The taxonomy and palaeobiogeography of small chorate dinoflagellate cysts from the Late Cretaceous to Quaternary of Antarctica

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Small chorate dinoflagellate cysts are common in Upper Cretaceous to Quaternary sedimentary successions from around the Antarctic margin. Taxonomic confusion surrounding dinoflagellate cysts and acritarchs of similar morphology throughout the southern high palaeolatitudes has hitherto limited investigation of their palaeoecological significance. This study aims to solve the taxonomic problems, and to allow a new assessment of dinoflagellate cyst acmes. A detailed morphological study of new material from the López de Bertodano Formation of Seymour Island, Antarctic Peninsula is presented. These dinoflagellate cysts are identified as *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov. Their gross morphology and their vast abundances in the James Ross Basin are strongly suggestive of dinoflagellate blooms. This scenario implies similarities to modern dinoflagellate cysts from the polar regions.

Keywords: dinoflagellate cysts; acritarchs; taxonomy; palaeobiogeography; Cretaceous-Quaternary; Antarctica

1. Introduction

Small chorate (spine-bearing) algal cysts have been recorded, but rarely illustrated, from Upper Cretaceous to Quaternary shallow marine sediments around the Antarctic margin, (Figure 1, Table 1). They have rounded to ellipsoidal cyst bodies, which are ~20 μm in diameter, and bear around 100 thin, solid, flexible non-tabular processes. The palaeoecology of these forms is poorly understood, but is likely to be significant in the southern high palaeolatitudes where they have been recorded in extremely high proportions (Askin 1988; Smith 1992; Bowman et al. 2012). Vast abundances of dinoflagellate cysts in the fossil record may represent the aftermath of dinoflagellate blooms (Noe-Nygaard et al. 1987). It has also been suggested that these acmes may represent phytoplankton blooms associated with the presence of seasonal sea ice (Wrenn et al. 1998; Warny et al. 2007; Warny and Askin 2011a). We consider that taxonomic confusion is hindering the interpretation of these abundant cysts in the geological record of the southern high palaeolatitudes.

Elucidating the detailed morphology of these small chorate cysts is difficult without scanning electron microscopy (Sarjeant and Stancliffe 1994; Schrank 2003). As most palynologists routinely work with transmitted light microscopy, the consistent differentiation of these morphotypes may be difficult. Small chorate cysts from the Late Cretaceous to Quaternary of the Antarctic margin have been attributed to the acanthomorph acritarch genus *Micrhystridium* Deflandre 1937 and the dinoflagellate cyst genus *Impletosphaeridium* Morgenroth 1966 (Table 1). Eaton et al. (2001) considered *Impletosphaeridium* to be a convenient genus to attribute problematical morphotypes (i.e. a “grab-bag”).

This paper assesses the taxonomy of these small chorate cysts using highly productive material from the Maastrichtian to Danian López de Bertodano Formation exposed on Seymour Island at the northeastern tip of the Antarctic Peninsula (Figures 1, 2). We consider that these cysts are *Impletosphaeridium clavus*, which is emended herein, extending its range back to the Late Campanian. The palaeogeographical distribution of small chorate cysts in Upper Cretaceous to Quaternary sediments around the Antarctic margin is reconsidered in the context of this study, which shows that many of these published records can be re-classified as *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

2. Geological background

Seymour Island is located in the James Ross Basin at the northeastern tip of the Antarctic Peninsula; in its southern part, shallow marine to deltaic sediments of the Coniacian to Danian Marambio Group are exposed (Figure 1; Pirrie et al. 1997a; Crame et al. 2004; Montes et al. 2007; Olivero et al. 2007; Olivero 2012). Here, the uppermost Snow Hill Island Formation (the Haslum Crag Member), the López de Bertodano Formation and the Sobral Formation crop out with the Cretaceous-Paleogene (K-Pg) boundary within the upper López de Bertodano Formation (Figure 2; Macellari 1988; Crame et al. 2004). The oldest beds exposed on Seymour Island are probably Maastrichtian in age (Bowman et al. 2012; Tobin et al. 2012). In the northern part of the island, the stratigraphical relationships within the Paleogene Seymour Island Group remain uncertain, but this succession is divided into the Cross Valley Formation (early Late Paleocene) and the La Meseta Formation (Eocene) (Figure 2; Sadler 1988; Marenssi et al. 2012).

A stratigraphical section (named D5.251), approximately 1100 m thick, was measured and sampled every 1-2 m throughout the highly fossiliferous Maastrichtian to Danian López de Bertodano Formation (Figure 1; Thorn et al. 2009; Bowman et al. 2012). The sedimentology is relatively monotonous, consisting of hundreds of metres of silty-clays and clayey-silts. The López de Bertodano Formation has yielded well-preserved palynofloras (Askin 1988; Thorn et al. 2009; Bowman et al. 2012) and is an exceptional locality for studying palaeobiology across the K-Pg transition.

The López de Bertodano Formation of southern Seymour Island was deposited at ca. 65°S palaeolatitude, at a similar latitude to the location today (Lawver et al. 1992). This unit represents a siliciclastic deltaic setting, with the sediment sourced from the rapidly rising volcanic arc to the west and deposited in a back-arc basin open to the current Weddell Sea region in the east (Hathway 2000; Crame et al. 2004; Olivero 2012). Dating of the López de Bertodano Formation has been established using strontium isotope analysis (McArthur et al. 1998), dinoflagellate cyst biostratigraphy (Bowman et al. 2012), magnetostratigraphy (Tobin et al., 2012) and the presence of an iridium anomaly at the K-Pg boundary horizon (Elliott et al. 1994).

3. Material and methods

Samples from section D5.251 were processed for palynomorphs using quantitative techniques (Wood et al. 1996). Twenty-five grammes of dry sediment from each sample were sieved at 180 µm and the smaller fraction treated with hydrochloric and hydrofluoric acids. The acidified residue was oxidized using nitric acid for one or two minutes, then the organic matter was gravity-separated from any resistant minerals using zinc chloride centrifugation and physical swirling. The organic fraction was then sieved at 10 µm and made up to 50 ml with distilled water. A standard aliquot of 1 ml (0.5 g of the initial 25 g dry weight) was then permanently mounted onto a microscope slide. All samples and slides are curated at the British Antarctic Survey, Cambridge, United Kingdom.

At least 300 marine and terrestrial palynomorph specimens were counted from each slide along regularly spaced transects allowing the calculation of palynomorphs per gramme of dry sediment. In many samples below 830 m in the measured stratigraphical section, small chorate cysts dominate the palynofloras. These were counted to 100 specimens thereby allowing their overall proportion in the assemblage to be calculated. One hundred well-preserved specimens of the small chorate cysts were measured from sample D5.930.1 (slide D5.930.1A) where they were most abundant (407 m from the base of section D5.251 and 340 m from the base of the López de Bertodano Formation; Bowman et al. 2012, Fig. 2). Despite extensive folding of the cyst bodies, the good preservation, the apparent homogeneity of sedimentology and sedimentation rate and their abundance in the samples compared to other obviously reworked palynomorphs led to the assumption that the small chorate cysts are autochthonous.

To illustrate the description of these cysts, transmitted light photomicrographs and scanning electron microscope images of selected well-preserved specimens are presented in Plates 1 to 3. Transmitted light images, and palynological analysis was undertaken on a Leica DM750P transmitted light microscope at the University of Leeds, United Kingdom. The scanning electron microscope images were taken on a FEI Nova 200 NanoLab high resolution Field Emission Gun Scanning Electron Microscope with precise Focused Ion Beam housed in the Faculty of Engineering of the same institution. The organic residue was evaporated directly onto aluminium stubs with no pre-treatment and was coated with platinum to 10 Nm. Fluorescence microscopy on slide D5.930.1A was undertaken at the British Geological Survey, Keyworth, United Kingdom, using a Zeiss Universal microscope fitted with a Zeiss ultraviolet epifluorescence attachment, which is powered by an Osram HBO® mercury short-wave arc lamp.

4. Results

Eighty-one samples from the López de Bertodano Formation of Seymour Island were analysed by Bowman et al. (2012) and all contain well-preserved marine and terrestrial palynomorphs. The marine component comprises acritarchs (e.g. *Nummus* Morgan 1975 spp.), dinoflagellate cysts (notably *Manumiella* Bujak & Davies 1983 spp. below the K-Pg transition) and other marine algae (such as *Palamblages* Wetzel 1961 spp. and *Tasmanites* Newton 1875 spp.). However, the most consistently abundant are small chorate cysts, identified herein as dinoflagellate cysts. The sedimentological homogeneity of this succession strongly suggests that palynomorph abundance reflects palaeoecological phenomena rather than facies changes. These small chorate dinoflagellate cysts vary dramatically between 2% and 99% of the marine palynomorph assemblage throughout the López de Bertodano Formation on Seymour Island.

5. Systematic palaeontology

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993
Subdivision DINOKARYOTA Fensome et al. 1993
Class DINOPHYCEAE Pascher 1914
Subclass PERIDINIPHYCIDAE Fensome et al. 1993
Order GONYAULACALES Taylor 1980
Family Uncertain

Genus: *Impletosphaeridium* Morgenroth 1966 emended Islam 1993
Type: *Impletosphaeridium transfodum* Morgenroth 1966

Remarks: *Impletosphaeridium* was established by Morgenroth (1966, p. 32) to encompass spherical to occasionally ellipsoidal chorate dinoflagellate cysts with smooth or slightly granular cyst bodies bearing solid processes. The process terminations are acuminate, capitate, conical or furcate, but no mention was made of the archaeopyle type or size by Morgenroth (1966). Stover and Evitt (1978, p. 232) stated that the archaeopyle type is uncertain. Masure (2004, p. 337-349) differentiated species assigned to "*Impletosphaeridium*" on the basis of the presence or absence of an apical archaeopyle and the nature of the processes. Specimens of *Impletosphaeridium* can be readily differentiated from similar genera, for example, solid processes in *Impletosphaeridium* differentiate it from the acritarch *Baltisphaeridium* Eisenack 1958, which has hollow processes. Similarly, the superficially similar dinoflagellate cyst *Cordosphaeridium* Eisenack 1963 is characterised by striate processes. However, there are certain issues pertaining to the differentiation of *Impletosphaeridium* from the chorate dinoflagellate cyst *Cleistosphaeridium* Davey et al. 1966 and the acanthomorph acritarch genus *Micrhystridium.*

A re-study of the type species of *Cleistosphaeridium*, *Cleistosphaeridium diversispinosum* Davey et al. 1966, by Islam (1993) revealed process complexes on the holotype. This made the genus superfluous and Islam (1993) transferred *Cleistosphaeridium diversispinosum* to *Systematophora* Klement 1960. Consequently, Islam (1993) transferred many former species of *Cleistosphaeridium* to *Impletosphaeridium*, emending the diagnosis of *Impletosphaeridium* to include an apical archaeopyle [type tA or (tA)] as evident in the illustration of the paratype of *Impletosphaeridium transfodum* Morgenroth 1966 (see Morgenroth, 1966, pl. 10, fig. 4). The emendation of Islam (1993) also included a weakly granulate or psilate, single or double-walled cyst body with nontabular processes with simple to complex distal terminations. Eaton et al. (2001) preferred to retain *Cleistosphaeridium*, although recognising that the differentiation of *Cleistosphaeridium* from *Impletosphaeridium* is highly problematical. Eaton et al. (2001) considered the types of these two genera might be conspecific, with that of the former type being the junior synonym. Masure (2004) agreed that the holotype of *Impletosphaeridium transfodum,* the type of *Impletosphaeridium,* might be referable to *Cleistosphaeridium.* However, the type material of *Impletosphaeridium transfodum* is lost and, with the images of Morgenroth (1966, pl. 10, figs. 4, 5) being unclear, doubt remains as to whether the holotype and paratype are conspecific. Therefore, Eaton et al. (2001) suggested that the use of the name *Impletosphaeridium* should only be used for material comparable to *Impletosphaeridium transfodum*, and that other species of *Impletosphaeridium* are questionable.

The findings of Eaton et al. (2001), and the lack of clarity regarding the archaeopyle type of *Impletosphaeridium*, does not allow the distinction of these cysts from the acritarch *Micrhystridium*. The original diagnosis of *Micrhystridium* is rather broad and includes all globular/spherical palynomorphs below 20 µm in diameter with various ornamentation and processes (Deflandre 1937). Subsequent emendations refined this generic concept, culminating in Sarjeant and Stancliffe (1994), to comprise approximately spherical, typically single-walled chorate cysts generally below 20 µm in diameter with a psilate to granulate wall and a slit or cryptosuture. Nine to 35 hollow or solid spines are present, which may be proximally flared and normally have simple distal terminations. Rarely the processes may be distally clavate or bifurcate (Sarjeant and Stancliffe 1994).

A comparison of the most recent generic diagnoses of *Impletosphaeridium* and *Micrhystridium* indicates that they are distinguishable only by an apical archaeopyle in the former and a slit or irregular opening (epitypche) in the latter. Cyst body size or number of spines is included in the diagnosis of *Impletosphaeridium*. Wrenn and Hart (1988) noted that archaeopyles were either not developed or indeterminate in their *Impletosphaeridium* spp. from the Cross Valley and La Meseta formations on Seymour Island. Warny and Askin (2011a,b) also noted the inconsistent occurrence of an archaeopyle in the small chorate cysts they observed in the SHALDRIL cores in the Weddell Sea, east of the Antarctic Peninsula. Where an archaeopyle is not evident in these small chorate cysts, identification is based on spine terminations. These are usually distally pointed and smooth in *Micrhystridium* (see Sarjeant and Stancliffe 1994). Clearly, the taxonomic confusion between *Impletosphaeridium* and *Micrhystridium* in the southern high latitudes is entirely understandable.

We suggest that cysts with a definite or probable archaeopyle (see *Impletosphaeridium clavus* below) and mainly complex distal process terminations be assigned to the dinoflagellate cyst *Impletosphaeridium.* Where an archaeopyle is not evident, but the cyst still possesses mainly complex distal process terminations, this material should be questionably assigned to *Impletosphaeridium*. If no archaeopyle is evident and the distal process terminations are mainly simple, these specimens should be referred to the acritarch *Micrhystridium.* Assignment to species level then relies on further morphological details, including the cyst and process surface texture, the density of processes and the detailed distal and proximal morphology of the processes.

Impletosphaeridium clavus Wrenn & Hart 1988 emend. nov.

Plate 1, figures. 1-10; Plate 2, figures 1, 4, 6; Plate 3, figures 1-6, 8

Synonymy:

Impletosphaeridium clavus Wrenn & Hart 1988. Wrenn and Hart (1988, p. 356, figs. 27.10, 27.11, 27.13) (latest Early Eocene, Seymour Island, Antarctic Peninsula)

Micrhystridium spp. Pirrie et al. (1991, fig. 7g) (Late Campanian to Late Maastrichtian, Vega Island, Antarctic Peninsula)

Impletosphaeridium clavus Wrenn & Hart 1988. Cocozza and Clarke (1992, fig. 4f) (?reworked Eocene, Seymour Island, Antarctic Peninsula)

Impletosphaeridium lorum Wrenn & Hart 1988. Cocozza and Clarke (1992, fig. 4g) (?reworked Eocene, Seymour Island, Antarctic Peninsula)

Micrhystridium sp. Dolding (1992, fig. 6l) (Late Campanian, Humps Island)

Micrhystridium sp. A Smith (1992, fig. 11a) (Late Campanian – Late Maastrichtian, Vega Island, Antarctic Peninsula)

Micrhystridium piliferum Smith (1992, fig. 11b) (Late Campanian – Late Maastrichtian, Vega Island, Antarctic Peninsula)

Impletosphaeridium clavus Wrenn & Hart 1988. Levy and Harwood (2000, pl. 7, figs. a, b) (Mid and Late Eocene glacial erratics, McMurdo Sound, Ross Sea, Antarctica)

Impletosphaeridium spp. Warny et al. (2007, figs. 2a-d) (reworked Eocene – Miocene, Weddell Sea, Antarctica)

Impletosphaeridium sp. Salzmann et al. (2011, fig. 4d) (Neogene, James Ross Island, Antarctic Peninsula)

Micrhystridium spp. Warny and Askin (2011a, figs. 2.4 - 2.6) (Mid Miocene and ?reworked Cretaceous, SHALDRIL core NBP0602A-5D, Weddell Sea, Antarctica)

Micrhystridium sp. Warny and Askin (2011b, fig. 4.9) (Late Pleistocene to Holocene, SHALDRIL core NBP0602A-3C, Weddell Sea, Antarctica)

Impletosphaeridium? sp. Warny and Askin (2011b, fig. 4.10 (Late Pleistocene to Holcene, SHALDRIL core NBP0602A-3C, Weddell Sea, Antarctica)

Impletosphaeridium clavus Wrenn & Hart 1988. Bowman et al. (2012, pl. 1, fig. 5) (Maastrichtian to earliest Danian) (Seymour Island, Antarctic Peninsula)

Original diagnosis of Wrenn and Hart (1988, p. 356): "A species of *Impletosphaeridium* characterized by its thin solid, nail-like processes. The processes taper slightly to pad-like terminations that may appear to be bifid, trifid, or multifurcate."

Emended diagnosis: A species of *Impletosphaeridium* with a rounded to ellipsoidal outline. Autophragm is externally microbaculate to microgranulate, and bears numerous solid, flexuous, nontabular processes. Process distal terminations are typically bifurcate or acuminate (commonly recurved); some may be capitate, trifurcate or multifurcate. Process bases are simple and contiguous with the autophragm. Archaeopyle apical, type (4A), operculum free or rarely adherent.

Emended description: Small skolochorate dinoflagellate cysts with a rounded, sub-rounded to ellipsoidal cyst body in outline. The autophragm is thin, with an external surface texture, which appears smooth under transmitted light but is microbaculate to microgranulate using scanning electron microscopy. Randomly-distributed dark granules, between less than 0.5 μm and 2 μm in diameter, adhere to the cyst body of most specimens. The density of these granules is variable. Up to around 100 solid, nontabular, randomly distributed processes are present on the cyst body. The processes are flexuous to straight, thin (0.5 μm at the base) and taper slightly distally. The process bases are simple and contiguous with the cyst body surface. The distal process terminations are dominantly bifurcate or acuminate, the latter commonly recurved. Many of the recurved processes have acuminate distal terminations which are angulate at close to 90°, i.e. are recurved in an angular sense; others are more smoothly curved. Some apparently angulate recurved terminations bear a minor accessory pinnule making them asymmetrically bifurcate. Some distal terminations may be capitate (slightly bulbous), trifurcate or multifurcate. A single specimen can exhibit various distal termination morphologies, all of which are resolvable using a transmitted light microscope. There is no indication of tabulation other than the apical, type (4A), archaeopyle. An angular principal archaeopyle suture is rarely observed; it is commonly irregular, but is consistently in an apical position; the operculum is free or rarely adherent. The cingulum and sulcus are not evident. Specimens of *Impletosphaeridium clavus* do not autofluoresce (i.e. emit induced light) under ultraviolet epifluorescence illumination.

Dimensions: All 63 measured specimens identified as *Impletosphaeridium clavus* are on slide A from sample D5.930.1, which is from the Maastrichtian of the López de Bertodano Formation (Bowman et al. 2012). Length of central body: 15 (22) 32 µm [minimum (mean) maximum]; breadth of central body: 12 (18) 28 µm; maximum process length: 5 (8) 14 µm. The process length was measured from the base to the furcation junction, and is approximate due to their frequently sinuous nature. The longest processes observed on each specimen were measured.

Remarks: Wrenn and Hart (1988) recorded four species of *Impletosphaeridium* from the Cross Valley and La Meseta formations on Seymour Island; these are *Impletosphaeridium clavus*, *Impletosphaeridium ligospinosum* (de Coninck 1969) Islam 1993, *Impletosphaeridium lorum* Wrenn & Hart 1988 and *Impletosphaeridium* sp. B. Separation of these taxa is based primarily on process morphology including the shape of the process bases, the flexibility of the process shafts and the nature of the process terminations. Wrenn and Hart (1988) stated that the archaeopyle is indeterminate or not developed. Despite the indeterminate nature of the archaeopyle in the original description, we consider that the small chorate cysts described in this paper from the López de Bertodano Formation are assignable to *Impletosphaeridium clavus.* This determination is on the basis of the frequent distally furcate solid processes, the finely granular autophragm and the size.

We consider that *Impletosphaeridium clavus* requires emendation in order to clarify certain features noted using scanning electron microscopy. These fine scale morphological features do not preclude its identification using transmitted light microscopy. The process terminations are largely furcate to acuminate (commonly recurved) on the same specimen (Plate 1, figures 4, 14; Plate 2, figures 3, 5; Plate 3, figures 5, 10). Many of the processes exhibit acuminate distal terminations which are angulate close to 90°; this means that they are recurved in an angular fashion (Plate 1, figures 3, 9, 16; Plate 2, figures 1, 3; Plate 3, figures 3, 5, 10). Other distal terminations are smoothly curved with acuminate terminations (Plate 3, figures 2, 3). Some bifurcate processes have strongly asymmetrical pinnules, superficially appearing to be distally angulate, but possessing one much smaller pinnule (Plate 3, figures 2, 3, 5). Some processes appear to be slightly capitate ("pad-like" of Wrenn and Hart 1988) under transmitted light (Plate 1, figures 4, 15; Plate 3, figures 5, 7). The complexity of rare multifurcate processes becomes evident when using the scanning electron microscope (Plate 3, figures 11, 12), although they are resolvable using transmitted light microscopy (Plate 1, figure 6). The species appears to be acavate; the microbaculate to microgranulate autophragm of the cyst body extends onto the processes, although this ornamentation is finer on the spines (Plate 2, figure 2; Plate 3, figures 11, 12). Moreover, a cross-section of the cyst wall at the principal archaeopyle suture indicates an autophragm only (Plate 2, figure 4). On the basis of these observations, it seems likely that *Impletosphaeridium clavus* may be synonymous with *Impletosphaeridium ligospinosum*; this would require a restudy of the type material of the latter.

Of the 100 specimens of *Impletosphaeridium* measured herein, 25 had definite apical archaeopyles with either angular or irregular principle archaeopyle sutures (Plate 1, figures 3, 4, 9, 10; Plate 2, figure 4). The former (Plate 1, figure 3) indicate dehiscence between the apical and precingular plates, however this is frequently difficult to comprehensively observe in a single specimen due to the small size and the susceptibility of these thin-walled cysts to folding. The somewhat irregular principal archaeopyle sutures (Plate 1, figures 4, 9, 10) may appear similar to acritarch epityches, but this again is perhaps a result of the thin autophragm causing folding of the autophragm at the cyst apex. A further 38 specimens probably have an archaeopyle, but they are unclear and the margin commonly appears as a flat, truncated edge of the cyst body in dorso-ventral compression (Plate 1, figures 5, 8; Plate 2, figure 1). Both these cyst types can be assigned to *Impletosphaeridium clavus*. The remaining 37 specimens showed no indication of an archaeopyle, but are otherwise identical to *Impletosphaeridium clavus*. We consider, due to the large number of specimens observed and their otherwise identical morphology, that they are cysts of the same species that had not yet excysted (Plate 1, figures 11, 14; Plate 2, figures 2, 3).

Impletosphaeridium clavus is abundant in the López de Bertodano Formation and was recorded as common by Wrenn and Hart (1988) throughout the overlying Cross Valley and La Meseta formations of the Seymour Island Group. On the basis of the generic emendation above, concluding that only specimens with definite or probable apical archaeopyles should be unequivocally assigned to *Impletosphaeridium,* we suggest that the material of Wrenn and Hart (1988) should be questionably referred to this genus until further study of the type material can be made. The material of Thorn et al. (2009, as *Micrhystridium* spp.) and Bowman et al. (2012, pl. 1, fig. 5) from the López de Bertodano Formation of Seymour Island is now confidently assigned to *Impletosphaeridium clavus*. Similarly, Askin (1988, fig. 8.5; 1999, fig. 3.2) referred to "swarms of acanthomorph acritarchs" and "abundant *Micrhystridium* spp." respectively from the López de Bertodano Formation. Pirrie et al. (1997a) also recorded "extremely abundant" *Micrhystridium* spp. from the lower part of the López de Bertodano Formation on Seymour Island. Study of the material of Askin (1988; 1999) and Pirrie et al. (1997a) was beyond the scope of this study, however, we confidently assume that the acritarchs referred to by these authors are *Impletosphaeridium clavus* because they are from the López de Bertodano Formation of Seymour Island.

A feature of *Impletosphaeridium clavus* from the López de Bertodano Formation of Seymour Island is the colour. In transmitted light, the cyst bodies of well-preserved specimens vary from almost transparent to having a dark golden brown colour; an indication of the range can be seen in greyscale throughout Plate 1. This variation in colour may reflect differential absorption of amorphous organic matter (the "humic staining" of Sarjeant and Stancliffe 1994), sporadic pigmentation possibly related to heterotrophy (Rochon et al. 1999; Brenner and Biebow, 2001) or different levels of thermal maturity suggestive of reworking. Due to the predominance and well-preserved nature of the small chorate cysts in many López de Bertodano Formation samples, we consider this colour variation is most likely attributable to humic staining implying the assemblage is autochthonous. In addition, during their study of the Cross Valley Formation and La Meseta Formation palynofloras on Seymour Island, Wrenn and Hart (1988) reported finding no evidence of reworking into the Upper Cretaceous and Paleocene in this basin. Higher in the regional stratigraphical succession, dinoflagellate cyst colour may still help to differentiate reworked Maastrichtian from much younger Neogene and Quaternary material (Warny and Askin 2011a, fig. 2.6; 2011b).

Comparison with other species: The earliest illustrated record of cysts assignable to *Impletosphaeridium clavus* in Antarctic sediments is that of Dolding (1992, Fig. 6l, as *Micrhystridium* spp.) from the Late Campanian Herbert Sound Member (Santa Marta Formation) of Humps Island. On Seymour Island, the similarity of *Impletosphaeridium lorum* to *Micrhystridium* sp. A of Wrenn and Hart (1988) from the Eocene La Meseta Formation was acknowledged by Wrenn and Hart (1988) who differentiated these forms by the more numerous, denser and shorter processes in the latter. *Impletosphaeridium clavus* differs primarily from *Impletosphaeridium lorum* in having furcate process terminations, in contrast to the entirely acuminate terminations of the latter. Furthermore, *Impletosphaeridium lorum* has 50-100 processes, whereas the diagnosis of *Micrhystridium* restricts this genus to forms with 9-35 processes (Sarjeant and Stancliffe 1994), suggesting that *Micrhystridium* sp. A of Wrenn and Hart (1988) requires further analysis. *Impletosphaeridium clavus* differs from *Impletosphaeridium* sp. B of Wrenn and Hart (1988) in being single-layered, having a microbaculate or microgranulate cyst body and simple, solid process bases.

Cocozza and Clarke (1992) recorded low abundances (0-5% of the marine assemblage) of both *Impletosphaeridium clavus* and *Impletosphaeridium lorum* from the Eocene La Meseta Formation of Seymour Island. Two similar specimens were illustrated, neither of which has a definite archaeopyle. They appear to be assignable to *Impletosphaeridium clavus* emend. nov. (see Cocozza and Clarke 1992, figs. 4f, g).

Warny et al. (2007, figs. 2a-d) illustrated reworked specimens of *Impletosphaeridium* spp. that occur unusually abundantly in piston cores from offshore Seymour Island, which are of Eocene to Miocene age. The images are mostly out of focus, but one specimen shows a probable archaeopyle (Warny et al. 2007, fig. 2a). These specimens are all comparable with the material described herein from the López de Bertodano Formation but without clearer illustration they can only be assigned to *Impletosphaeridium* sp. or ?*Impletosphaeridium* sp. However, Warny et al. (2007) suggested that the most common species observed was *Impletosphaeridium lorum* despite conceding that species of *Impletosphaeridium* are difficult to differentiate consistently. It is likely that *Impletosphaeridium lorum* represents an uncertain assignment by Warny et al. (2007). These authors noted the presence of closely related, undescribed species of very similar overall morphology and size, differing only in process thickness.

Stratigraphical range: Late Campanian to Holocene.

6. Discussion

Small chorate cysts comparable to *Impletosphaeridium clavus*, assigned either to *Impletosphaeridium* or *Micrhystridium*, are not restricted to Seymour Island but have been recorded from many localities around Antarctica (Figure 1, Table 1). *Micrhystridium* spp. was recorded in low abundances in the ?Valanginian and Hauterivian of ODP cores from offshore Dronning Maud Land (Mohr 1990) and from the Cenomanian to Coniacian (?to Early Santonian) of the Kerguelen Plateau (Mohr and Gee 1992). These were not illustrated so the taxonomic assignment of these records needs to be verified.

In the Antarctic Peninsula region, *Micrhystridium* spp. have been recorded from the Middle Albian to Campanian of James Ross Island (Keating 1992; Keating et al. 1992). Small chorate cysts identified as acanthomorph acritarchs from Cockburn Island (Askin et al. 1991) and common *Micrhystridium* spp. from Humps Island (Wood and Askin 1992) have been recorded from strata considered to be Late Campanian to Early Maastrichtian in age based on the presence of the ammonite genus *Gunnarites* (J.A. Crame, unpublished data). Dolding (1992) quantified the first common occurrence of these morphotypes as an acme of *Micrhystridium* spp., comprising up to 26% of the total palynomorphs in one sample, from the Upper Campanian Herbert Sound Member (Santa Marta Formation) of Humps Island. Records from the James Ross Basin indicate that these small chorate cysts increased dramatically in abundance during the Maastrichtian, reaching up to 99% of the marine palynomorph assemblage (Askin 1988; Pirrie et al. 1991, 1997a; Dolding 1992; Smith 1992; Thorn et al. 2009; Bowman et al. 2012; this study). For example, Pirrie et al. (1991, 1997a) recorded abundant forms tentatively referred to *Micrhystridium* throughout the Upper Campanian to Maastrichtian succession of Cape Lamb, Vega Island and the Spath Peninsula, Snow Hill Island. Smith (1992) recorded extremely abundant *Micrhystridium piliferum* (up to 91.2% of the assemblage) from the Cape Lamb Member (Snow Hill Island Formation) of Vega Island. We consider that all of these small chorate cysts from the Antarctic Peninsula are assignable to *Impletosphaeridium clavus*. Verification is required for those records that were not illustrated (e.g. Askin et al., 1991; Keating, 1992; Wood and Askin, 1992)

There are few data on the occurrence of these cysts around the Antarctic margin during the Paleocene, however they are recorded as rare in the Cross Valley Formation of Seymour Island (Wrenn and Hart 1988). Wrenn and Hart (1988) recorded *Impletosphaeridium clavus* in the overlying Eocene La Meseta Formation of Seymour Island, however, they discuss evidence for significant reworking of marine and terrestrial palynomorphs into Eocene sediments on Seymour Island. It is likely that the low abundances of *Impletosphaeridium clavus* and *Impletosphaeridium lorum* recorded by Cocozza and Clarke (1992) from the La Meseta Formation are also reworked. *Impletosphaeridium* spp. has also been noted from the Lower Eocene sediments of Cockburn Island (Askin et al. 1991). In the Ross Sea region, Levy and Harwood (2000) recorded rare specimens comparable to *Impletosphaeridium clavus* from modern glacial erratics composed of Eocene sediments. These authors noted a rare undescribed *Impletosphaeridium* with short, solid, bifurcate or trifurcate process terminations, a type that is apparently absent from Seymour Island. The rarity of all these forms suggests that they may be reworked.

Palynomorph assemblages in Upper Eocene to Holocene sediment cores to the east of the James Ross Basin in the Weddell Sea (the NBP0602A-3C SHALDRIL core) have also revealed abundant small chorate cysts. The majority occurring in the youngest sediments (as *Micrhystridium* spp.) are dark in colour, are associated with reworked Cretaceous dinoflagellate cysts (for example, *Isabelidinium cretaceum* and *Manumiella* spp.) and hence are interpreted as being reworked from Cretaceous sediments themselves (Warny and Askin 2011b). These authors distinguished dark coloured specimens of *Micrhystridium* from rare 'presumed in-place' translucent forms with capitate processes and occasional apical archaeopyles assigned to *Impletosphaeridium.* They also noted variation in process base and shaft morphology in *Micrhystridium,* and compared this material to the abundant *Micrhystridium* spp. of Askin (1988, 1999) in association with *Isabelidinium cretaceum* (Cookson 1956) Lentin & Williams 1977 and *Manumiella seymourensis* Askin 1999 on Seymour Island. We consider that all these abundant small chorate cysts from this core are referable to *Impletosphaeridium clavus* (probably including *Impletosphaeridium ligospinosum*). This suggests the youngest occurrence of cysts assignable to *Impletosphaeridium clavus* is from Upper Pleistocene to Holocene sediments recovered in the NBP0602A-3C SHALDRIL core from the Weddell Sea. The illustrations of *Micrhystridium* sp. and *Impletosphaeridium*? sp. by Warny and Askin (2011b, figs. 4.9, 4.10 respectively) appear indistinguishable using transmitted light microscopy, and are comparable to *Impletosphaeridium clavus* described herein. Similarly, small chorate cysts are dominant in the lower SHALDRIL cores NBP06602A-12A and NBP0602A-5D (Warny and Askin 2011a) and are also deemed referable to *Impletosphaeridium clavus*. Salzmann et al. (2011) also noted abundant *Impletosphaeridium* spp. in Neogene diamictites from James Ross Island, which could be a mixture of autochthonous cysts and marine palynomorphs reworked from the underlying Cretaceous. Further, from the Ross Sea region, Hannah et al. (2001) recorded *Impletosphaeridium clavus* and *Impletosphaeridium* sp. B of Wrenn and Hart (1988) from the Lower Oligocene in the CRP-3 core, but did not illustrate these morphotypes.

We have demonstrated that *Impletosphaeridium clavus* is ubiquitous, and frequently extremely abundant, in the Upper Cretaceous to Quaternary of the James Ross Basin and the Weddell Sea. Bijl et al. (2011) also recognised its extensive distribution by including it within the endemic "Transantarctic Flora", a suite of dinoflagellate cysts considered to be characteristic of Eocene Antarctic palynofloras. However, we consider that all Eocene records of small, chorate cysts comparable to *Impletosphaeridium clavus* from around the Antarctic region are likely to have been reworked, probably from the Campanian to Maastrichtian acmes, and should not therefore be included within the Transantarctic Flora.

Warny et al. (2007) selected several modern dinoflagellate cyst taxa as analogues for *Impletosphaeridium* spp. that are found in polar regions, although the affinity of these cysts is currently unknown. These are *Echinidinium karaense* Head et al. 2001, *Islandinium*? *cezare* (de Vernal et al. 1989) Head et al. 2001 and *Islandinium minutum* (Harland & Reid in Harland et al. 1980) Head et al. 2001. These species are produced by heterotrophic dinoflagellates within cold, polar/subpolar waters (Harland and Pudsey 1999; De Vernal et al. 2001; Head et al. 2001; Marret and Zonneveld 2003; De Vernal and Rochon 2011). They all have spherical, thin-walled cyst bodies (the largest ranges up to 45 μm in diameter) and are covered in processes with a variety of terminations. De Vernal and Rochon (2011) noted that only minute morphological differences separate these species, however, details of process and archeopyle structure in these taxa differ from *Impletosphaeridium* spp. (Kenneth N. Mertens, personal communication 2012). Warny et al. (2007) also suggested the cyst of *Pentapharsodinium dalei* Indelicato & Loeblich III as an analogue for *Impletosphaeridium* spp. This is a small, spherical, spiny cyst found in cold regions (e.g. Dale, 1983; Indelicato and Loeblich III 1986; Harland et al. 1998; Ribeiro et al. 2011; Candel et al. 2012). It belongs to the family Thoracosphaeraceae and is autotrophic (Gottschling et al. 2005; 2012). The specimen of *Pentapharsodinium dalei* figured by Harland et al. (1998, pl. 2, fig. 5) from the

Weddell Sea compares closely with *Impletosphaeridium clavus* in terms of size, number of processes (with both recurved acuminate and bifurcate process terminations) and exhibiting adherent organic granules on the cyst body. However Harland et al. (1998) expressed doubt about the taxonomic assignment. Other illustrations of cysts now assigned to *Pentapharsodinium dalei* in the literature have a similar gross morphology to *Impletosphaeridium clavus*, but differ especially in the details of process terminations and wall thickness (e.g. Rochon et al. 1999; Price and Pospelova 2011; Ribeiro et al. 2011). Furthermore, cyst pigmentation and the lack of autoflorescence in *Impletosphaeridium clavus* (compared with dull red/brown autofluorescence colours exhibited by the other dinoflagellates in the same slide) may imply that the parent dinoflagellate was heterotrophic (Brenner and Biebow, 2001). Therefore, there is no known direct analogue for *Impletosphaeridium clavus* currently, but clearly cysts of a similar gross morphology and size are found in cold, high latitude oceans today.

Several undescribed species of *Micrhystridium* spp., superficially similar in morphology to *Impletosphaeridium clavus*, have been recorded from Lower Oligocene to Pliocene sediments from the Ross Sea region (Hannah et al. 1998, 2000, 2001; Wrenn et al. 1998; M.J. Hannah, unpublished data). These cysts have relatively few solid and hollow processes, with mostly simple process terminations and flared bases, and have not yet been recorded from the lower palaeolatitude James Ross Basin. These morphotypes, correctly identified as *Micrhystridium* spp., may reflect an adaptation to colder conditions, perhaps along the margins of floating ice shelves.

Dolding (1992) and Smith (1992) interpreted acmes of *Micrhystridium* (now referred to *Impletosphaeridium clavus*) in Upper Campanian to Maastrichtian sediments of the James Ross Basin as representing shallow water, nearshore deposition in comparison with the work of Wall (1965) who studied Early Jurassic microplankton from England and Wales. Acmes of *Micrhystridium* in the low to mid palaeolatitudes apparently imply shallow water conditions (e.g. Downie et al. 1971; Firth 1987; Oloto 1992; Prauss 2006; Götz and Feist-Burkhardt 2012). Further work is required to clarify whether it is reasonable to apply this interpretation to the highly variable temperature and light regime of the southern high latitudes. This inner neritic interpretation is likely to be overly simplistic on a global scale, and there was probably a latitudinal pattern in palaeoecological preference for chorate cysts of this type.

7. Conclusions

Small chorate algal cysts have been recorded, but rarely illustrated, in Upper Cretaceous to Quaternary sediments from the southern polar palaeolatitudes. However, taxonomic confusion has hitherto limited investigation of their palaeoecological significance. A detailed taxonomic analysis of *Impletosphaeridium clavus* from Seymour Island, Antarctic Peninsula, has helped resolve these issues for this species. We now recognise that this cyst, previously termed *Impletosphaeridium* spp. or *Micrhystridium* spp., is present, often in high numbers, throughout the James Ross Basin and rarely in other localities around the Antarctic margin.

In the light of this taxonomic clarification, a reassessment has been made of the published occurrences of what is now recognised as *Impletosphaeridium clavus* in the south polar region. We have found that many authors have recorded this species in extremely high numbers (up to 99% of marine palynomorphs) during the Late Campanian to Maastrichtian interval. However, during the Eocene, their numbers were significantly reduced. The available evidence, including rare occurrences from glacial erratics from McMurdo Sound, suggests that all *Impletosphaeridium* spp. recorded from Eocene sediments around the Antarctic margin are probably reworked. We therefore suggest the removal of *Impletosphaeridium clavus* from the “Transantarctic Flora” of Bijl et al. (2011). Additional later acmes are present in the mid Miocene of the Joinville Plateau (Warny and Askin 2011a).

Building on the work of Warny et al. (2007), detailed comparison of *Impletosphaeridium clavus* with modern cysts produced no unequivocal direct analogue. However, it is clear that diverse cysts of similar gross morphology are known from cold high latitude oceans today.

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Captions for the display materials:

Figure 1. The locations around the Antarctic margin where small chorate cysts (*Impletosphaeridium* and *Micrhystridium*) have been recorded. Further details for each numbered location are listed in Table 1. Note that there may be several publications per locality. The outcrop of Aptian-Coniacian to Eocene sediments in the James Ross Basin is illustrated (refer to Fig. 2 for a lithostratigraphical

summary). D5.251 = the stratigraphical section throughout the oldest sediments cropping out on Seymour Island from which sample D5.930.1 was collected. Boxes indicate geographical regions enlarged elsewhere in the figure.

Figure 2. Upper Cretaceous to Neogene lithostratigraphy for the James Ross Basin, Antarctic Peninsula (not to scale). Based on biostratigraphical and lithostratigraphical information (Ineson et al. 1986; Pirrie et al. 1991, 1997a, 1997b; Keating 1992; Keating et al. 1992; Riding et al. 1992; Barnes and Riding 1994; Jonkers and Kelley, 1998; Riding and Crame 2002; Crame et al. 2004; Nývlt et al. 2011; Pirrie et al. 2011; and references therein). LDBF, López de Bertodano Formation.

Table 1. The occurrences of small chorate cysts (*Impletosphaeridium* and *Micrhystridium*) in the Late Cretaceous to Quaternary of the Antarctic margin. ODP = Ocean Drilling Program. The superscript location numbers refer to the starred localities in Figure 1.

Plate 1. Transmitted light images of specimens of *Impletosphaeridium clavus* from sample D5.930.1 (slide A). The images were taken using Differential Interference Contrast using an oil immersion objective. LF, MF and HF – low, mid and high focus respectively. England Finder coordinates are quoted for each specimen. All images are at the same scale; the scale bar in Figure 1 represents 10 µm. Note the distal terminations of the relatively densely-inserted slender, nontabular processes which may be acuminate, recurved, capitate, bifurcate, trifurcate or multifurcate. Many of these are recurved in an angular sense (close to 90°), and a single specimen can exhibit various distal termination morphologies. Several process terminations are enlarged in Plate 3.

Figures 1-10 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

Figures 1, 2. Note that the operculum of the apical archaeopyle is attached to the cyst body; M64-3. 1 - LF; 2 - HF.

Figure 3. A specimen with an apical archaeopyle having a clear angular principal archaeopyle suture (A); N62-2, MF.

Figure 4. Note the apical archaeopyle with an irregular suture (A); X61-1, LF.

Figures 5-7. A specimen with many furcate process terminations. The truncated edge in 5 (A?) strongly suggests an apical archaeopyle. Note the trifurcate process termination (arrowed) in 6; X62-0. 5 - MF; 6 - LF; 7 - HF.

Figure 8. The truncated edge (A?) suggests an apical archaeopyle; X62-2, HF.

Figure 9. Note the apical archaeopyle with an irregular suture (A); X66-0, HF.

Figure 10. Note the apical archaeopyle with an irregular suture (A); U63-3, MF.

Figures 11-16 - *Impletosphaeridium*? *clavus* Wrenn & Hart 1988 emend. nov.

Figures 11, 12. W65-1. 11 - MF; 12 - HF.

Figure 13. W60-1/2, LF.

Figure 14. R63-2, MF.

Figure 15. P64-4, HF.

Figure 16. N64-0, HF.

Plate 2. Scanning electron microscope images of specimens of *Impletosphaeridium clavus* from sample D5.930.1. These specimens illustrate further examples of process terminations recurved in an angular sense (close to 90°). The scale bars all represent 5 µm.

Figures 1, 4, 6 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

Figure 1. The flat truncated edge (A?) at the top of the cyst body suggests an apical archaeopyle suture.

Figure 4. The principal archaeopyle suture of the apical archaeopyle (A) indicates a single wall layer (autophragm).

Figure 6. A possible apical archaeopyle (A?).

Figures 2, 3, 5 - *Impletosphaeridium*? *clavus* Wrenn & Hart 1988 emend. nov.

Figure 2. The microbaculate surface ornamenatation on the central body extends as finer granules onto the surfaces of the processes.

Figure 3. A specimen with a mixture of acuminate recurved and furcate process terminations.

Figure 5. A specimen with a multifurcate process termination which is highlighted within a square; enlarged in Plate 3, figure 12.

Plate 3. High-magnification images of process terminations observed on specimens of *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov and *Impletosphaeridium*? *clavus* Wrenn & Hart 1988 emend. nov. Figures 1-10 - transmitted light images comprising enlargements of specimens illustrated in Plate 1 (slide D5.930.1A). The scale bars all represent 5 μm. Figures 11, 12 - Scanning electron microscope images of specimens observed in sample D5.930.1. The scale bars represent 0.5 μm.

Figures 1-6, 8 - *Impletosphaeridium clavus* Wrenn & Hart 1988 emend. nov.

Figure 1. Bifurcate process terminations on a free and adherent apical archaeopyle; M64-3, LF (entire specimen illustrated in Plate 1, Figure 1).

Figures 2, 3. 2 - recurved process terminations (close to 90°), one bifurcate with minor accessory pinnule (arrowed). 3 - acuminate, recurved and bifurcate process terminations. Examples of both smooth and angular recurved terminations can be seen, one bifurcate with minor accessory pinnule (arrowed). N62-2, MF (entire specimen illustrated in Plate 1, figure 3).

Figures 4, 5. 4 - acuminate and smoothly recurved process terminations. 5 - capitate (slightly bulbous termination), angular recurved and bifurcate (with minor accessory pinnule; arrowed) process terminations. X61-1, LF (entire specimen illustrated in Plate 1, figure 4).

Figures 6, 8. 6 - bifurcate process terminations. 8 - angular recurved and a trifurcate process termination (arrowed). X62-0, (entire specimen illustrated in Plate 1, figures 5-7).

Figures 7, 9-12 – *Impletosphaeridium*? *clavus* Wrenn & Hart 1988 emend. nov.

Figure 7. Note the capitate and angular recurved process terminations; P64-4, HF (entire specimen illustrated in Plate 1, figure 15).

Figure 9. Note the bifurcate process terminations; W60-1,2, LF (entire specimen illustrated in Plate 1, figure 13).

Figure 10. Bifurcate and angular recurved process terminations; R63-2, MF (entire specimen illustrated in Plate 1, figure 14).

Figures 11, 12. Process shafts show detail of microgranular surface texture. 11 - multifurcate process termination with minor accessory pinnule. 12 - complex multifurcate process termination (entire specimen illustrated in Plate 2, figure 5).