channel shows typical characteristics of a fjord with estuarine dynamics controlled by important seasonal fluvial inputs and by tidal currents from both the east (Atlantic) and the west (Pacific) (Isla et al. 1999). The Beagle Channel receives input from numerous rivers that drain the intermontane basins of the Grande, Navarino and Hoste Islands. The water column is stratified mainly during the summer. Sea-surface salinity varies from 27 to 33.5 PSU, with minimum values during summer due to the meltwater discharge into the channel. The Beagle Channel is ice-free all year round, and has an average sea-surface temperature of 6.5 °C (Isla et al. 1999).

For palynological analysis, 22 surface sediment samples were collected from the bottom of the Beagle Channel, Tierra del Fuego (Figure 1B–C). The lithology consists of dark grey clays and dark brown medium-coarse sands with abundant shells. The palynological assemblage shows the predominance of terrestrial palynomorphs (pollen and spores) over aquatic forms (dinoflagellate cysts, acritarchs, chlorophyte algae, copepod eggs and foraminiferal linings). The dinoflagellate cyst assemblages are characterised by a relatively low diversity of species, and perinidinialean taxa, mainly protoperidiniacean, dominate over the Gonyaulacales. Besides, specimens characterised by high degradation, compression and dark yellow to brownish colours were grouped as reworked dinoflagellate cysts and are present in the marine assemblages in low percentages ($<2\%$) (Candel 2010; Candel et al. 2012).

2.2. ***Laboratory treatments and palynological analyses***

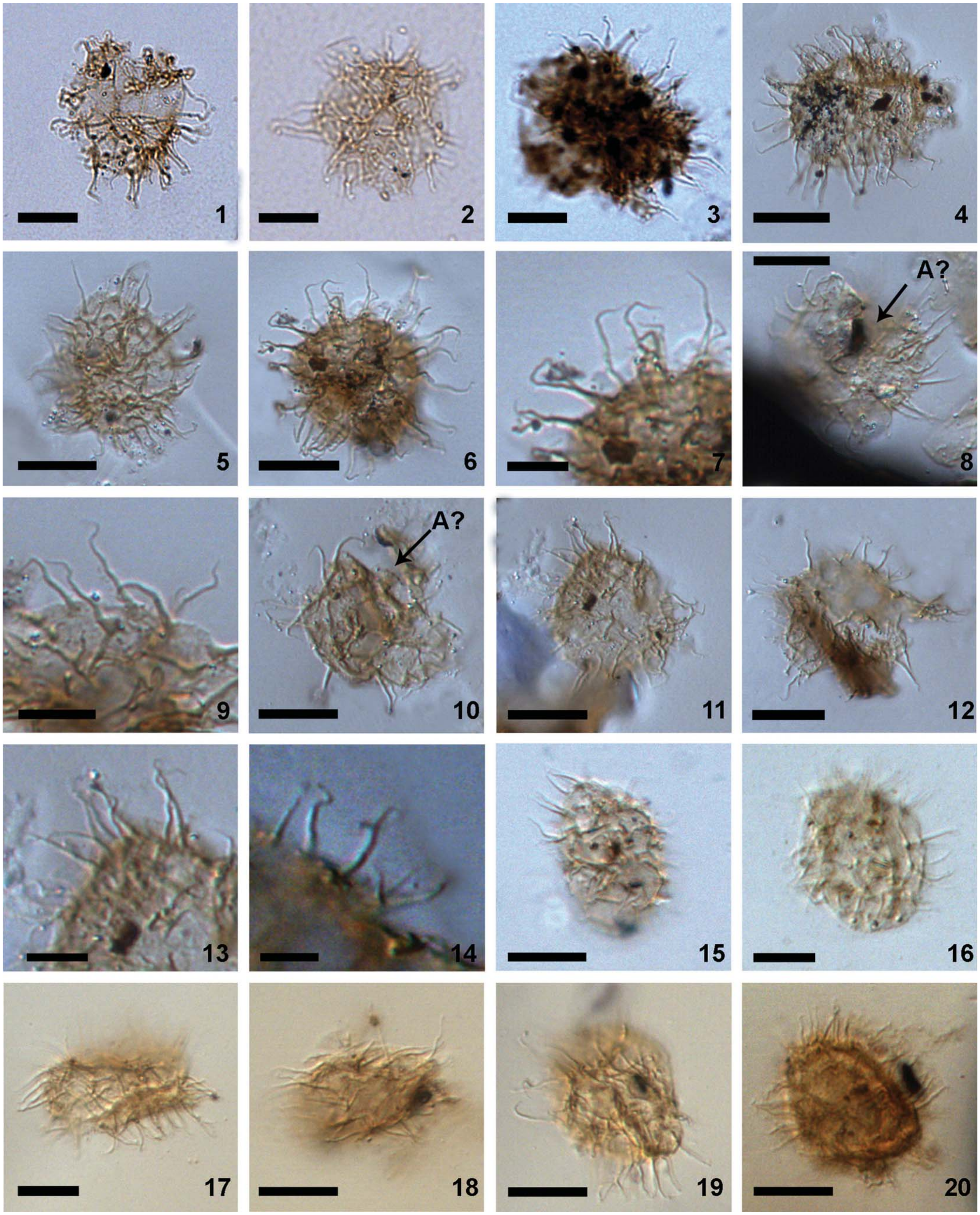
The Cretaceous and some of the Cenozoic samples were processed using palynological procedures involving the extraction of the organic matter from 10 g of dry sediment by digesting the carbonates with hydrochloric acid (HCl; 10%) and silicates with hydrofluoric acid (HF; 70%) followed by several washings with water. The residue was sieved with 25 μm and 10 μm meshes and finally mounted on slides with glycerin gel (Wood et al. 1996). The fraction sieved at 10 μm was used to detect small spiny palynomorphs. This procedure was carried out at the Laboratorio de Palinología, Universidad de Buenos Aires. The remaining Cenozoic samples were processed in the Laboratorio de Palinología at the Universidad Nacional del Sur, using HCl (10%) and silicates with HF (40%) and the residues were sieved with 10 μm mesh. In this case, the separation of the organic fraction was conducted by heavy liquid gravity separation procedures (zinc chloride, $ZnCl_2$).

In all the Cretaceous and Cenozoic samples, it was possible to count a minimum of 200 palynomorphs including dinoflagellate cysts, pollen, spores and other palynomorphs (algae, organic foraminiferal linings, scolecodonts, fungi, etc.), using a transmitted light microscope at 400 and 1000× magnifications.

Holocene samples were prepared for palynological analysis according to the laboratory procedures at Centre de recherche en géochimie et géodynamique (GEOTOP) (de Vernal et al. 1999). Samples containing 5 to 10 g of dry sediment were wet sieved at 106 and 10 μm in order to remove particles above and below this size range. In order to dissolve carbonates and silicates, the 106–10 μm fraction was treated several times with HCl (10%) and HF (49%). Neither oxidation nor treatment with heavy liquids was applied, in order to prevent the loss of more fragile protoperidiniacean cysts. A tablet containing a known number of *Lycopodium clavatum* spores was added to each sample for the calculation of palynomorph concentrations (Stockmarr 1971). The final residue was sieved at 10 μm, in order to eliminate particles smaller than this size, and it was mounted between a slide and coverslip in glycerin gel.

In most of the Holocene samples, a minimum of 200 dinoflagellate cysts and other non-pollen palynomorphs were counted using a transmitted light microscope at 400 and 1000× magnifications.

Selected specimens from Antarctica and Tierra del Fuego are illustrated in Plates 1–3. Antarctic figured specimens are denoted by the prefix BAFC-Pl, corresponding to the repository of the Laboratorio de Palinología, Universidad de Buenos Aires, Argentina, where the slides are stored, followed by the slide number and the England Finder coordinates. Holocene slides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from Tierra del Fuego are stored in the Laboratorio de Palinología, Universidad Nacional del Sur, Bahía Blanca, Argentina, under the name UNSP followed by the denomination of the study area (Fondo Canal Beagle, FCB).

The taxonomic nomenclature of modern dinoflagellate cysts used in this study is that of Dale (1977), Zonneveld (1997), Rochon et al. (1999), Head et al. (2001) and Candel et al. (2012). The systematic references that do not appear in the bibliography can be found in Fensome et al. (2008) and Raine et al. (2011).

3. Results

3.1. Cretaceous material

Cretaceous material analysed in this study comes from Ekelöf Point (James Ross Island) and Sanctuary Cliffs (Snow Hill Island), Antarctica (Figure 1A). In both localities, small dinoflagellate cysts are present. Those forms assigned to *Impletosphaeridium* found in the Ekelöf Point are here assigned to *Impletosphaeridium clavus*. The small spiny cysts obtained from Sanctuary Cliffs referred to *Micrhystridium piliferum* by di Pasquo et al. (2006) and Amenábar & di Pasquo (2008) are also here reassigned to *Impletosphaeridium clavus.*

Bowman et al. (2013a) emended the species *Impletosphaeridium clavus* and described the autophragm as microbaculate to microgranulate bearing numerous solid, flexuous, non-tabular processes. Distal process terminations are mostly bifurcate or acuminate (commonly recurved), in some cases capitate, trifurcate or multifurcate. Process bases are simple and contiguous with the autophragm. The archaeopyle is an apical (4A) type with an operculum free or rarely adherent. The morphology of the Upper Cretaceous Antarctic specimens at Ekelöf Point and Sanctuary Cliffs are in agreement with the emendation proposed by Bowman et al. (2013a). However, some other features have been observed in our specimens: (i) The external surface of thin autophragm appears smooth under transmitted light microscopy (Plate 1, figures 1–2) but when highlighted using Differential Interference Contrast (DIC) the cyst wall is observed as microgranulate (Plate 1, figures 4, 8–11, 13, 15–16, 20). Furthermore, some specimens show a microstriate surface under SEM (Plate 2, figures 6–9); (ii) many processes appear to be smooth but the SEM images highlight the presence of microgranules along the process (Plate 2, figures 3–4, 6–8). Bowman et al. (2013a) proposed that microbaculate surface ornamentation on the cyst body extended as finer granules onto the surfaces of the processes (Plate 2, figure 2 of Bowman et al. 2013a). Nevertheless, our specimens show that the microgranulation along the processes can also be present in non-granulated but striated vesicles (Plate 2, figures 6–8). Despite the fact that many specimens were analysed, the archaeopyle is not clear or evident; some specimens show an irregular opening (Plate 1, figures 8, 10) that could be considered an apical archaeopyle according to Bowman et al. (2013a), but most of the specimens observed do not show a clear indication of excystment.

Dimensions. Central body diameter (measured along the major axis): 17 (24) 34 μm; length of the processes: 4.5 (6.4) 10 μm; breadth of the processes 0.5 μm (14 specimens measured).

Remarks. Cretaceous specimens from Ekelöf Point and Sanctuary Cliffs show both yellow translucent and dark brown colours (Plate 1, figures 5–6, 15–16, 20).

3.2. Cenozoic material

The Cenozoic material studied herein comes from Ekelöf Point (James Ross Island) and Cape Lamb

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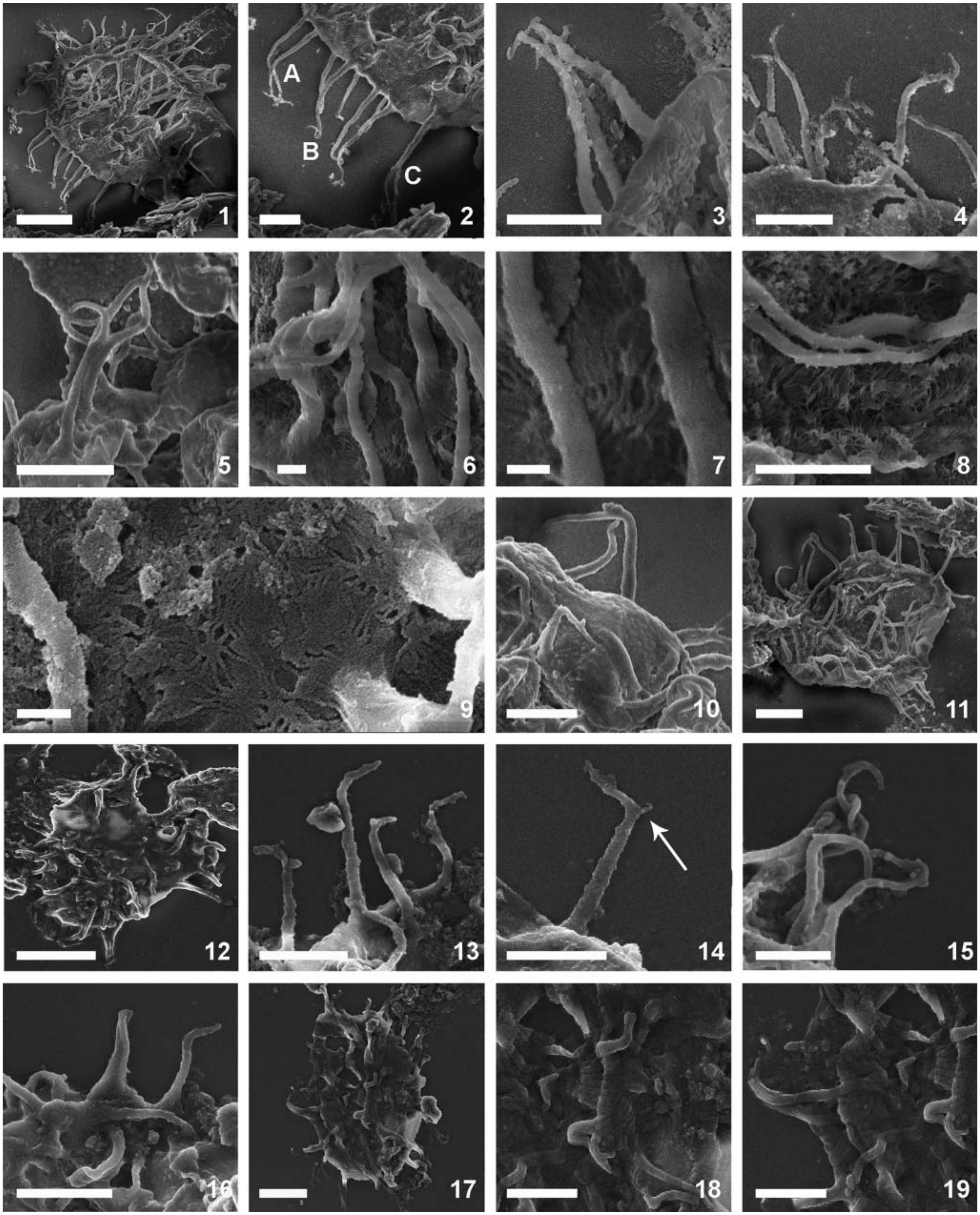
Plate 1. Specimens of *Impletosphaeridium clavus* from the Upper Cretaceous sediments at Ekelöf Point and Sanctuary Cliffs, Antarctica. All images are at the same scale; scale bar: 10 μm. England Finder coordinates are given for each specimen after the sample number. Most of the figures were taken using Differential Interface Contrast (DIC) light microscopy and Figures 1–3 were obtained without DIC. Figures 1–14. Ekelöf Point, James Ross Island. Figures 15–20. Sanctuary Cliffs, Snow Hill Island. Figures 1, 2. Specimens with circular central body and smooth wall; 1. BAFC-Pl 2458, X34/3–4; 2. BAFC-Pl 2458, W35/0. Figure 3. A dark brown specimen; BAFC-Pl 2458, X34/2. Figure 4. Specimen with granulate cyst wall. Note the high density of processes in one specimen; BAFC-Pl 2458, H34/3. Figure 5. A yellow translucent specimen; BAFC-Pl 2458, O38/0. Figure 6. A dark brown specimen close to the translucent one in figure 5 in the same slide; BAFC-Pl 2458, O38/0. Figure 7. Detail of non-tabular processes of the specimen illustrated in figure 6. Note the commonly recurved terminations; BAFC-Pl 2458, O38/0. Figures 8, 10. Specimens with an irregular opening, maybe an archaeopyle (?A); 8. BAFC-Pl 2458, M30/2; 10. BAFC-Pl 2458, M37/2. Figure 9. Detail of the slender and curved process terminations (close to 90°) and a granulate cyst wall; BAFC-Pl 2458, P39/2. Figure 11. Specimen with circular central body; BAFC-Pl 2458, B40. Figure 12. Specimens with somewhat deformed central body and few processes; BAFC-Pl 2458, H35/0. Figure 13. Detail of processes of the specimen illustrated in figure 11; BAFC-Pl 2458, F23. Figure 14. Detail of processes of the specimen illustrated in figure 12; BAFC-Pl 2458, H35/0. Figures 15–16. Specimens with scarce and short processes; 15. BAFC-Pl 2064, L26/3, 16. BAFC-Pl 2064, L35/3. Figures 17–19. Specimens with somewhat deformed central body and curved and long processes; 17. BAFC-Pl 2064, K52/2, 18. BAFC-Pl 2064, F52/1, 19. BAFC-Pl 2064, H36/1. Figure 20. Specimen with circular central body, slightly darker than the rest of the specimens from the same locality illustrated in figures 15–19; BAFC-Pl 2064, G40/2.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(Vega Island), Antarctica (Figure 1A). Both localities contain small spiny palynomorphs, assigned to *Impletosphaeridium* at the first locality and attributed to *Micrhystridium piliferum* at the second one.

All of these specimens are reassignable to *Impletosphaeridium clavus*. They are morphologically similar to those recovered from the Cretaceous units at Ekelöf Point and Sanctuary Cliffs. However, some features have not been observed in the Cretaceous material studied here. One of them is a well-defined striate cyst wall surface (Plate 2, figures 18–19).

Some Cenozoic specimens from Ekelöf Point and Cape Lamb are in general more poorly preserved than those from the Cretaceous of Ekelöf Point and Sanctuary Cliffs, due to fragmentation or deformation (Plate 3, figures 1, 3, 5).

Dimensions. Central body diameter: 15 (20) 26 μm; length of processes 2.5 (5.9) 9 μm; breadth of processes 0.5 μm (12 specimens measured).

Remarks. As in the Cretaceous samples from Ekelöf Point and Sanctuary Cliffs, some specimens show both yellow translucent (Plate 3, figure 4) and dark brown colours (Plate 3, figure 3).

3.3. *Holocene material*

Specimens from Holocene sediments in the Beagle Channel are considered to be reworked (Candel 2010; Candel et al. 2012, 2013) are comparable to *Impletosphaeridium clavus.* They are illustrated in Plate 3, figures 9–13. The Holocene reworked specimens have a spherical to sub-spherical shape. Their wall surface is microgranulate, medium brown, and ornamented by numerous processes. The processes are solid with acuminate terminations, in some cases with minutely expanded tips. An archaeopyle was not clearly observed.

Dimensions. Central body diameter: 26 (37.5) 45.5 μm; length of the processes: 4.2 (8.1) 12 μm (26 specimens measured).

Remarks. In general, the reworked specimens found in the Holocene marine sediments of the Beagle Channel are characterised by a brown colour which is lighter than the typical dark brown present in the Holocene protoperidiniacean RBSCs.

3.4. *Comparison between* Impletosphaeridium clavus *and some modern RBSCs*

Taking into account the fact that the gross morphology of *Impletosphaeridium* resembles some modern RBSCs, as previously observed by different authors, we carried out a detailed comparison between *Impletosphaeridium* and some species of modern RBSCs belonging to the family Protoperidiniaceae, as well as other small spiny dinoflagellate cysts species. We use the term RBSCs in the sense applied by Radi et al. (2013), who used this abbreviation to define the ‘round brown spiny cysts’, which represent brown cysts with a spherical central body bearing numerous non-tabular spines (processes) distributed more or less randomly. In this study, the following RBSCs species are considered for comparison with *Impletosphaeridium clavus*: *Islandinium minutum*, *Islandinium cezare*, *Echinidinium granulatum*, *Echinidinium* cf. *E. delicatum*, *Selenopemphix quanta* and *Selenopemphix* cf. *S. quanta.* The small cyst with a spherical central body and a variable density of processes belonging to the species *Pentapharsodinium dalei* is also used for comparison.

Figure 2 and Table 1 summarise the main characteristics of RBSCs and other small spiny dinoflagellate cysts present in Holocene sediments from the Beagle Channel and *Impletosphaeridium clavus* recorded in James Ross and Vega Islands. Figure 2 illustrates the

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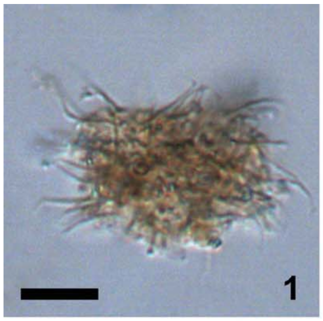
Plate 2. Scanning electron microscope (SEM) images of *Impletosphaeridium clavus* recorded from the Upper Cretaceous sediments at Sanctuary Cliffs, Snow Hill Island, and from the Cenozoic diamictites at Ekelöf Point, James Ross Island, Antarctica. Images are at different scales; scale bar: 10 μm (figures 1, 11–12, 17), 5 μm (figures 2–5, 8, 10, 13–16, 18–19), 1 μm (Figures 6–7, 9). Figures 1–11. Sanctuary Cliffs, Snow Hill Island (1–9 and 11, sample BAFC-Pl 2064 and figure 10, sample BAFC-Pl 2074). Figures 12–19. Ekelöf Point, James Ross Island (Sample BAFC-Pl 2468). Figure 1. Specimen with a lightly broken wall. Figure 2. Details of processes of the specimen illustrated in figure 1. Note the heterogeneity observed in the processes for a single specimen: multifurcate tips with asymmetric terminations (A), recurved tips at an angle of 90° (B) and bifurcate process (C). Figures 3–4. Detail of the processes. Note the asymmetric bifurcation tips and the microgranulation along the processes. Figure 5. Detail of the processes showing a bifurcate process. Note how the processes are intertwined with each other. Figures 6–8. Detail of a microstriate surface of cyst wall and the development of microgranules along the processes. Figure 9. Detail of the microstriate surface of cyst wall. Figure 10. Detail of a specimen with a smooth process and a microbaculate surface of the cyst wall. Figure 11. Deformed complete specimen. Figure 12. Complete specimen showing a subcircular outline. Figure 13. Detail of the processes with recurved tips and microgranules along the process. Figure 14. Detail of a process with recurved tips at an angle of 90° (indicated with arrow) and asymmetric termination with a minor accessory pinnule. Figure 15. Detail of the processes with greatly curved tips and intertwined with each other. Figure 16. Detail of the processes; the process on the left is shorter and has a wider base, and the one on the right is thinner and has a curved termination. Figure 17. Complete specimen showing a subcircular outline. Figures 18–19. Detail of the specimen illustrated in figure 17, showing a striate surface of the cyst wall, in different sections of the specimen.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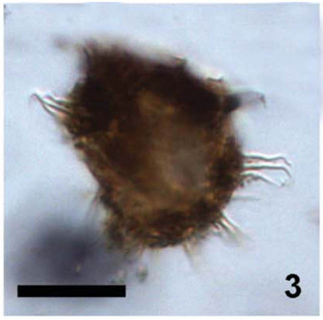
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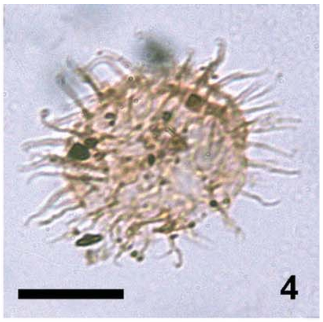
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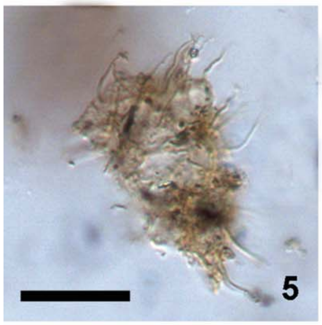
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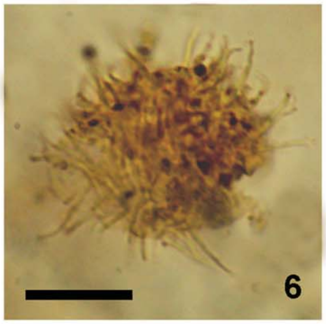
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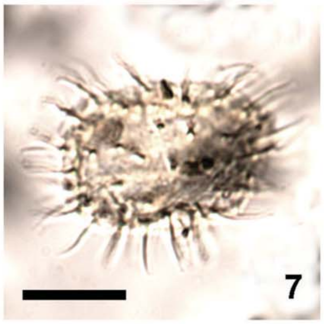
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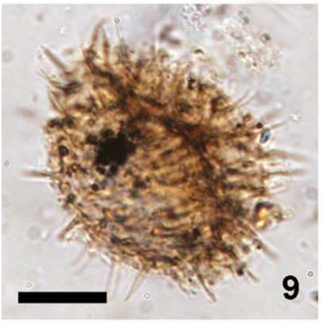
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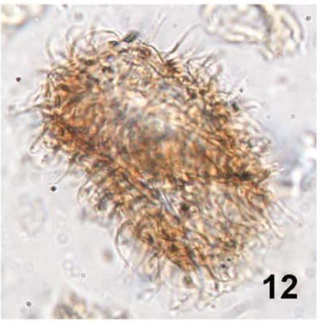
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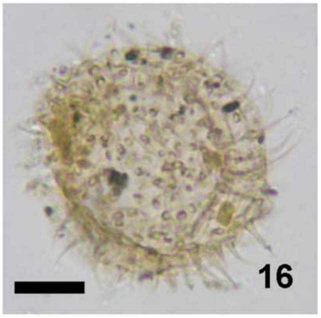
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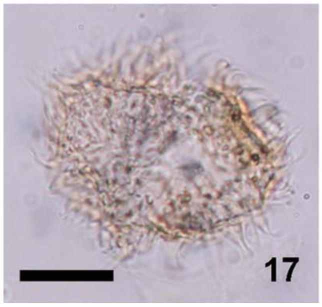
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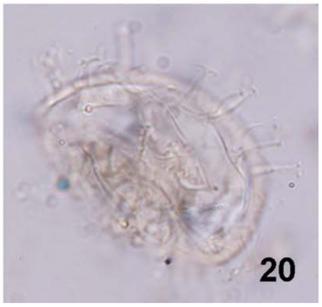
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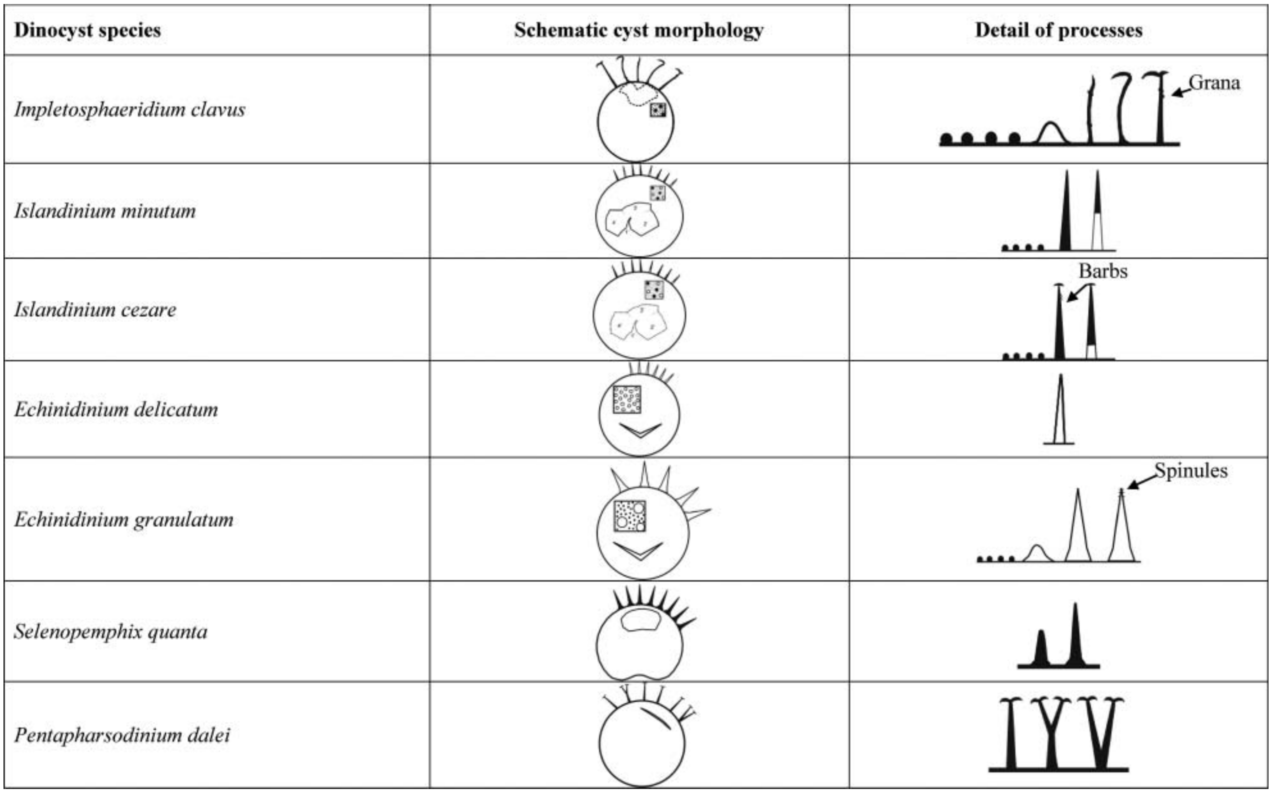

Figure 2. Line drawings of different dinoflagellate cyst species analysed in this study. The first column corresponds to a schematic cyst morphology showing the archaeopyle, surface wall structure and processes. A detail of the processes is drawn in the second column (modified from Zonneveld 1997).

schematic features of *Impletosphaeridium clavus*. Some additional RBSC characteristics are based on the type species described by different authors in recent sediments, both in the Northern and Southern Hemispheres. Figure 3 shows the relationship between central body diameter and process length of the Cretaceous, Cenozoic and Holocene (reworked and *in situ*) specimens. Cretaceous and Cenozoic specimens yielded similar values and overlap one another in the scheme. Reworked specimens presented a wide range of values. Some values match those of the Cretaceous and Cenozoic specimens but, overall, the central body diameters are larger and the processes are longer. Conversely, Holocene (*Echinidinium-Islandinium in situ*) specimens have similar central body sizes to older specimens but shorter processes in comparison to the body cyst

Plate 3. Reworked specimens of *Impletosphaeridium clavus* recorded from the Cenozoic (Pliocene) diamictites at Ekelöf Point, James Ross Island, and Cape Lamb diamictite (Pleistocene) from Vega Island, Antarctica, and from Recent (Holocene) sediments of the Beagle Channel, Tierra del Fuego, Argentina. All images are at the same scale; scale bar: 10 μm. England Finder coordinates are given for each specimen after the sample number. Some illustrations (figures 1–2, 5) were taken using Differential Interface Contrast (DIC) light microscopy and the rest were obtained without DIC. Figures 1–6. Ekelöf point diamictite, James Ross Island, Antartica. Figures 7–8. Cape Lamb diamictite, Vega Island, Antarctica. Figures 9–13. Reworked material from the Beagle Channel, Tierra del Fuego, Argentina. Figures 1–2. Specimens with circular outline; 1. BAFC-Pl 2465, V27/4. 2. BAFC-Pl 2465, N29/0. Figure 3. Dark brown specimen; BAFC-Pl 2465, N30/0. Figure 4. Yellow translucent specimen; BAFC-Pl 2468, V24/1. Figure 5. Broken and slightly distorted specimen; BAFC-Pl 2465, N30/4. Figure 6. Specimen with densely distributed non-tabular processes; BAFC-Pl 2468, S24. Figures 7, 8. Specimens with randomly distributed non-tabular processes. Note the colourless characteristic of Vega Island material; 7. BAFC-Pl 2024–1, C20/3. 8. BAFC-Pl 2026–1, H49/3–4. Figure 9. UNSP FCB 2347–5, Q36/4. Figure 10. UNSP FCB 2347–3, F45. Figure 11. UNSP FCB 2347–3, N59/3. Figure 12. UNSP FCB 2347–5, D3. Figure 13. UNSP FCB 2347–2, X18/1. Figures 14–20. Modern species of dinoflagellate cysts from the Beagle Channel used to compare with reworked cysts identified in this study. Figure 14. *Islandinium minutum*; UNSP FCB 2347–4, Q46/2. Figure 15. *Islandinium cezare*; UNSP FCB 2349–4, X17/3. Figure 16. *Echinidinium granulatum*; UNSP FCB 3166, Z13/4. Figure 17. *Echinidinium* cf. *E. delicatum*; UNSP FCB 2347–3, M53. Figure 18. *Selenopemphix quanta*; UNSP FCB 2347–2, J44/2. Figure 19. *Selenopemphix* cf. *S. quanta*; UNSP FCB 2347–5, W20/4. Figure 20. *Pentapharsodinium dalei*; UNSP FCB 2347–1, L44.

Table 1. Main morphological differences of *Impletosphaeridium clavus* recorded from James Ross and Vega Islands and Holocene sediments in the Beagle Channel. Also, some round brown spiny cysts (RBSCs) are shown in relation to the type species described by different authors from sediments in the Northern and Southern Hemispheres.

	Central body			Processes					
Dinoflagellate cyst	diameter (μm)	shape	cyst wall	length (μm)	form	characteristics	Archaeopyle	Specimens measured	Illustration
Impletosphaeridium clavus Cretaceous *(in situ)*	17 (24) 34	spherical to sub-spherical	smooth, granulate, striate, perforate, baculate	4.5 (6.4) 10	branched (asymmetrical bifurcate, trifurcate to multifurcate)	solid, with or without grana developed along the processes, with curved tips	?apical to unknown	14	Plate 1, figures 1–20 Plate 2, figures 1–9
Impletosphaeridium clavus Pliocene and Pleistocene (reworked)	15 (20) 26	spherical to sub-spherical	smooth, granulate, striate, perforate, baculate	2.5 (5.9) 9	branched (asymmetrical bifurcate, trifurcate to multifurcate)	solid, with or without grana developed along the processes, with curved tips	?apical to unknown	12	Plate 2, figures 12–19 Plate 3, figures 1–8
Impletosphaeridium clavus Holocene (reworked)	26 (37.15) 48	spherical to sub-spherical	smooth, granulate	4.2 (8.1) 12	acuminate	solid, with curved tips	?apical to unknown	27	Plate 3, figures 9–13
Islandinium minutum	24 (35) 64	spherical to sub-spherical	granulate	2.5 (4) 6.5	acuminate	solid, circular and unexpanded bases	apical, not clearly observable	22	Plate 3, figure 14
Islandinium cezare	25 (32.5) 46.8	sub-spherical	smooth to microgranulate	3 (5.5) 9	minutely expanded tips	usually solid, circular and unexpanded bases	saphopylic	11	Plate 3, figure 15
Echinidinium granulatum	19 (28.5) 41.6	spheroidal	granulate	3 (5.2) 8	acuminate	hollow with circular expanded bases	chasmic	45	Plate 3, figure 16
Echinidinium cf. *E. granulatum*	21 (28.3) 43	spherical to sub-spherical	granulate	4 (5) 9	acuminate	hollow and solid with circular expanded bases	split along suture	15	— — — — —
Echinidinium cf. *E. delicatum*	19 (23.2) 28	spherical	smooth	2 (4.1) 5	acuminate	hollow with sub-circular bases	split along suture	15	Plate 3, figure 17
Selenopemphix quanta	30 (45.1) 66	sub-spherical to reniform	smooth	4 (10.5) 14.4	sharp and blunt	solid with expanded bases	intercalary	30	Plate 3, figure 18
Selenopemphix cf. *S. quanta*	30 (38.4) 48.8	sub-spherical	smooth	5 (9.8) 13	sharp and blunt	solid, without expanded bases	intercalary, not clearly observable	22	Plate 3, figure 19
Pentapharsodinium dalei	19 (26) 33.8	spherical	smooth	3 (4.6) 6.5	branched (symmetrical bifurcate) or unbranched	solid with expanded bases	split (chasmic)	25	Plate 3, figure 20

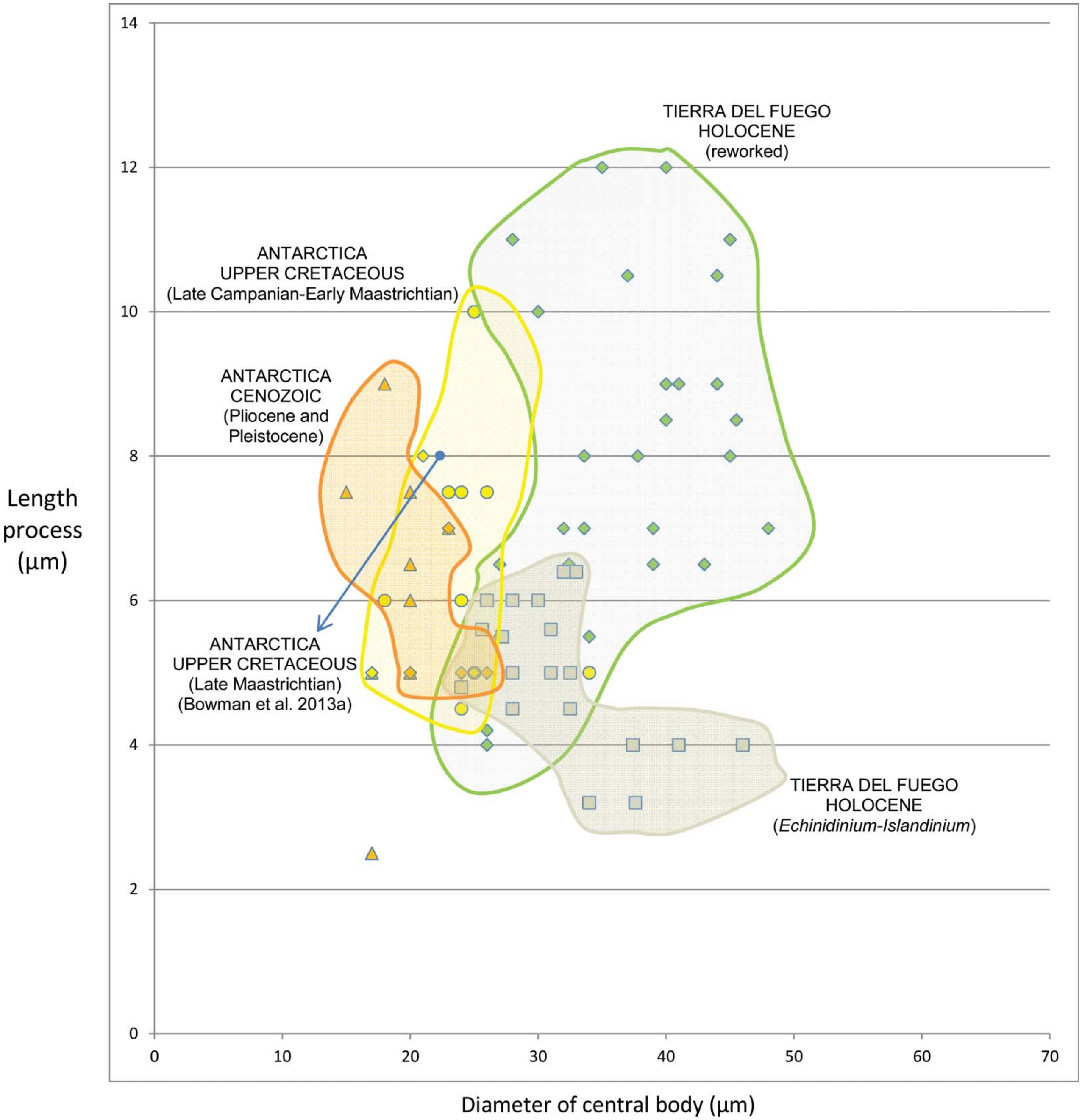

Figure 3. Relationship between the central body diameter and length of the processes observed in specimens from the Cretaceous and Cenozoic of Antarctica and Holocene (reworked and *in situ*) of Tierra del Fuego. Studied localities: Antarctica, Upper Cretaceous: Ekelöf Point (James Ross Island) and Sanctuary Cliffs (Snow Hill Island). Antarctica, Cenozoic: Ekelöf Point (James Ross Island) and Cape Lamb (Vega Island). Tierra del Fuego, Holocene: Beagle Channel. One point is also plotted in the figure which corresponds to the average of the specimen's dimensions (maximum diameter of central body and process length, 22 µm and 8 µm, respectively) measured by Bowman et al. (2013a) from the Maastrichtian of the López de Bertodano Formation, at Seymour Island, Antarctica. One specimen of the Cenozoic samples is outside of the analysis (perhaps it is a fragmented specimen) because of its extremely low vesicle (central body diameter: 17 µm) and process (process length: 2.5 µm) dimensions that deviate from the values of the rest of the specimens measured.

diameters with values falling in the lower part of the diagram. The average of the specimen dimensions measured by Bowman et al. (2013a) from the Maastrichtian of the López de Bertodano Formation, of Seymour Island, Antarctica, falls into the Cretaceous group as studied here.

The comparison leads to the following observations: *Echinidinium* and *Islandinium* have acuminate processes and are not branched like *Impletosphaeridium.* In addition, the processes in *Echinidinium* and *Islandinium* are shorter in relation to the central body diameter (Plate 3). The latter genus presents more rigid processes which do not curve as occurs in *Impletosphaeridium. Echinidinium granulatum* has hollow, acuminate processes with circular expanded bases, in contrast with *Impletosphaeridium clavus* which has branched processes with unexpanded bases. However, *Selenopemphix quanta* has solid and sharp, in some cases truncated (or blunt), processes with expanded bases. Expanded bases have not been observed in *Impletosphaeridium clavus*. Cysts of *Pentapharsodinium dalei* have solid and branched, or usually unbranched, processes with expanded bases, and the branches or bifurcations may occur at any point along their length, dividing the processes into two equal parts. It is understandable for some authors (Warny et al. 2007; Bowman et al. 2013a) to include *Pentapharsodinium dalei* in their analysis and compare it with *Impletosphaeridium*, because of its bifurcatet processes, a feature which is also present in *Impletosphaeridium clavus*. However, the branches of *Impletosphaeridium clavus* are bifurcate to multifurcate and are also asymmetrically bifurcate or, in rare cases, they do not even ramify.

Reworked specimens from the Holocene of the Beagle Channel, Tierra del Fuego, show morphological characteristics similar to *Impletosphaeridium clavus*, although some are larger than those documented for the Cretaceous and Cenozoic of Antarctica (Figure 3).

4. Discussion

The recognition of *Impletosphaeridium* as an *in situ* or reworked palynomorph in Antarctic Cenozoic deposits is central to determine interpretations of palaeoenvironment and age. In this sense, Warny and Askin (2011a, 2011b) suggested the use of the cyst wall coloration as a means to distinguish *in situ* and reworked specimens amongst these small spiny palynomorphs (as *Micrhystridium*) recorded in the Antarctic Cenozoic. They considered that the cysts with light-coloured, almost transparent walls, were native, while those with dark colours (with a golden hue), indicating a thermally more mature status, were reworked from the Upper Cretaceous.

The small cysts found in palynological assemblages from the Antarctic Cenozoic diamictites (Ekelöf Point and Cape Lamb), could not be distinguished from those observed in the Upper Cretaceous deposits of Antarctica (Ekelöf Point and Sanctuary Cliffs). The coloration of the cysts may be variable in both Cretaceous and Cenozoic assemblages. Moreover, the same Upper Cretaceous sample usually contains cysts with different colours (Plate 1, 3–4, 5–6). Some specimens, especially from Cape Lamb (Vega Island), are 'beautifully preserved' (p. 15, Dettman & Thomson 1987) and have a translucent pale yellow colour (C.R.A., personal observation). The reworked Cretaceous material recovered from Cenozoic the can be found in excellent condition, and is not necessarily darker than that found in *in situ* samples. For that reason, the colour of the cysts recovered in Cenozoic samples cannot be used as a criterion to decide whether they are penecontemporaneous or recycled from older deposits. Accordingly, when the preservation does not contribute to the distinction between *in situ* and reworked palynomorphs, only the stratigraphical ranges of the species allow the differentiation both groups. However, it is worth noting that some specimens of *Impletosphaeridium clavus* appear to be better preserved in the Upper Cretaceous of Ekelöf Point and Sanctuary Cliffs, retaining their original shape with more rounded central bodies (Plate 1). In contrast, most of the *Impletosphaeridium clavus* specimens from the diamictites (mainly from Ekelöf Point) are generally broken, and the central bodies tend to be deformed (Plate 3, figure 5).

In contrast, *Impletosphaeridium clavus* specimens from Antarctic Cenozoic diamictites studied herein (Ekelöf Point and Cape Lamb) are recorded together with the reworked Late Cretaceous dinoflagellate cysts, such as *Odontochitina porifera*, *Trichodinium castanea*, *Phelodinium exilicornutum* and *Isabelidinium pellucidum* (Adamonis et al. 2010), associated with reworked pollen and spores, i.e. *Perotrilites majus*, *Leptolepidites verrucatus* (C.R.A., personal observation). Other authors have also noted the presence of reworked dinoflagellate cysts from Upper Cretaceous (Campanian–Maastrichtian) in Cenozoic samples. Salzman et al. (2011) reported the presence of species *Isabelidinium pellucidum*, *Odontochitina porifera* and *Nelsoniella tuberculata* in several Cenozoic diamicites (Early Pliocene) from James Ross Island. Similarly, Warny and Askin (2011b) recorded the dinoflagellate cysts *Isabelidinium cretaceum* and *Manumiella seymourensis* in the upper part of the core NBP0602A-3C (middle to ? upper Miocene) on the Joinville Plateau, Weddell Sea, northern Antarctic Peninsula. Hence, *Impletosphaeridium clavus* specimens recorded from Cenozoic Antarctic diamictites are morphologically identical to the Late Cretaceous specimens, regardless of the colour of the cysts. In addition, these specimens found in the diamictites are associated with definitely recycled Upper Cretaceous dinoflagellate cysts and pollen-spores. For these reasons, we assume the presence of *Impletosphaeridium clavus* in Cenozoic Antarctic samples is a consequence of Upper Cretaceous recycling produced by glacial action. Thus, we can confirm the *in situ* nature of *Impletosphaeridium clavus* only in the Upper Cretaceous.

Most of the middle Eocene dinoflagellate cyst assemblages in circum-Antarctic areas contain small spiny palynomorphs with a barely visible archaeopyle, illustrated as different species of *Impletosphaeridium*. The specimens illustrated fit into the emended description of *Impletosphaeridium clavus* by Bowman et al. (2013a). Quantitative palynological studies showed that this species represented less than 5% of the total number of dinoflagellate cysts. The assemblages analysed contain species that represent reworked material from Upper Cretaceous deposits (Cocozza & Clarke 1992; Mao & Mohr 1995; Guerstein et al. 2008). Archangelsky (1969) and Guerstein (personal observation) recorded less than 5% of *Impletosphaeridum* spp. in the assemblages in cores drilled by Yacimientos Carboníferos Fiscales in southeastern Santa Cruz Province, Patagonia region, southern Argentina (Figure 1B), but did not note the presence of Upper Cretaceous reworked material. This information cannot determine whether *Impletosphaeridium clavus* is *in situ* or reworked in the middle Eocene of Antarctica and Patagonia, except to conclude that no acme of this species is present.

Warny et al. (2007) were the first to compare specimens of *Impletosphaeridium* recovered from Eocene to Miocene Antarctic deposits with modern dinoflagellate cysts species. These authors selected some RBSCs species (*Echinidinium* spp., *Islandinium cezare*, *Islandinium minutum*) and *Pentapharsodinium dalei* as potential modern analogues. However, they failed to specify the morphological features shared by modern and fossil groups, and thus did not confirm the proposed affinity. Besides, Bowman et al. (2013a) resumed the hypothesis of the morphological resemblance between *Impletosphaeridium clavus* and some modern RBSCs, but they did not indicate which features both groups had in common either. The detailed morphological analysis of the fossil dinoflagellate cysts and their potential modern analogues carried out here demonstrates that, although *Impletosphaeridium clavus* is roughly similar to some RBSCs, some differences in the processes and cyst wall characteristics prevent ensuring a complete equivalence to confirm the analogy.

Another important point to reassess is the order in which the genus *Impletosphaeridium* should be classified. Originally, it was included in the order Gonyaulacales. This classification was consecutively followed by Wrenn and Hart (1988) and Bowman et al. (2013a). Due to their autotrophic habits, gonyaulacacean cysts emit green to yellow fluorescence under ultraviolet epifluorescence illumination (Brenner & Biebow 2001). However, Bowman et al. (2013a) pointed out that *Impletosphaeridium clavus* specimens do not autofluoresce. In consequence, the lack of autofluorescence in these dinoflagellate cysts might indicate their affinity to some peridinacean cysts (Family Protoperidinaceae) or, at least, to some other family with heterotrophic habits which is not characteristic of gonyaulacacean taxa. This hypothesis, which relates parent dinoflagellates of *Impletosphaeridium clavus* with heterotrophy, has already been outlined by Bowman et al. (2013a).

Conversely, all of the RBSCs are assigned to Order Peridiniales, Family Protoperidiniaceae, based on the archaeopyle type (even though it is hardly visible), the brown pigmentation of their cyst walls, the lack of epifluorescence and the non-tabular process distribution (cf. Head et al. 2001; Radi et al. 2013). In reference to the archaeopyle of *Impletosphaeridium clavus,* Bowman et al. (2013a) described the presence of an apical archaeopyle (4A) in their emended diagnosis, assuming that the opening was in an apical position. This feature would bring *Impletosphaeridium clavus* closer to the gonyaulacacean tabulation. However, the presence of that type of archaeopyle is not convincing in the specimens illustrated by Bowman et al. (2013a) nor in hundreds of specimens studied herein. The archaeopyle margin is never clear enough to determine the number of plates involved, or the exact apical position. If the apical archaeopyle (4A) is not confirmed in *Impletosphaeridium clavus*, and the opening type of this species is similar to some RBSCs (intercalary archaeopyle), *Impletosphaeridium clavus* may be related to species with heterotrophic habits, which is also supported by the lack of fluorescence. Regarding the cyst coloration, low pigmentation of the cyst wall, or its complete absence, does not represent a valid feature to discard the affinity with protoperidiniaceans. For example, *Trinovantedinium applanatum* is a fossil protoperidiniacean species with no pigmentation. The cyst *Trinovantedinium applanatum* is produced by the dinoflagellate *Protoperidinium pentagonum* and the species of the genus *Protoperidinium* are considered to be heterotrophic and feed primarily on medium to large diatoms and other dinoflagellates (Gribble et al. 2007).

Considering that *Impletosphaeridium* resembles some RBSCs, Warny et al. (2007) related these extant small spiny cysts to ice-cover conditions developed around Seymour Island, possibly at the end of the Eocene. However, it is necessary to take into account that, although an unequivocal analogy between *Impletosphaeridium clavus* and RBSCs cannot be demonstrated, not all the RBSCs are linked to the ice-cover, since many of them are also produced in low and middle latitudes. For instance, some RBSCs species, such as *Echinidinium delicatum*, *E. granulatum* and *Selenopemphix quanta,* have a polar to equatorial distribution, but their highest relative abundances are observed in the subtropical and tropical regions (Zonneveld et al. 2013). Species of *Islandinium* are characteristic of cold, polar/sub-polar regions. The species *Islandinium minutum* has a bipolar distribution restricted to temperate to polar regions, while *Islandinium cezare* is endemic for the high latitudes of the Northern Hemisphere (Marret & Zonneveld 2003; Zonneveld et al. 2013). Even though *Islandinium* species may have polar or bipolar distributions and exhibit apical archaeopyles involving the loss of three plates (Head et al. 2001), this feature has not been observed in our specimens of *Impletosphaeridium*.

The assemblage obtained from marine Holocene deposits in the Beagle Channel, Tierra del Fuego, provides a good example of Southern Hemisphere high-latitude assemblages, which illustrates the fact that RBSCs are present in cold waters without sea-ice development. This palynological assemblage contains both *Islandinium* and *Echinidinium* species (Table 1; Figure 2). The Beagle Channel is characterised by cold waters, with an average sea-surface temperature of 6.5 °C (4–9 °C, winter–summer, respectively) and is ice-free all year round (Isla et al. 1999). It was possible to demonstrate that *Impletosphaeridium clavus* does not have unequivocal modern analogues, but it is likely that these small spiny cysts could have been produced by dinoflagellates similar to those that generate some of the RBSCs or other similar small spiny cyst today. On the basis of this information, we can speculate that the existence of similar climatic conditions in the Beagle Channel during the Late Cretaceous in the Antarctic Peninsula would have favoured the development of *Impletosphaeridium clavus* in such marine high latitude environments. From correlation with the delta-oxygen-18 (δ^{18}O) data, Bowman et al. (2013b) inferred a possible toleration of near-freezing conditions for this species.

5. Climatic implications for the high latitudes during the Late Cretaceous

In all likelihood, the Late Cretaceous of Antarctica experienced cold climatic conditions, but it did not necessarily lead to the development of sea-ice cover. This assumption agrees with Miller et al. (2005), who argued that throughout Late Cretaceous–Eocene greenhouse conditions, ice sheets were ephemeral and apparently stayed during short intervals of peak Milankovitch insolation (on the order of 100 ky), leaving Antarctica ice free for a considerable part of this interval. This implies that ice sheets did not reach the Antarctic coast in the Late Cretaceous (Santonian–Maastrichtian); therefore, coastal Antarctica remained relatively warm despite the significant changes in sea level resulting from glaciations. Antarctic ice sheets remained well inland, having little to no influence on coastal regions. Thereby, Miller et al. (2005) explained how ice conditions reconcile with relative warm temperatures on the Antarctic coastline. The warm palaeoclimates for high latitudes are also supported by the terrestrial floral records. Continental temperatures were equable; 13.6 °C in the Santonian and 11.7 °C in the Maastrichtian. These could have allowed the development of a floristically diverse and structurally complex vegetal community, characterised by a perhumid, tall, open forest during the Santonian–Maastrichtian in the Antarctic Peninsula (Specht et al. 1992).

What would be the reasons for the *Impletosphaeridium* acme during the Late Cretaceous of Antarctica? Thorn et al. (2009) noted that a great abundance of small spiny cysts (assigned to *Micrhystridium* spp., then to *Impletosphaeridium clavus* by Bowman et al. 2013b and quantified up to 99% of marine assemblage) occurred together with an acme of *Manumiella seymourensis*. These observations were obtained from levels 250 m below the Cretaceous/Paleogene (K/Pg) boundary in the uppermost López de Bertodano Formation on Seymour Island. Recently, Bowman et al. (2013a) completed the analysis of the lowermost 700 m of the López de Bertodano Formation, and detected two additional abundance peaks of *Impletosphaeridium clavus* (intervals A and B) in addition to the one (interval C) in the uppermost part of the unit. These authors related the acmes of *Impletosphaeridium clavus* with the presence of Antarctic winter sea-ice during cold episodes during the Maastrichtian. They suggested that only this environmental factor could have influenced the blooms of the parent dinoflagellate, and hence the *Impletosphaeridium clavus* acmes. This is based on the fact that no other marine palynomorph exhibited an abundance pattern similar to that of *I. clavus* in their section. Nevertheless, an important point on dinoflagellates is that not all species produce resting cysts with a probability of being preserved, so care should be taken when comparing the abundances of different genera when they are present in large abundances. Dinoflagellate cyst assemblages may be altered pre- and post-depositionally as a result of species-selective degradation (Zonneveld et al. 2007). Not only temperature influences the rate of excystment but also nutrients and light intensity (Godhe et al. 2001). We consider that other factors, such as nutrient availability and physico-chemical properties of marine waters, should not be excluded from the interpretation, especially if we take into account that other species, in this case *Manumiella seymourensis*, are also abundant in the dinoflagellate cyst assemblages of the López de Bertodano Formation, and a peak of abundance of this taxa matches the acme of *I. clavus* (Thorn et al. 2009).

The Upper Cretaceous units out cropping at Ekelöf Point are the Rabot and Snow Hill Island formations, which are located stratigraphically below the López de Bertodano Formation (Olivero 2012 and references therein). In Upper Campanian–Lower Maastrichtian palynological assemblages at Ekelöf Point, *Impletosphaeridium clavus* shows a peak of abundance representing 73.5% of marine palynomorphs (see *Section 3.1*). This species is associated with rare specimens of *Odontochitina porifera*, *Spiniferites ramosus*, *Oligosphaeridium* sp., *Palaeocystodinium* spp., *Phelodinium exilicornutum* and indeterminate peridinacean dinoflagellate cysts. However, the large numbers of *Impletosphaeridium clavus* in this locality do not seem to be associated with ice-sea cover, because Late Campanian–Early Maastrichtian temperatures were warm to cool towards the Late Maastrichtian, based on the chemical index of alteration ratio of feldspars (CIA) data which relates the temperature with the sediments (Dingle & Levelle 2000). This climatic tendency shows the transition from a warm Turonian–latest Campanian to a cool Early Maastrichtian and then to a cool-cold Late Maastrichtian–Mid-Paleocene. Thus, the bloom of *Impletosphaeridium clavus* at Ekelöf Point would not be related with glaciation in Antarctic coastal areas, but it could be the case that the glaciation did influence the acme of this species in the Maastrichtian section of the López de Bertodano Formation on Seymour Island. *Impletosphaeridium Clavus* is well represented in the Upper Campanian–Lower Maastrichtian of on Ekelöf point and Sanctuary Cliffs localities but it becomes even more abundant as the climate deteriorated towards the K/Pg boundary, where *I. clavus* represents up to 99% of the marine assemblage. This observation concurs with the proposal by Bowman et al. (2013b), who suggested that dinoflagellate blooms that produced resting cysts of *I. clavus* may have occurred during periods when shelf waters off the Antarctic Peninsula were particularly cool during the Maastrichtian.

Returning to the peak of *Impletosphaeridum clavus* in the Late Cretaceous at Ekelöf Point, it should be noted that the assemblage of the entire section is dominated mainly by peridinoid dinoflagellate cysts, where the best represented as regards numbers of species and numbers of specimens are *Isabelidinium*, *Manumiella* and *Palaeocystodinium*. Taking into account that Thorn et al. (2009) observed a spectrum of the peridinioid genera *Manumiella* and *Isabelidinium* in samples near to the K/Pg boundary and related it with a change in nutrient availability, temperature or chemistry of Antarctic marine environments. They considered the assumption that the peridinioid genera *Manumiella* and *Isabelidinium* were heterotrophic, as mentioned by several authors (e.g. Jacobsen & Anderson 1986; Pearce et al. 2009), and their dominance in the assemblages might suggest eutrophic surface waters during the Late Cretaceous (cf. Warny & Askin 2011b). The source of nutrients could have been generated by coastal upwelling zones or by continental input from deltaic complexes (Warny & Askin 2011b). There is no sedimentological evidence of upwelling currents in the Late Cretaceous of the Antarctic Peninsula region, so a high nutrient input into the marine basin coming from the continent is a plausible explanation. Consequently, in a nutrient-rich or eutrophic surface waters context, the abundance of *Impletosphaeridium* may have occurred, which also accords with the assumption of a heterotrophic lifestyle of the dinoflagellates that produced these cysts. In any case, the causal factors responsible for the acmes of *Impletosphaeridium* still require further study.

6. Conclusions

Despite the fact that *Impletosphaeridium clavus* shows similar morphological characteristics to some modern species of RBSCs, the detailed comparison conducted in this study between different specimens from the Upper Cretaceous and Holocene demonstrated that *Impletosphaeridium clavus* does not have unequivocal modern analogues. Still, this species presents some similarities to the RBSCs (archaeopyle, lack of fluorescence, brown pigmentation in some specimens and nontabular process distribution), which lead us to consider that the dinoflagellates that produced them had a similar lifestyle.

The acmes of *Impletosphaeridium clavus* recorded in the Early and Late Maastrichtian of Seymour Island (Thorn et al. 2009; Bowman et al. 2013a, 2013b) have been linked to the presence of Antarctic winter sea-ice during cold episodes taking place at those times. An abundance peak of *Impletosphaeridium clavus* identified in a single level of Upper Campanian–Lower Maastricthian from Ekelöf Point (James Ross Island) could be a response to a cold pulse during the Late Cretaceous, but does not necessarily imply the development of sea-ice cover. The arrival of cold water in marine settings could possibly be the result of ice fluctuations on the continent. The Late Cretaceous *Impletosphaeridium* acme recorded in high latitudes could be a combination of cold waters and a marine environment with nutrient-rich surface waters that would have favoured the increase in numbers for such species and finally its dominance in the palynological assemblages towards to the end of the Cretaceous.

Bowman et al. (2013a) proposed that *Impletosphaeridium clavus* ranged from the Late Campanian to the Holocene. Specimens of *Impletosphaeridium clavus* recorded in the middle Eocene of southern high latitudes (Antarctica and Patagonia) cannot be certainly determined as *in situ* or reworked palynomorphs since this species is present in low proportions in assemblages where reworking is not significant, if present at all. However, we can conclude that no acmes of *Impletosphaeridium clavus* have been recorded in the middle Eocene of Antarctica and Patagonia. Considering that we cannot confirm *Impletosphaeridium clavus* as *in situ* in the Antarctic Cenozoic diamictites, we propose to restrict the stratigraphical range of *Impletosphaeridium clavus* from the late Campanian to the Late Eocene.

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Appendix. List of the marine palynomorphs identified in the samples studied from Antarctica, Patagonia and Beagle Channel areas

Echinidinium cf. *E delicatum* Zonneveld 1997

Echinidinium granulatum Zonneveld 1997

Echinidinium cf. *E. granulatum* Zonneveld 1997

Impletosphaeridium clavus Wrenn & Hart, 1988 emend. Bowman et al. 2013a

Islandinium? *cezare* (de Vernal et al. 1989 ex de Vernal in Rochon et al. 1999) Head et al. 2001

Islandinium minutum (Harland & Reid in Harland et al. 1980) Head et al. 2001

Pentapharsodinium dalei Indelicato & Loeblich III 1986

Selenopemphix quanta (Bradford 1975) Matsuoka 1985

Selenopemphix cf. *S. quanta* (Bradford 1975) Matsuoka 1985

List of the palynomorphs cited in the text

Dinoflagellate cysts and acortarchs

Chatangiella tripartita (Cookson & Eisenack 1960) Lentin & Williams 1976

Chatangiella victoriensis (Cookson & Manum 1964) Lentin & Williams 1976

Exochosphaeridium bifidum (Clarke & Verdier 1967) Clarke et al. 1968.

Isabelidinium cretaceum (Cookson 1956) Lentin & Williams 1977

Isabelidinium korojonense (Cookson & Eisenack 1958) Lentin & Williams 1977

Isabelidinium pellucidum (Deflandre & Cookson 1955) Lentin & Williams 1977

Malvinia escutiana Houben, et al. 2011

Manumiella seelandica (Lange 1969) Bujak & Davies 1983, emend. Firth 1987

Manumiella seymourensis Askin 1999

Micrhystridium piliferum Deflandre 1937

Nelsoniella tuberculata Cookson and Eisenack 1960

Odontochitina indigena Marshall 1988

Odontochitina porifera Cookson 1956

Operculodinium radiculatum Smith 1992

Palaocystodinium lidiae (Górka 1963) Davey 1969

Phelodinium exilicornutum Smith 1992

Spiniferites ramosus (Ehrenberg 1838) Mantell 1854

Trichodinium castanea Deflandre 1935

Trinovantedinium applanatum (Bradford 1977) Bujak and Davies 1983

Xenikoon australis Cookson & Eisenack 1960

Pollen and spores

Baculatisporites comaumensis (Cookson 1953) Potonié 1956

Ceratosporites equalis Cookson & Dettmann 1958

Cyathidites minor Couper 1953

Evansispora senonica Raine 2008

Franseria meyeniana Sch. Bip. (illustrated by Heusser 1971)

Haloragacidites trioratus Couper 1953

Leptolepidites verrucatus Couper 1953

Nothofagidites dorotensis Romero 1973

Peninsulapollis gillii (Cookson 1957) Dettmann & Jarzen 1988

Perotrilites majus (Cookson & Dettmann 1958) Evans, 1970

Phyllocladidites mawsonii Cookson 1947 ex Couper 1953

Retitriletes austroclavatidites (Cookson 1953) Doring et al. in Krutzsch 1963

Algae

Botryococcus braunii Kützing 1849

Palambages sp.

Paralecaniella indentata (Deflandre & Cookson 1955) Cookson & Eisenack 1970 emend. Elsik 1977.