

Original Article

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# Dinoflagellate cysts of the La Meseta Formation (middle to late Eocene), Antarctic Peninsula: implications for biostratigraphy, palaeoceanography and palaeoenvironment

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## Abstract

Dinoflagellate cyst assemblages recovered from the La Meseta Formation cropping out in Seymour Island, Antarctic Peninsula, are studied herein and their distribution is compared with the biostratigraphic scheme available for the Palaeogene of the Southern Ocean and other high-latitude regions. In this way, the La Meseta Formation is dated as middle Lutetian to Priabonian (46.2–36 Ma), which differs from the age provided by other fossils, isotopes and also with the magnetostratigraphic scheme recently performed for the unit. The dinoflagellate cyst data support the proposal of ocean circulation patterns on the South American Shelf prior to the opening of Drake Passage. Assemblages from the La Meseta Formation contain Antarctic-endemic taxa which are also dominant in several circum-Antarctic sites, located south of 45° S. Their distribution reflects an ocean-circulation scheme with wide clockwise gyres surrounding Antarctica that were disrupted as a consequence of the deepening and definitive apertures of the Tasmanian Gateway and Drake Passage towards the Eocene/Oligocene transition. The palaeoenvironmental inference based on the S/D ratio (sporomorphs versus dinoflagellate cysts) and the P/G ratio (peridinioid versus gonyaulacoid dinoflagellate cysts) suggests an overall trend through the section from marine-dominated assemblages with poorly productive waters in the lower part of the section to more terrestrially dominated assemblages with increasing productivity in the upper part of the unit, reflecting a shallowing trend to the top.

## 1. Introduction

The La Meseta Formation (LMF) crops out in Seymour (Marambio) and Cockburn islands, both located at the northeastern tip of the Antarctic Peninsula. The LMF forms the upper part of Late Jurassic – Cenozoic sedimentation of the James Ross Basin and provides the best palaeontological record of marine and terrestrial Cenozoic biota in Antarctica. The fossils that have been found in the LMF include marine invertebrates such as echinoderms, bryozoans, corals, decapods, brachiopods and molluscs (e.g. Stillwell & Zinsmeister, 1992; Álvarez *et al.* 2014), vertebrates including fishes, reptiles, aquatic birds, whales and marsupials (e.g. Reguero *et al.* 2012 and references therein), plants (e.g. Gandolfo *et al.* 1998; Pujana *et al.* 2014), microfossils such as foraminifera and ostracods (Gaździcki & Majewski, 2012), and palynomorphs mainly comprising dinoflagellate cysts, pollen and spores (e.g. Wrenn & Hart, 1988; Cocozza & Clarke, 1992; Askin, 1997; Douglas *et al.* 2014).

The fossil record of the LMF is extremely diverse and abundant, and fossils exhibit an excellent to exceptional preservation. Due to these peculiar characteristics, the LMF is a focus of attention for several palaeontologists and geologists worldwide. This palaeontological wealth exposed in the LMF is crucial not only for studying the taxonomic and phylogenetic relationship among fossil groups, their radiation and the palaeobiogeographic links between Antarctic and Patagonian faunas, but also in reconstructing the Antarctic environments prior to the significant climate deterioration and the onset of glaciation of Antarctica at the beginning of the Oligocene (e.g. Tatur *et al.* 2011), which has been triggered with the Drake Passage opening and deepening (Livermore *et al.* 2005).

The LMF was assigned to a late early Eocene to late Eocene / ?Oligocene age once the first fossils, including palynology (Wrenn & Hart, 1988; Cocozza & Clarke, 1992; Askin, 1997), were

studied together with isotopic data from bivalve shells (e.g. Dutton *et al.* 2002; Ivany *et al.* 2008). However, a subsequent age model based on dinoflagellate cyst biostratigraphy and strontium isotopes proposed for the LMF (Douglas *et al.* 2014) suggested a mid- to late Eocene age (45 to 34 Ma, middle-Lutetian – Priabonian). In spite of this, many researchers still support the older age, and indeed a magnetostratigraphic scheme recently performed in the LMF proposes ~58.4 Ma (upper Thanetian) to ~45.8 Ma (lower Lutetian) (Montes *et al.* 2019a).

It is evident that the mid- to late Eocene age for the LMF is not entirely accepted and there are still debates about whether is early, middle or late Eocene. Elucidating and confirming the correct chronology of the LMF has crucial implications, as the LMF has a rich palaeontological record of vertebrates, including the first Antarctic mammals (Woodburne & Zinsmeister, 1982; Gelfo *et al.* 2015), invertebrates and flowering plants (Gandolfo *et al.* 1998) and also constitutes a significant archive of palaeoclimate data. Given the importance of the Eocene strata on Seymour Island for palaeoclimatic reconstructions, a re-examination of its chronostratigraphy is warranted. It is especially important to confirm the age of the LMF in order to make comparisons with other Eocene assemblages of the Southern Ocean and to understand the events that occurred around the Drake Passage and the consequences that brought about its opening.

Thus, the aim of this contribution is to document the dinoflagellate cyst assemblages recovered throughout the LMF and discuss the stratigraphical distribution of the species in order to complement and firm up the age proposed by Douglas *et al.* (2014) and thus contribute to an accurate chronology. This analysis also provides quantitative data on the dinoflagellate cyst assemblages of the LMF that will be available to seek a robust comparison with other localities of the Drake Passage area. In addition, palaeoceanographical implications and a palaeoenvironmental reconstruction for the LMF based on the dinoflagellate cyst assemblages are presented herein.

## 2. Geological setting, stratigraphy and age of the La Meseta Formation

### 2.a. Geology

Seymour (Marambio) Island is located in the Weddell Sea near the NE margin of the Antarctic Peninsula (64° 15' S, 56° 40' W) (Fig. 1a). It is located in the most external (SE) area of the Maastrichtian and Palaeogene outcrops in the James Ross Basin (Elliot, 1988).

The sedimentary sequences exposed in Seymour (Marambio) Island are more than 2000 m thick and represent the youngest part of the infill of the James Ross Basin. These sediments are part of the Marambio and Seymour Island Groups (Rinaldi, 1982 and Elliot & Trautman, 1982, respectively; Fig. 1b). In Seymour, the Marambio Group comprises the Haslum Crag Formation (Olivero *et al.* 2008), López de Bertodano Formation and Sobral Formation (Rinaldi *et al.* 1978), with ages spanning from the Maastrichtian to the Danian. The group consists of fine-grained sandstone and shales, highly fossiliferous, with subordinate conglomerates and fossiliferous bioclastic concentrations deposited in a middle-external to internal shelf that represent an extended prograding platform in the Weddell Sea for more than 100 km to the east (Olivero *et al.* 2008). The rest of the Palaeogene sediments of Seymour Island are represented by the Seymour Island Group (Elliot & Trautman, 1982), which comprises the Cross Valley –

Wiman Formation (Montes *et al.* 2008), the LMF (Rinaldi *et al.* 1978; Marensi *et al.* 1998) and the Submeseta Formation (Montes *et al.* 2013, 2019a, b). The sediments of this group (Palaeocene–Oligocene) represent the final stage of filling of the James Ross Basin and were deposited in incised valleys on an emergent marine platform (Marensi *et al.* 1998).

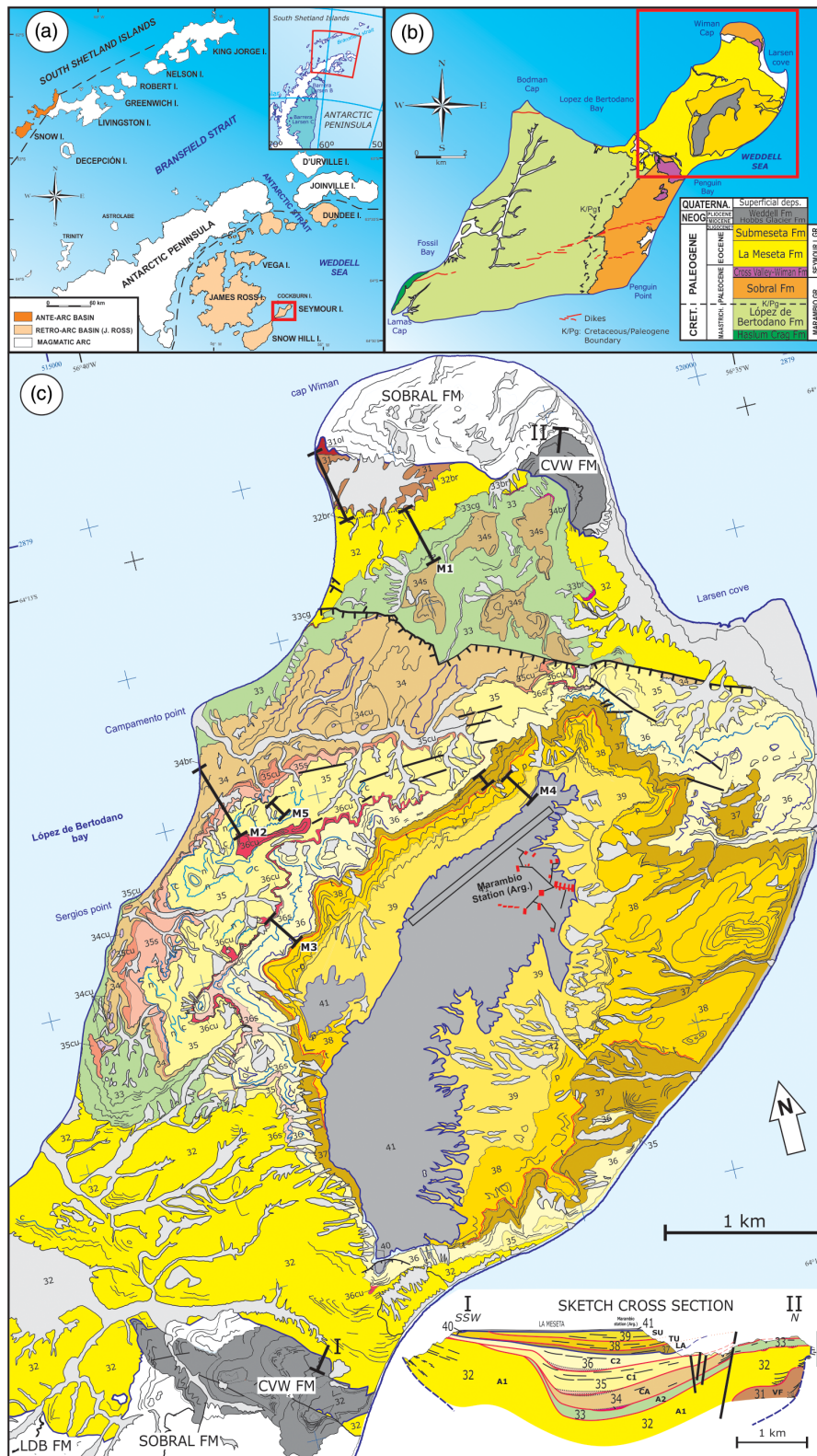
During deposition of the Marambio and Seymour Groups, the eastern edge of the James Ross Basin acted as a passive continental margin receiving sediments mainly from the magmatic arc located in the Antarctic Peninsula (Marensi *et al.* 2002). After a period of emersion and erosion between the Oligocene and the early Miocene, glaciomarine sediments of the Hobbs Glacier Formation were deposited overlying the LMF (Marensi *et al.* 2010).

Later, in the terminal Miocene (Zinsmeister & Webb, 1982), a complex of several eruptive phases of alkaline volcanic rocks of the James Ross Volcanic Group (JRVG) defines a post-subduction ensialic volcanism, with eruptions on the NE flanks of the magmatic arc and related to an extensional tectonic period in the area of the Antarctic Peninsula (Smellie *et al.* 1988). The youngest sediments of the James Ross Basin correspond to the Weddell Formation, interpreted as glacial deposits of latest Pliocene–Holocene age (Gaździcki *et al.* 2004).

### 2.b. Stratigraphy of the La Meseta Formation

The LMF (Elliot & Trautman, 1982) consists of poorly consolidated and bioturbated sandstones and siltstones, with tractive structures, alternating with rhythmical alternations of very fine sandstone-siltstone and mudstone with inclined heterolithic stratification and coquina. Its sediments contain very abundant and relatively well-preserved marine and continental vertebrate fauna, marine invertebrates and plant remains. The base of this formation is a diachronic surface that cut older stratigraphic units on the island. The lenticular geometry and the architecture of the internal units were interpreted as the filling of an incised valley, eroded on an emerging platform after the tilting of the Marambio Group and the Cross Valley – Wiman Formation strata (Marensi *et al.* 1998).

Based on the architecture of the lithosomes, the relationship between facies and sedimentary palaeoenvironments, the Eocene filling of Seymour Island has been divided into six allomembers (Marensi *et al.* 1998; Montes *et al.* 2013), namely: Valle de las Focas (Telm 1), Acantilados I and II (Telm 2 and Telm 3 in partim), Campamento (Telm 3 in partim and Telm 4), and *Cucullaea* I and II (Telm 5 and Telm 6 in partim). The uppermost Eocene / ? Oligocene sediments previously considered as the upper unit of the LMF, named the Submeseta Allomember (Marensi *et al.* 1998), are now considered a new formation, the Submeseta Formation (Montes *et al.* 2013). This was divided into three allomembers denominated Submeseta I or Laminado (Telm 6 in partim and Telm 7 in partim), Submeseta II or *Turritella* (Telm 7 in partim) and Submeseta III or Superior (upper Telm 7). The correlation between these allomembers and the informal lithofacies, named as Telm 1 and 7 and defined by Sadler (1988), are shown in Marensi *et al.* (1998, fig. 4, p. 140). The Submeseta Formation consists of c. 162 m of muddy shales; fine sandstones with mollusc coquinas and sandstone packages with gravels. The top of the Submeseta Formation unconformably underlay the Plio-Quaternary glaciomarine deposits of the Weddell Formation, in most of its extension. However, in small outcrops located in the SW of Seymour Island, the unit unconformably underlies the Hobbs Glacier Formation (Marensi *et al.* 2010).



**Fig. 1.** (Colour online) (a) Location map of Seymour Island related to the Antarctic Peninsula. (b) Location of the La Meseta Formation, showing the study area at Marambio (Seymour) Island. The box shows the area mapping with more resolution in (c) The scheme of stratigraphic units follows that of Montes *et al.* (2013). (c) Location of stratigraphic columns in the Geological Map of the La Meseta and Submeseta formations of Seymour Island (modified from Montes *et al.* 2013). Numbers 32–41 correspond to cartographic units defined by Montes *et al.* (2013). The geometry of the units is shown in sketch cross-section (number and name units in Fig. 2). Abbreviations: LDB FM: Lopez de Bertodano Formation; CVW FM: Cross Valley - Wiman Formation. **ol** breccia and ostolites; **cr** sandstones with concretions; **cg** conglomerates and sandstones; **br** breccia and conglomerates; **v** veneroidea (bivalve) levels; **s** sandstones; **cu** canalized level with gravel and *Cucullaea* (bivalve) coquinas; **c** *Cucullaea* (bivalve) levels; **t** *Turritella* (gastropod) level.

## 2.c. The age of the La Meseta Formation

### 2.c.1. Previous palynological studies

The first palynological studies of the LMF were presented by Hall (1977) who reported the presence of pollen and spores and provided the first analysis of fossil dinoflagellate cysts, assigning a late Eocene – early Oligocene age to the unit. Later, Wrenn & Hart (1988) used the dinoflagellate cyst assemblages to subdivide the LMF into two units: interval A (upper lower Eocene) and interval B (middle–upper Eocene).

Cocozza & Clarke (1992) analysed the marine palynoflora (dinoflagellate cysts, acritarchs and Chlorophyta) obtained from the lower part of the LMF (Telm 1 – Telm 2 according to Uchman & Gaździcki, 2006, p. 155) and divided the section into three assemblages: Association 1 (late early Eocene), Association 2 and Association 3 (possible middle–late Eocene).

Askin (1997) subdivided the LMF into four provisional zones based on terrestrial and marine palynomorphs. The lower zone (including Valle de las Focas, Acantilados and basal Campamento allomembers) was dated as late early Eocene; the overlying zone (including the upper Campamento and the basal Submeseta allomembers) was assigned likely to the middle Eocene. The third zone (Submeseta Allomember) was proposed to be late Eocene in age while the upper zone, considered to be the top of the LMF (the uppermost 25 m of the formation), was dated as earliest Oligocene.

Recently, Douglas *et al.* (2014), in order to reconstruct the Eocene climatic variability in southern high latitudes, proposed a biostratigraphic age model for the LMF based on five dinoflagellate cyst samples (from Telm 2 – Telm 7) and concluded that the LMF was deposited during the middle to late Eocene (between 45 and 34 Ma), in contrast to previous early to late Eocene age assignments.

Exclusively terrestrial palynomorph (pollen and spores) studies of the LMF were also carried out (Askin & Elliot, 1982; Askin & Fleming, 1982; Askin 1997). However, they focused on recycled pollen and spores in the Cenozoic Seymour Island sediments; the taxonomy of some pollen genera and species; and the diversity and compositional change of terrestrially derived assemblages in relation to climatic conditions, without engaging in specifying age.

### 2.c.2. Other palaeontological and isotopic data

Initially, Zinsmeister & Camacho (1980) studied mollusc faunas and proposed a late Eocene – early Oligocene age for the LMF which was then sustained by Stilwell & Zinsmeister (1992) based on a biostratigraphic provisional zonation using marine gastropods. Considering that proposed age, Marensi (2006) related the basal erosion surface of the LMF to the sea-level lowstand established by Sadler (1988) in the late Ypresian (49 Ma).

On the other hand, Dutton *et al.* (2002) examined selected *Cucullaea* bivalve specimens for strontium isotope ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) analyses of Telms 2, 5 and 7 of the LMF and suggested that the deposition of the unit took place during the early–late Eocene. Ivany *et al.* (2008) analysed the  $^{87}\text{Sr}/^{86}\text{Sr}$  bivalve shell ratios of Telms 2–7 and indicated that the LMF spanned almost the entire Eocene, and suggested the presence of an early middle Eocene unconformity. However, Douglas *et al.* (2014) disagree with the age proposed by the above-mentioned authors, pointing out that the strontium-isotope data may be biased because of the presence of freshwater mixing or the incorporation of trace minerals into the shells. They also found that the uncertainty of the data is intensified

by the small degree of variation of the global seawater strontium-isotope curve for the early to middle Eocene of McArthur *et al.* (2001). Therefore, Douglas *et al.* (2014) applied the dinoflagellate cyst biostratigraphic framework proposed by Bijl *et al.* (2013a) for the early Palaeogene of the Southern Ocean, which is magnetostratigraphically calibrated to the 2012 geologic timescale, suggesting that the lower part of the LMF is no older than the base of the middle Eocene, contrary to previous assignments that consider that the formation also spanned the early Eocene.

A recent age model based on a combination of magnetostratigraphy, isotopic data ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) and lithostratigraphy was performed in the LMF by Montes *et al.* (2019a). According to this model, the age of the LMF ranges from the upper Thanetian (~58.4 Ma) to the lower Lutetian (~45.8 Ma).

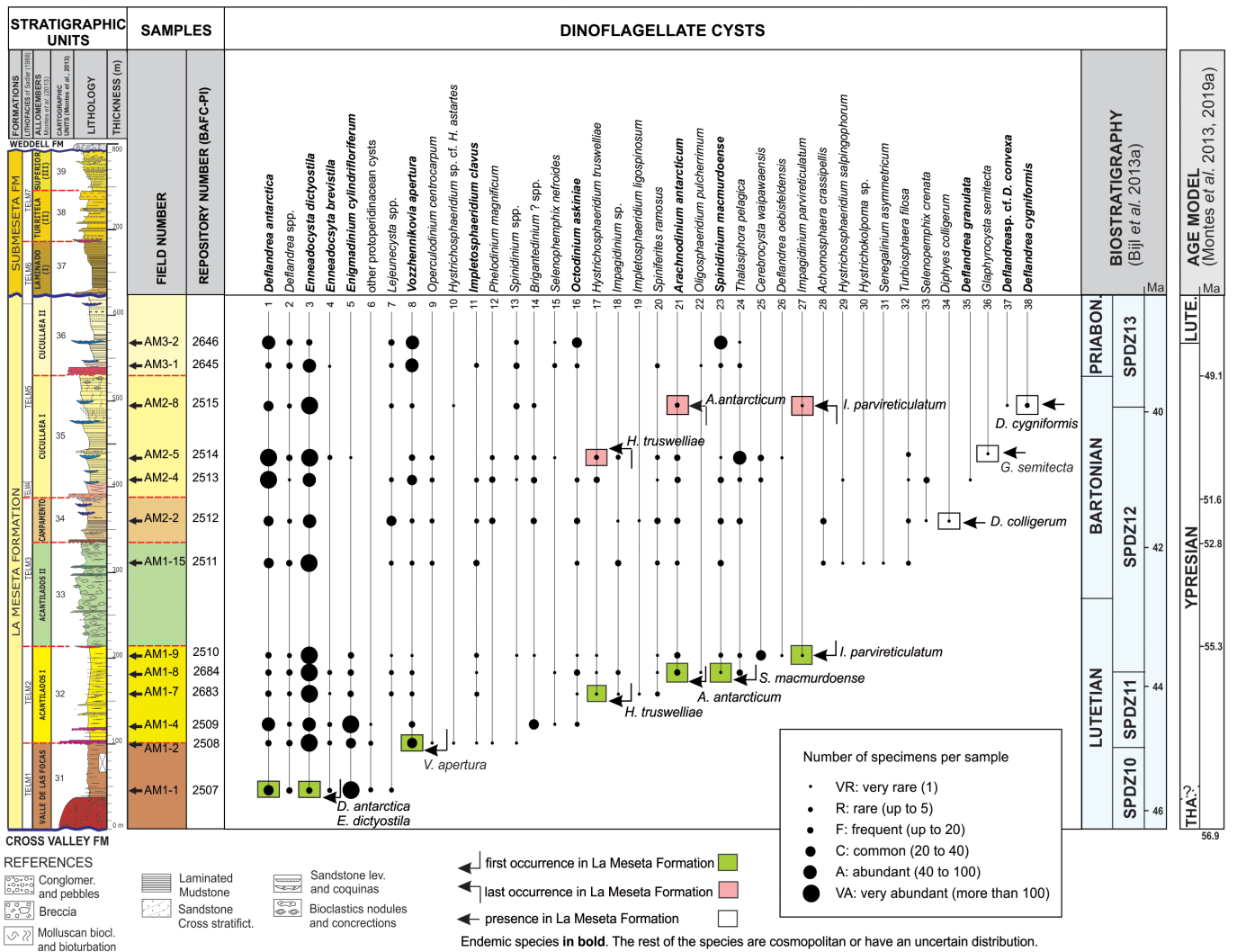
The vertebrate fossil records also allowed inferences to be made about the age of the LMF. The age of terrestrial fossil mammals, especially ungulates (i.e. astrapotheres and litopterns), recovered from the *Cucullaea* I and *Cucullaea* II allomembers, is based on the assumption that Patagonian and Antarctic faunas were similar because they shared some taxa (Gelfo *et al.* 2009; Tejedor *et al.* 2009; Reguero *et al.* 2013). Gelfo *et al.* (2009) and Tejedor *et al.* (2009) proposed that the Paso del Sapo fauna of west-central Patagonia, whose age, based on the  $^{40}\text{K}/^{40}\text{Ar}$  method (~49.5 Ma), is late early Eocene (Ypresian/Lutetian boundary), was putatively coeval and biogeographically related to the LMF fauna. However, Bond *et al.* (2011) pointed out that terrestrial mammals from the LMF closely resemble, but are not exactly similar to those of late early Eocene faunas from southern Patagonia. Besides, the finding of Antarctic whales (basilosaurids) in the *Cucullaea* I Allomember (Buono *et al.* 2016) indicates an early middle Eocene age for that part of the section, consistent with the stratigraphic record of basilosaurids worldwide.

## 3. Material and methods

The studied material consists of 13 productive samples collected from all the allomembers of the LMF (*sensu* Marensi *et al.* 1998): Valle de las focas, Acantilados I, Acantilados II, Campamento, *Cucullaea* I and *Cucullaea* II (Fig. 2). The upper allomembers (Laminado, *Turritella* and Superior) considered as the Submeseta Formation by Montes *et al.* 2013, 2019a, b) are excluded from this study. Stratigraphic sections were measured by some of the authors (S.S., M.M. and F.N.) as part of the new geological cartography of Seymour Island (Montes *et al.* 2013, 2019b).

Palynomorphs were extracted from rocks using palynological procedures that involved the removal of the organic matter from 10 g of dry sediment by digesting the carbonates with HCl (10 %) and silicates with HF (40 %) followed by several washings with water. The residue was sieved with 40 µm and 10 µm meshes and finally mounted on slides with glycerin jelly (Wood *et al.* 1996). Light microscopy observation was at 400× and 1000× magnifications using a Nikon Eclipse 80i, and images were taken with a Nikon Coolpix 950 digital camera, both pieces of equipment being available at the Laboratorio de Bioestratigrafía de Alta Resolución of the Universidad de Buenos Aires (FCEN-UBA), Argentina.

For each sample, it was possible to count a minimum of 300 specimens including dinoflagellate cysts, pollen, spores and other palynomorphs (see Appendix, and the online Supplementary Material available at <https://doi.org/10.1017/S0016756819000591>).



**Fig. 2.** (Colour online) Occurrence of dinoflagellate cyst species in the La Meseta Formation on Seymour Island, Antarctic Peninsula. On the left, stratigraphic columns of the La Meseta Formation with stratigraphic units (allomember and number in Fig. 1) and sample positions (modified from Montes *et al.* 2013, 2019a, b). On the right, two different age models are shown: one is the dinoflagellate cyst zonation of the early Palaeogene South Pacific Ocean by Bijl *et al.* (2013a), which is adopted here. The other is the alternative magnetostratigraphic model performed in the La Meseta Formation by Montes *et al.* 2013, 2019a). Note the age contradiction between the two age models, whose difference is ~11 Ma. Biogeographic distribution: endemic (E) in bold and cosmopolitan (C) according to Wrenn & Hart (1988), Bijl *et al.* (2013a) and Houben *et al.* (2013). The dinoflagellate cyst assemblages were semi-quantitatively characterized using the following scale: very rare: **VR** (1), rare: **R** (up to 5), frequent: **F** (up to 20), common: **C** (up to 40) and abundant: **A** (up to 100), very abundant: **VA** (more than 100) specimens per slide.

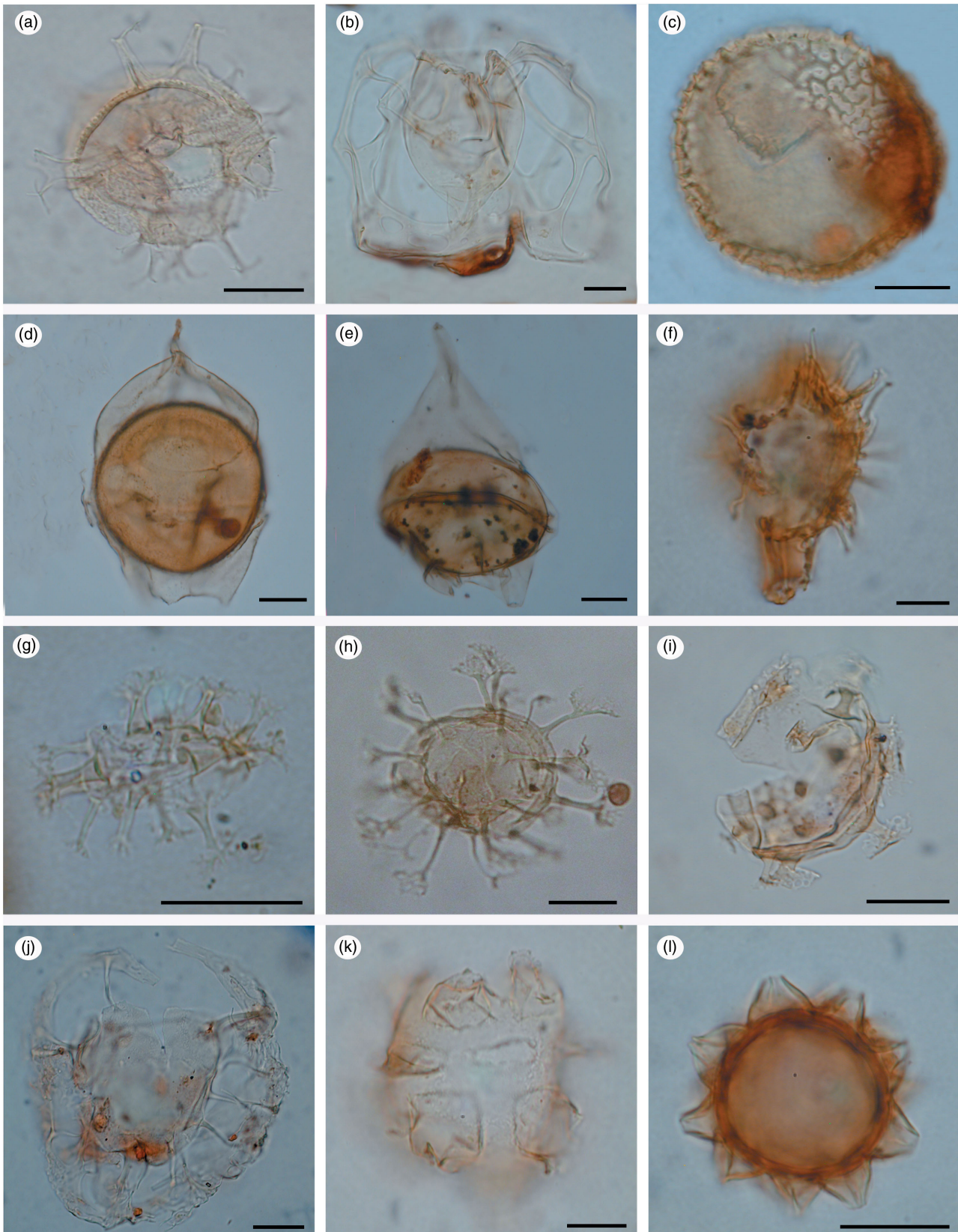
Selected specimens are illustrated in Figures 3 and 4. In this work, only marine palynomorphs (mainly dinoflagellate cysts) were identified in terms of species level and analysed with the aim of obtaining biostratigraphic information. Pollen and spore analysis will be presented in a future contribution. The taxonomic nomenclature of dinoflagellate cysts used in this study was based on the database DINOFLA3 of Williams *et al.* (2017).

The dinoflagellate cyst assemblages were semi-quantitatively characterized using the following scale: very rare (1), rare (up to 5), frequent (up to 20), common (20 to 40), abundant (40–100) and very abundant (more than 100) specimens per slide (Fig. 2). The absolute values can be seen in the online Supplementary Material at <https://doi.org/10.1017/S0016756819000591>.

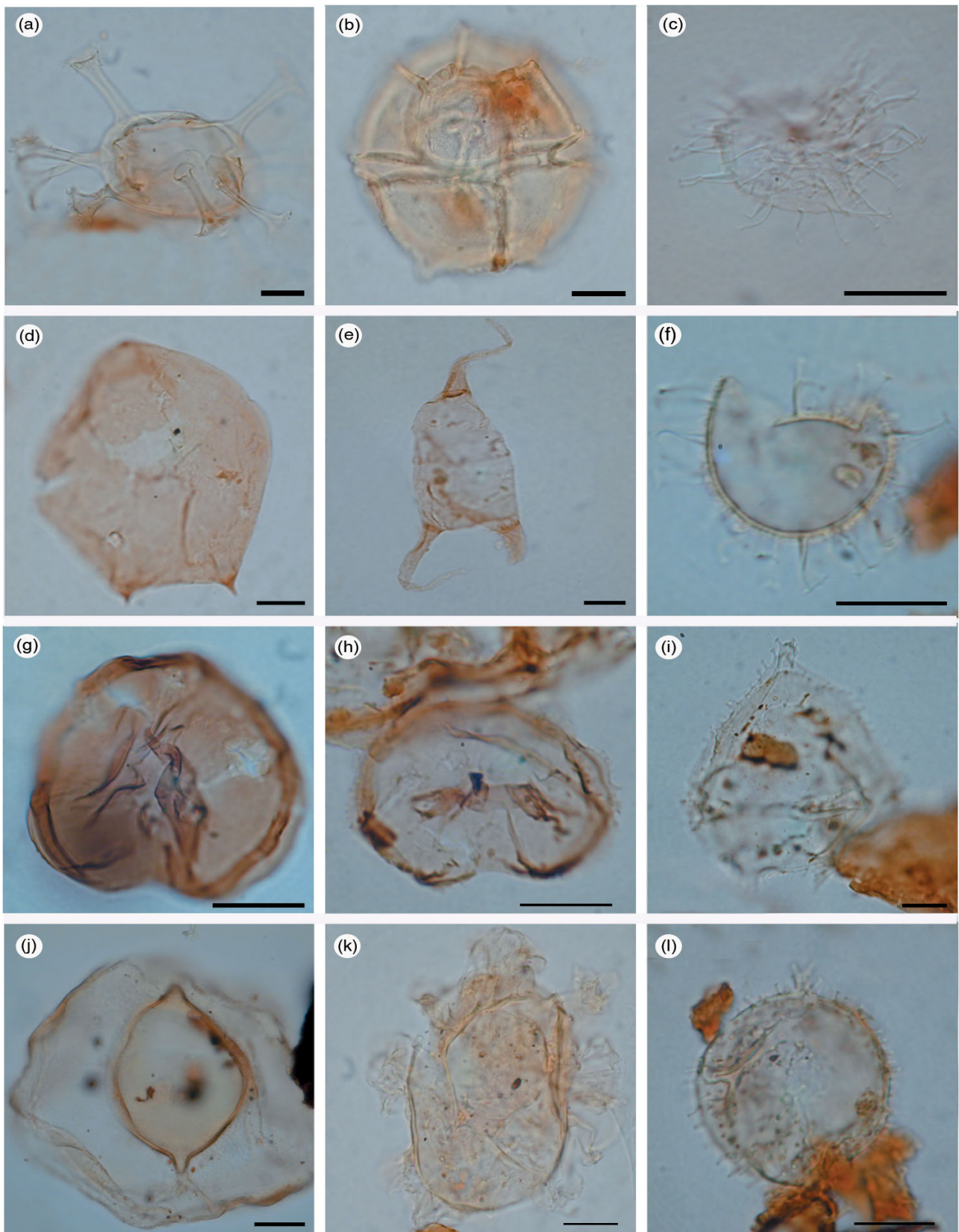
For palaeoenvironmental analyses, the following indexes proposed by Versteegh (1994) were considered: the P/G ratio,

peridinioid versus gonyaulacoid dinoflagellate cysts and the S/D ratio, sporomorphs versus dinoflagellate cyst (Fig. 5). The P/G cyst ratio characterizes the palaeoproductivity of surface water and is obtained by the equation  $P/G = nP/(nP + nG)$ , where n is the number of specimens counted, P are the peridinioid (or Proto-peridinioid) dinoflagellate cysts and G include the Gonyaulacoid dinoflagellate cysts. The S/D ratio is used as a measure for terrestrial influence relative to marine influence and is calculated as follows:  $S/D = nS/(nD + nS)$  where n is the number of counted specimens, S is represented by sporomorphs (pollen and spores) and D by dinoflagellate cyst and acritarchs.

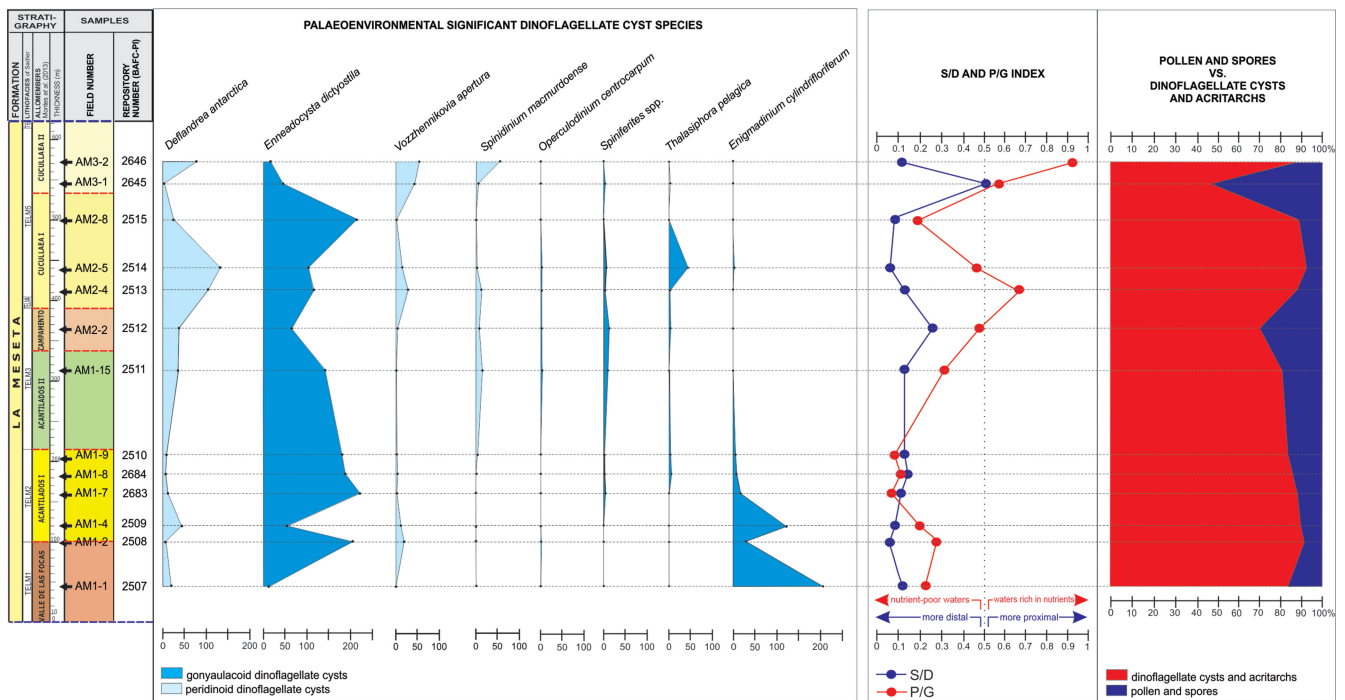
Palynological slides are stored in the Palynological Collection of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCEN-UBA), Argentina, under the acronym BAFC-PI and the slide numbers 2507–2515, 2645–2646 and 2683–2684.



**Fig. 3.** (Colour online) Dinoflagellate cysts recovered from the La Meseta Formation, Seymour Island, Antarctic Peninsula. (a) *Achomosphaera crassipellis*, sample AM1-15 (BAFC-PI 2511: X24). (b) *Arachnodinium antarcticum* Wilson & Clowes, 1982, sample AM2-5 (BAFC-PI 2514: L40). (c) *Cerebrocysta waipawaensis* (Wilson, 1988) Fensome *et al.* 2009, sample AM1-9 (BAFC-PI 2513: L59/3). (d) *Deflandrea antarctica* Wilson, 1967, sample AM2-4 (BAFC-PI 2513: K21). (e) *Deflandrea cygniformis* Pöthe de Baldi, 1966, sample AM2-8 (BAFC-PI 2515: W43/4). (f) *Diphyes colligerum* (Deflandre & Cookson, 1955) Cookson, 1965, sample AM2-2 (BAFC-PI 2512: W34). (g) *Enigmadinium cylindrifloriferum*, sample AM1-9 (BAFC-PI 2510: L17/1). (h) *Enneadocysta dictyostila* (Menéndez, 1965) Stover & Williams, 1995 emend. Sarjeant, 1981, sample AM1-2 (BAFC-PI 2508: K22). (i) *Enneadocysta brevistila* Fensome *et al.* 2006, sample AM1-1 (BAFC-PI 2507: S46). (j) *Glyphyrocysta semitecta* (Bujak in Bujak *et al.* 1980) Lentini & Williams, 1981, sample AM2-5 (BAFC-PI 2514: K28/1). (k) *Hystrichokolpoma* sp., sample AM1-15 (BAFC-PI 2511: L46). (l) *Hystrichosphaeridium* sp. cf. *H. astartes* (Sannemann, 1955) in Wrenn & Hart, 1988, sample AM1-2 (BAFC-PI 2508: S49/4). Scale bar: 20 µm.



**Fig. 4.** (Colour online) Dinoflagellate cysts recovered from the La Meseta Formation, Seymour Island, Antarctic Peninsula. (a) *Hystrichosphaeridium truswelliae* Wrenn & Hart, 1988, sample AM2-5 (BAFC-PI 2514: V27/2). (b) *Impagidinium parvireticulatum*, sample AM1-15 (BAFC-PI 2511: B25/1). (c) *Impletosphaeridium clavus* (Wrenn & Hart, 1988) emend. Bowman *et al.* 2013, sample AM1-15 (BAFC-PI 2511: P22/3). (d) *Lejeunecysta* sp., sample AM2-5 (BAFC-PI 2514: C33/2). (e) *Octodinium askinia* Wrenn & Hart, 1988, sample AM1-15 (BAFC-PI 2511: T24). (f) *Operculodinium centrocarpum* (Deflandre and Cookson, 1955) Wall, 1967, sample AM1-15 (BAFC-PI 2511: 22). (g) *Selenopemphix nephroides* Benedek, 1972, sample AM2-5 (BAFC-PI 2514: O39/2). (h) *Selenopemphix crenata* Matsuoka & Bujak, 1988, sample (BAFC-PI 2513: X21/3). (i) *Spinidinium macmurdoense* (Wilson) Lentini & Williams, 1976, sample AM1-15 (BAFC-PI 2511: E29). (j) *Thalassiphora pelagica* (Eisenack, 1954) Eisenack & Gocht, 1960, sample AM2-4 (BAFC-PI 2513: M32). (k) *Turbiosphaera filosa* (Wilson, 1967) Archangelsky, 1969, sample AM2-5 (BAFC-PI 2514: Z17/4). (l) *Vozzhennikovia apertura* (Wilson, 1967b) Lentini & Williams, 1976, sample AM2-4 (BAFC-PI 2513: V19/1-3). Scale bar: 20  $\mu$ m.



**Fig. 5.** (Colour online) Abundances (number of species) of gonyaulacoides and peridinoides cyst species per sample. Peridinioid/Gonyaulacoid curve (G/P index). The ratio of the abundance of gonyaulacoid versus peridinioid dinoflagellate cysts can reflect the productivity (Versteegh, 1994). Sporomorph/Dinoflagellate cyst curve (S/D index). The S/D curve plots the continental versus marine influences. The presence of dinoflagellate cysts is indicative of marine influence, whereas the presence of spores and pollen reflects terrestrial influences.

**4. Results**

**4.a. Dinoflagellate cysts**

All samples provided abundant and well-preserved marine palynomorphs including dinoflagellate cysts, acritarchs, microforaminiferal linings, as well as continental taxa such as spores and pollen, freshwater algae and fungi, in variable percentages along the whole section. Reworked Permian taeniate pollen, and Late Cretaceous and Palaeocene dinoflagellate cysts are also present in the analysed samples (Fig. 2).

A total of 38 dinoflagellate cyst species were recorded, 12 of which are part of the Antarctic-endemic assemblage, that consist of species whose distribution is restricted to latitudes south of 45° S (see definition in Bijl et al. 2011). The rest of the species have a cosmopolitan distribution (Lentin & Williams, 1980; Bijl et al. 2011, 2013a).

Among the endemic species, *Emeadocysta dictyostila* is well represented in all samples, reaching high values in most of them (Fig. 2). The closely related species *E. brevistila* is recorded only in some samples and in small amounts. Together with *E. dictyostila*, *Deflandrea antarctica* was also present throughout the whole unit in variable abundances (Fig. 2). *Vozzhennikovia apertura* is also an endemic species. It occurs in most of the samples, being abundant in the upper part of the section, in Acantilados I (sample AM1-2) and *Cucullaea* I horizons (samples AM2-4 and AM2-5). *Arachnodinium antarcticum*, *Spinidinium macmurdoense* and *Octodinium askinia* are documented throughout the section, with different abundances.

The small dinoflagellate cysts that are also members of the endemic assemblages are the species *Enigmadinium cylindrifloriferum* and *Impletosphaeridium clavus*. The first one is abundant in

the lowest samples, in Valle de las Focas (sample AM1-1) and Acantilados I (sample AM1-2) allomembers, and occasionally appears in some of the uppermost samples but is poorly represented. *Impletosphaeridium clavus* was recorded in some of the samples but always in very low proportions (Fig. 2).

Species with cosmopolitan distribution were recorded along the whole section but, except for *Lejeunecysta* spp. which is well-represented in the Campamento Allomember (sample AM2-2) and *Thalassiphora pelagica* which was particularly abundant in one sample of the *Cucullaea* I Allomember (sample AM2-5), they never dominate the assemblages (Fig. 2). Other cosmopolitan taxa that are present as frequent elements in the LMF are *Achomosphaera crassipellis*, which was recorded in the Campamento Allomember (sample AM2-2 with 15 specimens), and *Cerebrocysta waipawaensis* in Acantilados I (sample AM1-9) and *Cucullaea* I (samples AM2-4 and AM2-5) allomembers.

Other marine palynomorphs recorded in the section include the marine algae *Paralecaneia indentata* in Acantilados II (sample AM1-15), *Palambages* sp. in Campamento (sample AM2-2) and *Cucullaea* I (samples AM2-4 and AM2-5) and other prasinophytes in *Cucullaea* I (sample AM2-8). Just one specimen of the acritarch *Veryhachium* sp. is found in the Valle de las Focas (sample AM1-1) Allomember while microforaminiferal linings are spread over some samples but in all cases with few specimens.

The reworked specimens documented in this study include the Late Cretaceous species *Isabelidinium cretaceum*, *Isabelidinium* sp., *Odontochitina operculata*, *Oligosphaeridium pulcherrimum* and *Palaeocystodinium australinum*, and *Palaeoperidinium pyrophorum* was probably reworked from lower Palaeocene Seymour sections (online Supplementary Material, at <https://doi.org/10.1017/S0016756819000591>).



## 5. Discussion

### 5.a. Comments about the middle Eocene index species *Enneadocysta dictyostila*

In palynological studies carried out prior to 1995, the species *Enneadocysta dictyostila* (Menéndez, 1965) Stover & Williams, 1995 emend. Sarjeant, 1981 was published as *Areosphaeridium diktyoplokum* (Klumpp, 1953) emend. Eaton, 1971, Stover & Williams, 1995; the latter being wide-distribution taxa from the Northern Hemisphere. Nevertheless, Stover & Williams (1995) taxonomically differentiated *Enneadocysta dictyostila* (as *E. partridgei*) from *Areosphaeridium diktyoplokum*, and this allowed assigning the specimens of the Southern Hemisphere as *Enneadocysta dictyostila*, separating them from *Areosphaeridium diktyoplokum*, from the Northern Hemisphere. It was only after this separation that *Enneadocysta dictyostila* was recognized as a member of the Antarctic-endemic assemblage, and it was subsequently reinforced by other authors (e.g. Hannah, 1997; Truswell, 1997; Sluijs *et al.* 2003). Moreover, Stover & Williams (1995) established a spatial differentiation between the two species based on the recognition that all records of *Areosphaeridium diktyoplokum* correspond to the Northern Hemisphere while *Enneadocysta dictyostila* (as *E. partridgei*) is restricted to the Southern Hemisphere with a wide distribution (different localities of the SW Atlantic Ocean, Antarctica, Tasmania, Australia and New Zealand; Guerstein & Daners, 2010; Bijl *et al.* 2011; Douglas *et al.* 2014; Daners *et al.* 2016).

Fensome *et al.* (2006) re-examined specimens from eastern Canada and southern Argentina in order to differentiate the two genera. They concluded that, although both species are superficially similar, they differ in the number of the antapical processes, the shape of the central body and the morphology of the processes. While *Enneadocysta* has two antapical processes (more or less equal size at the antapex, neither of which is centrally located or distinctively large), *Areosphaeridium* has a single one, centrally located, that is commonly larger than other processes on the same specimen. Besides, *Enneadocysta* tends to have a lenticular central body and an asymmetrical overall shape while *Areosphaeridium* has a subspherical central body and symmetrical shape (Fensome *et al.* 2006). Regarding the process morphology, both *Enneadocysta* and *Areosphaeridium* can have lirate (solid or closed processes in which the distal endings are drawn out, commonly asymmetrically, into two orthogonal or curved branches that are serrate or denticulate on the outer margin *sensu* Sarjeant, 1982 in Fensome *et al.* 2006) or clypeate (a process bearing a distal perforate, quadrate to polygonal platform processes *sensu* Fensome & Williams (2005) in Fensome *et al.* 2006) processes. Nevertheless, in *Enneadocysta dictyostila* the processes vary distally from bifid to most commonly ragged clypeate and, in contrast, *Areosphaeridium diktyoplokum* has predominantly entire clypeate distal process terminations (Fensome *et al.* 2006).

Most of the palynological contributions on Antarctic sections (Wrenn & Hart, 1988; Coccozza & Clarke, 1992; Askin, 1997) agree to assign Antarctic specimens to *Areosphaeridium cf. diktyoplokus*, which first appears in the late early Eocene in the Northern Hemisphere. Therefore all the mentioned authors dated LMF as late early to late Eocene. For instance, Wrenn & Hart (1988) reported the presence of *Areosphaeridium diktyoplokum* in the LMF. They based the age of the unit on the stratigraphical range of *Areosphaeridium diktyoplokum* and they also considered it as a cosmopolitan species that spans from the late early Eocene to the Oligocene. They dismissed the comments of Goodman &

Ford (1983) who stated that the specimens referable to *Areosphaeridium diktyoplokus* from localities of the Southern Hemisphere have incomplete margins similar to those specimens they recovered from the uppermost Eocene / lower Oligocene from the Falkland Plateau (SW Atlantic) and they referred to *Areosphaeridium* sp. cf. *A. diktyoplokum*. Goodman & Ford (1983) pointed out that none of the Southern Hemisphere specimens should be attributed to *A. diktyoplokus* s.s. Finally, Wrenn & Hart (1988) end up stating that Northern and Southern dinoflagellate cysts assigned to *Areosphaeridium diktyoplokum* are a single species whose biostratigraphical distribution ranges from the late early Eocene to early Oligocene. But lastly, Douglas *et al.* (2014) assigned the Antarctic specimens to *Enneadocysta dictyostila* following the dinoflagellate cyst zonation applied to the Southern Ocean (Bijl *et al.* 2013a).

Based on all the above remarks and in agreement with Douglas *et al.* (2014) we consider that the specimens here studied from the LMF are assignable to *Enneadocysta dictyostila* instead of *Areosphaeridium cf. diktyoplokum*.

### 5.b. Biostratigraphy and correlation based on dinoflagellate cysts

The biostratigraphic analysis here presented is based on dinoflagellate cyst zonation applied to the entire Southern Ocean proposed by Bijl *et al.* (2013a). These authors calibrated the Palaeogene dinoflagellate cyst assemblages obtained from the Ocean Drilling Program (ODP) holes from the Tasmanian Platform and the Wilkes Land margin with the Geomagnetic Polarity Time Scale of Vandenberghe *et al.* (2012) using magnetostratigraphy and stable isotope stratigraphy. They distinguished 13 dinoflagellate cyst zones (SPDZ 1–13) for the late Palaeocene to late Eocene (58–36 Ma) using the first occurrences (FO), last occurrences (LO), first common (~25 %) occurrences (FCO) and last common (~25 %) occurrences (LCO) of dinoflagellate cyst species to define boundaries between the zones. In the present work, it is assumed the synchronicity of bioevents occurred at the East Tasmania platform (65° S palaeolatitude), Wilkes Land (67° S) and Marambio (Seymour) Island (64° S). So, considering the Bijl *et al.* (2013a) zonation scheme, we observed the following occurrence of dinoflagellate cyst species in the LMF (Fig. 2).

*Deflandrea antarctica* (FO: 58.20, LO: ~36.00 Ma) and *Enneadocysta dictyostila* (FO: 46.2 Ma; FCO: 45.20, LCO: 35.5 Ma; LO: 33.40 Ma) are recorded in all samples in the whole section. This indicates that the age of the LMF is between 46.20 and 36.00 Ma, where the base is defined by the FO of *Enneadocysta dictyostila* and the top is marked by the co-occurrence of *Deflandrea antarctica* and *Enneadocysta dictyostila*.

*Arachnodinium antarcticum* (FO: 48.70, LO: 36.00 Ma) and *Spinidinium macmurdoense* (FO: 55.50, LO: 35.95 Ma) first occur in the upper part of the Acontilados I Allomember (sample AM1-9). The first species reaches the upper sample of *Cucullaea* I Allomember (sample AM2-8) while the second extends to the top of the LMF.

*Impagidinium parvireticulatum* (FO: 43.7 Ma, LO: 35.5 Ma) is present in the Acontilados I (AM1-9) and the Acontilados II (AM1-15) allomembers. This means that sample AM1-15 could not be younger than 43.7 Ma.

*Glaphrocysta semitecta* (FO: 39.70, LO: 39.10 Ma) and *Deflandrea cygniformis* (FO: 40.00, LO: 35.90 Ma) occur in sample AM2-5 in the *Cucullaea* I Allomember. *G. semitecta* is present only

in this allomember, but *D. cygniformis* continues in sample AM2-8. Thus, from sample AM2-5 to AM2-8 (*Cucullaea* I Allomember) the unit has a maximum age of 39.10 Ma.

The FO of *Deflandrea convexa* is 58.20 Ma (Bijl *et al.* 2013a), and Brinkhuis *et al.* (2003) gave a LO at 35.8 Ma. The presence of a single specimen of *Deflandrea* sp. cf. *D. convexa* in sample AM2-8 (BAFC-Pl 2515) indicates that the *Cucullaea* I Allomember could not be younger than 35.8 Ma.

*Diphyes colligerum* (FO: 40.60, LO: 39.10 Ma) occurs in sample AM2-2 (Campamento Allomember), indicating that this allomember could not be younger than 39.10 Ma.

Some long-ranging species are also part of the assemblage and their ranges fall within the lapse between 45.20 and 36.00 Ma. They are *Thalassiphora pelagica* (FO: 55.30, LO: ~ 36.00 Ma), *Vozzhennikovia apertura* (FO: 65.10, LO: 35.5 Ma) and *Spinidinium macmurdoense* (FO: 55.50, LO: 35.95 Ma) among others.

The base of the LMF (the lowest sample AM1-1 in Valle de las Focas Allomember) is correlatable with Zone SPDZ10 (middle Lutetian, 46.2–45.2 Ma) in which *Enneadocysta dictyostila* has its FO. This zone is characterized by the alternation of *Deflandrea antarctica*, *Enneadocysta multicornuta* and *Enneadocysta dictyostila*. Although *E. multicornuta* is not recorded in the LMF, the fluctuation of *D. antarctica* and *E. dictyostila* is observable in the unit and the species are present as abundant and common elements, respectively (Fig. 2). Samples AM1-2 to AM1-8 (Valle de las Focas to Acantilados I Allomembers) of LMF are comparable to Zone SPDZ11 (middle Lutetian, 45.2–44.0 Ma) defined by the FCO of *Enneadocysta dictyostila*, and samples AM1-9 to AM2-8 (Acantilados I to *Cucullaea* II Allomembers) are comparable to Zone SPDZ12 (44.0–40.0 Ma, middle Lutetian to early Bartonian) defined by the FO *Impagidinium parvireticulatum* of Bijl *et al.* (2013a). The SPDZ13 (Bartonian–Priabonian, 40.0–35.95 Ma) is not easily correlated with LMF because neither the species of the base nor the top are found in the Antarctic samples; only the characteristic species of the zone such as *Spinidinium macmurdoense*, *Vozzhennikovia apertura* and *Glaphyrocysta semitecta* are recorded. Nevertheless, a significant event in Zone SPDZ13 is the FO *Deflandrea cygniformis*; this species occurs in sample AM2-8 (*Cucullaea* I Allomember), but only in this sample, and has no continuous record in the section. It is important to point out that *Spinidinium macmurdoense* is an abundant element in the uppermost sample (AM3-2) of the LMF and in Zone SPDZ13 this species has its FCO, suggesting that Zone SPDZ13 would be recognized in the LMF, but the equivalence of both dinoflagellate cyst assemblages is not assured.

LMF is also equivalent to zones RTF1 (middle Lutetian, ~46 Ma) and RTF2 (middle Lutetian to late Bartonian, 46–39 Ma) and probably to RTF3 (late Bartonian to middle Priabonian, 39–36 Ma) as proposed by González Estebenet *et al.* (2016) for the Río Turbio Formation (upper member), Santa Cruz province, Austral Basin, Argentina. The zones of the Austral Basin were calibrated with the South West Pacific Ocean zonation (Bijl *et al.* 2013a) and complemented with isotopic ages of  $^{87}\text{Sr}/^{86}\text{Sr}$  (Casadio *et al.* 2009), foraminifera (Malumián, 1990) and calcareous nannofossils (Concheyro, 1991) data obtained from the Río Turbio Formation (upper member). Zone RTF 1 is correlated with Zone SPDZ10 of Bijl *et al.* (2013a), because of the co-dominance of *Deflandrea antarctica* and *Enneadocysta dictyostila*, being the FO of the *E. dictyostila*, a significant event in this zone. The same is observed in the lowermost LMF (sample AM1-1). The base of RTF 2 is equivalent to the base of Zone SPDZ11, both defined by the FCO of *Enneadocysta dictyostila*, while the upper part of

RTF 2 is correlated with the SPDZ12 based on the range of the characteristic species of both zones. The FCO of *Enneadocysta dictyostila* is recorded in samples AM1-2 to AM3-1 of the LMF (Valle de las Focas to *Cucullaea* II allomembers). Zone RTF 3 is equivalent to Zone SPDZ 13 of Bijl *et al.* (2013a) due to the FCO of *Spinidinium macmurdoense* that is recognizable in both the Austral and South Pacific Ocean dinoflagellate cyst biozonation schemes. Although in the uppermost LMF (sample AM3-2) *S. macmurdoense* increases in number of specimens in comparison with the samples below it, the species is considered as an abundant (A: 40 to 100 specimens, Fig. 2) and not very abundant (VA: more than 100 specimens, Fig. 2) element as in the biozonation schemes. Besides, the base of Zone RTF 3 is defined by the LO of *Arachnodinium antarcticum* and *Hystrichosphaeridium truswelliae*, but in the LMF the *H. truswelliae* disappears earlier than *A. antarcticum* (Fig. 2). However, the LO of *Impagidinium parvireticulatum* and the LCO of *Enneadocysta dictyostila* are two significant events dated at the middle Priabonian (Bijl *et al.* 2013a). The same is seen in sample AM2-8 (*Cucullaea* I) of the LMF, which could indicate its equivalence to Zone RTF 3. Because the distribution of the dinoflagellate cyst species of the LMF has some important differences from Zone RTF 3, the correlation between the two assemblages is not well defined. The same occurs with the correlation between the LMF and Zone SPDZ13.

González Estebenet *et al.* (2016) recognized Zone RTF 1 in the base of La Despedida Formation, Tierra del Fuego province (Argentina), while Zone RTF 2 was documented in the Man Aike Formation, Santa Cruz province, and in the Leticia Formation (Río de la Turba section), Tierra del Fuego province, both in Argentina. Thus, the lowest LMF (sample AM1-1) is correlatable with Río Turbio (upper member) and the base of La Despedida formations, whereas the rest of the LMF is correlatable with the Río Turbio (upper member), Man Aike and Leticia (Río de la Turba section) formations. The correlation and comparison between high south latitude localities of the Austral Basin have been carried out by González Estebenet *et al.* (2016) taking into account the presence/absence of species rather than abundance data. Comparison of the dinoflagellate cyst assemblages of the James Ross Basin (Antarctic Peninsula) and the Austral Basin (south of Argentina), based on the quantitative data, is a work in progress and will give more strength to the correlation from localities of the Drake Passage area.

The new analysis of dinoflagellate cysts presented here complements the study of Douglas *et al.* (2014), confirming the age of the LMF, and especially adding to the study the lowest part of the unit (corresponding to Telm 1 that has not been analysed by the mentioned authors) suggesting a middle Lutetian to Priabonian age (~46.2 to ~36 Ma) for the LMF, younger than the one documented so far.

As was mentioned in Section 2.c.2 above, there is a recent age model proposed for the LMF. This model merits inclusion in this discussion since it has been carried out in the LMF itself and the palynological samples analysed herein were collected during the geological mapping of the succession for the new geological cartography of Seymour Island proposed by Montes *et al.* (2013, 2019b). Based on the combination of isotopic data ( $^{87}\text{Sr}/^{86}\text{Sr}$ ), magnetostratigraphy and lithostratigraphy in relation to the global curves of sea level, the age model offers a late Thanetian to early Lutetian age (~56.4 to ~45.8 Ma) for the LMF. So, the age here obtained based on dinoflagellate cysts involves a hiatus of 11 Ma at the base of the LMF with respect to the top of the underlying Cross Valley – Wiman Formation (56.9 Ma; Beamud *et al.* 2015;

Montes *et al.* 2019a). This hiatus would imply the absence of the Ypresian (lower Eocene) and a large part of the lower Lutetian. Such a hiatus of 11 Ma, would not be caused by eustatic sea-level drop alone; rather, it could be due to tectonic–erosive mixed origin and thus a tectonic control for the incised valley of LMF considering the proposal of Marenssi *et al.* (1998) about the cause of the unconformities in the unit. In contrast, the age for the LMF proposed in the magnetostratigraphic scheme by Montes *et al.* (2019a) would not involve such a hiatus, explaining how continued sedimentation would have prevailed during the regressive and gradual evolution in the filling of the James Ross Basin.

## 6. Palaeoceanographic and palaeoenvironmental implications

### 6.a. Palaeoceanography during the Eocene in the Southern Ocean and surrounding areas

Climatic and tectonic changes occurring during the Palaeogene strongly influenced the distribution of dinoflagellate cyst assemblages in the Southern Ocean (Stickley *et al.* 2004; Bijl *et al.* 2013a; Guerstein *et al.* 2016). During the Palaeocene and the early Eocene circum-Antarctic dinoflagellate cysts, assemblages were dominated by cosmopolitan early Palaeogene taxa while Antarctic-endemic species were rare (Bijl *et al.* 2013a, b). In the early middle Eocene (50–48 Ma), endemic taxa began to dominate the dinoflagellate cyst assemblages in the Southern Ocean south of 45° S, i.e. areas east of the Tasmanian Gateway and Drake Passage (Bijl *et al.* 2011). The dominance of endemic dinoflagellates became stronger at least until the mid- to late Eocene (38–36 Ma). Huber *et al.* (2004) and González Estebenet *et al.* (2014) explained that the distribution of the middle–late Eocene endemic taxa in the Southern Ocean would be in response to surface ocean-circulation pattern characterized by wide clockwise subpolar gyres surrounding Antarctica that favoured the endemism of the species tolerant to relatively low surface-water temperatures. Towards the Eocene/Oligocene transition, endemic species became extinct as a consequence of the deepening of the Tasmanian Gateway and Drake Passage (Sluijs *et al.* 2003; Stickley *et al.* 2004; Guerstein *et al.* 2008; Houben *et al.* 2013), and were replaced by Oligocene cosmopolitan taxa, typically heterotrophic species (protoperidinaean) with modern analogues that live today in sea-ice environments (Houben *et al.* 2013).

In reference to the establishment of dominantly Antarctic-endemic assemblage in the middle Eocene, Bijl *et al.* (2011) considered that in the early middle Eocene (~50 Ma) the dominance of the Antarctic-endemic taxa has little relation to the sea surface temperature (SST) because the SSTs did not decrease abruptly at that time. In contrast, during the middle Eocene, when the endemic assemblage was well established, the SST controlled the abundances of endemic species. The causes of the proliferation of the endemic assemblage just after 50 Ma would be linked to other physicochemical parameters of the surface waters, such as large-scale changes in surface-ocean nutrient availability. That ocean richness would be generated by a significant diatom production recorded at 47 Ma onward, as a consequence of the global cooling occurring in the middle Eocene that increased latitudinal gradients and stimulated upwelling, bringing waters enriched in silica to the surface for utilization by the diatom walls. Besides, increased weathering may have led an additional nutrient supply to the oceans, especially the co-limitation diatom nutrients, Si and Fe. The diatom production caused a rapid reorganization of

Southern Ocean dinoflagellate cyst assemblages. Once the endemic dinoflagellate cyst species came to dominate the assemblages in the early middle Eocene, they were more controlled by SST variations than during the Palaeocene and early Eocene (Bijl *et al.* 2010, 2011).

On the other hand, González Estebenet *et al.* (2014) carried out a qualitative comparison (presence/absence of species) between the middle Eocene dinoflagellate cyst assemblages from localities to the north (upper member of Río Turbio, Man Aike and Leticia formations of the Austral Basin) and south (La Meseta Formation of the Antarctic Peninsula and core IO1578-59 in Bruce Bank of the Scotia Sea) of the Drake Passage area. They observed that, although both areas surrounding the Drake Passage were characterized by a high presence of the Antarctic-endemic species, a notable difference in non-endemic taxa existed between the north and the south localities and these differences might be due to the influence of surface waters from different sources. The sites located to the south of Drake Passage (Antarctic Peninsula and the Scotia Sea) would reflect the influx of surface waters originating from Antarctic coasts and directed northwards through the clockwise subpolar gyre known as the proto-Weddell Gyre (p-WG). On the other hand, the shallow flows through the incipient opening of Drake Passage in the early Eocene (Scher & Martin, 2006; Livermore *et al.* 2007; Barbeau *et al.* 2009) would have allowed the input of shallow waters with cosmopolitan taxa from the Pacific to the South Atlantic Ocean. Thus, the cosmopolitan taxa would have been subsequently transported together with the Antarctic-endemic components into the Austral Basin by the northwestern sector of the p-WG.

### 6.b. Palaeoenvironment of the La Meseta Formation

The usefulness of dinoflagellate cysts in providing age determinations within the Palaeogene of the South Atlantic Ocean and, consequently, their potential for stratigraphically correlating different basins of that region has been well established (e.g. Pross & Brinkhuis, 2005). Besides this, dinoflagellate cysts are also useful as proxy indicators for environmental conditions (Sluijs *et al.* 2005) because of their high sensitivity to physicochemical changes of surface water, such as salinity, temperature and depth, and also in productivity (i.e. the trophic levels). Thus, the palaeoproductivity of surface water can be estimated using the relationship between peridinioid (P) cysts and gonyaulacoid (G) cysts by means of the P/G cyst ratio. We assumed that the dinoflagellate generators of P cysts of extinct species would have had the same heterotrophic habit as the living dinoflagellate genus *Protoperidinium*, while the G cysts would have been originated by dinoflagellates with an autotrophic or mixotrophic behaviour (Sluijs *et al.* 2005; Esper & Zonneveld, 2007). Therefore, the high relative abundance of P cysts could indicate a high concentration of dissolved nutrients of surface water, e.g. upwelling or estuaries (Goodman & Ford, 1983; Mao & Mohr, 1995; Brinkhuis *et al.* 2003; Sluijs *et al.* 2003, among others). In contrast, the high relative abundance of G cysts would suggest nutrient-poor waters, e.g. outer shelf or oceanic waters. In terms of the index values, a ratio of 0.5–1 is indicative of higher-productivity waters, while the ratio of 0–0.5 indicates less productive waters.

On the other hand, the S/D ratio, sporomorphs (pollen and spores) versus dinoflagellate cysts, is used as a measure for terrestrial influence relative to marine influence whereby an increase in pollen and spores relative to dinoflagellate cysts is interpreted as a sea level lowering as the section becomes more proximal to the

coast. Therefore, an S/D ratio of 0.5–1 indicates more proximal environments while a ratio of 0–0.5 means a more distal position. Thus, the S/D ratio was employed together with the P/G ratio in deducing the depositional environment and the direction of the trend line which reflects the regression or progression of the shoreline.

Previous sedimentological evidence suggests that LMF is indeed a composite valley fill containing not only estuarine but also deltaic and shallow-marine sediments (Stilwell & Zinsmeister, 1992; Marensi *et al.* 1998, 2002). So, the joint analysis of the frequency distribution of dinoflagellate cysts, P/G and S/D ratios and the results of the sedimentological study of the LMF allows us to reconstruct the palaeoenvironment and surface water conditions during the middle to late Eocene in the study area.

The P/G ratio varied little throughout the section. In Valle de las Focas, Acantilados I and Acantilados II allomembers, the P/G values are below 0.5, indicating poor productive waters; these samples are characterized by a high number of autotrophic dinoflagellates (G – note the large number of *Enneadocysta* specimens counted; Fig. 2; online Supplementary Material at <https://doi.org/10.1017/S0016756819000591>). The samples with the lowest P/G values are AM1-7 (P/G: 0.07), AM1-9 (P/G: 0.08) and AM1-8 (P/G: 0.11); they would indicate the least productive waters (Fig. 5). That lowest productivity is coincident with the presence of calcareous nannofossils which were recorded only in these three samples from the thirteen processed samples of the entire LMF (Concheyro *et al.* 2016) suggests somewhat more open marine conditions. Moreover, dinoflagellate cyst assemblages from the Southern Ocean (ODP Leg 189, Site 1170) recorded the highest *Enneadocysta* spp. that is correlatable with high CaCO<sub>3</sub> content in sediments possibly reflecting more offshore, less eutrophic marine conditions (Röhl *et al.* 2004). Turning to the LMF, the P/G ratio values greater than 0.5 are observed in samples AM3-2 (P/G: 0.92), AM2-4 (P/G: 0.67) and AM3-1 (P/G: 0.57), i.e. Campamento, *Cucullaea* I and *Cucullaea* II allomembers, evidencing more productive waters. This means that from Campamento to *Cucullaea* II allomembers, a tendency to more productive waters or closer to the coast is suggested. In these samples an increase in the number of heterotrophic peridinioid dinoflagellates, such as *Deflandrea* and *Vozzhennikovia* (Fig. 5), is noticeable.

Referring to the S/D ratio, LMF displays low values in most of the samples (S/D < 0.5, Fig. 5). These low values fluctuate throughout the section, but in sample AM2-2 (Campamento Allomember) the S/D ratio is c. 0.5, reaching the highest value in sample AM3-1 of the *Cucullaea* II Allomember (S/D: 0.515, Fig. 5). Sample AM3-1 reflects the closest condition to the coast and is the only sample in which the number of pollen and spore specimens exceeds the number of dinoflagellate cysts. The scarce dinoflagellate cysts are represented by *Enneadocysta dictyostila* and *Vozzhennikovia apertura*. The general increase in the S/D ratio observed from Campamento to *Cucullaea* II allomembers means an increase in terrestrial influence. This compositional change reflects a shift in the depositional environment from a more distal setting to one closer to the shoreline, i.e. a shallowing-upwards trend, or deposition further up inside the La Meseta estuary. The overall trend through the section is for a move from marine-dominated assemblages (Valle de las Focas to Acantilados II allomembers) to more terrestrially dominated assemblages (from Campamento to *Cucullaea* II allomembers). This would probably be a consequence of infilling of the incised valley estuary system within which these sediments were being deposited; within this are smaller-scale changes (cf. JC Greenhalgh, unpub. PhD thesis, UCL, Univ.

London, 2003). Fluctuations within the individual members can be attributed to the large variation in environments and energy settings within an estuary. Differences between the individual members, e.g. across unconformable boundaries, reflect relative sea level change, caused by eustatic sea level changes, localized tectonism, sedimentary infill or a combination of these events (Porebski, 1995).

Worth taking into consideration is the small spiny palynomorph assigned to the species *Enigmadinium cylindrifloriferum* which is abundant in the Valle de las Focas and lower samples of Acantilados I allomembers (Fig. 5). This species was defined by Wrenn & Hart (1988) as a chorate dinoflagellate cyst of the Order Gonyaulacales, while recently Williams *et al.* (2017) considered it as an acritarch. This duality in the assignment is founded on the position of the processes (non-tabular) and the doubtful existence of an archaeopyle in these spiny forms. Depending on whether it is considered to be an acritarch or a dinoflagellate cyst, the palaeoenvironmental interpretation differs. In this sense, some authors (Smith, 1992; Schrank, 2003) proposed that the abundance of small acritarchs may be related to depositional environment; e.g. the small spiny acritarch *Micrhystridium* reaches greater abundances and diversity in shallow marine sandstones (in relatively coarse sediments), while it is much less frequent in open marine facies (finer-grained sediments) characterized by diverse dinoflagellate cyst assemblages. However, assuming that these small spiny palynomorphs are dinoflagellate cysts, it is expected to be considered that the lifestyle of the dinoflagellates produced these cysts; this implies their affinity to gonyaulacacean or peridinacean cysts, with autotrophic or heterotrophic habits, respectively. Taking into account the highest relative abundances of *E. cylindrifloriferum* registered in the lowest samples of the LMF (Fig. 5), this can be linked to a more distal environment with low productivity reflected by the low S/D and P/G ratio values (whether it is considered as a dinoflagellate cyst or an acritarch). Coccozza & Clarke (1992) suggested stressed marine depositional conditions in a shallow water environment for the lowermost part of the LMF. They support such palaeoenvironment on the assumption that low-diversity, high-dominance dinoflagellate cyst assemblages are compatible with shallow, inshore conditions (e.g. Goodman, 1979), i.e. low-salinity or estuarine/brackish. *E. cylindrifloriferum* seems to be restricted to the lower part of the LMF, suggesting that the stressed marine-influenced conditions existed only in that part of the section, e.g. deposition was occurring more proximally. In spite of the fact that the species decreases in abundance towards to the middle and upper part of the section until it almost disappears, a single specimen is registered in sample AM2-5 (*Cucullaea* I allomember). This would indicate that its presence in the assemblage is related to a facial factor or the stress palaeoenvironmental conditions.

## 7. Conclusions

Although the LMF has previously been analysed in terms of its dinoflagellate cyst assemblages, the re-study of the unit presented here has allowed us to reach new conclusions as follows:

- The age of the LMF – from Valle de las Focas to *Cucullaea* II allomembers (*sensu* Montes *et al.* 2013) – is middle Lutetian to Priabonian (46.2–36 Ma), supported by the co-occurrence of *Enneadocysta dictyostila* and *D. antarctica*, allowing the establishment of a maximum and minimum age for these

deposits. The proposed age, which is in agreement with Douglas *et al.* (2014), is based on the dinoflagellate cyst biostratigraphic scheme of the early Palaeogene of the Southern Ocean performed by Bijl *et al.* (2013a), which at the moment is the most accurate scheme for the Eocene assemblages of southern high-latitudes sections. The LMF is correlatable with zones SPDZ 10, 11 and 12 of the Palaeogene biozonation of the Southern Ocean, but the correlation with Zone SPDZ 13 is not very clear. The LMF is also equivalent to zones RTF1 and RTF2 of the Austral Basin defined for the Río Turbio Formation (upper member), Austral Basin, Argentina, but the correlation between the LMF and Zone RTF 3 is not well established.

- There is an apparent contradiction between dinoflagellate cyst data presented herein and the magnetostratigraphic age model performed for the LMF (Beamud *et al.* 2015; Montes *et al.* 2019a) that suggests a late Thanetian to early Lutetian (~58.4–45.8 Ma) age. The consistency of the absolute age model offered by the magneto-, litho- and Sr-isotope data would imply the earliest appearance of the *Enneadocysta dictyostila* in the LMF (Antarctic Peninsula), compared with the later occurrence of the species in the rest of the Southern Ocean localities. If we consider that these differences exist, a convincing explanation should be found, or alternatively, a hiatus of 11 Ma between the LMF and the underlying Cross Valley – Wiman Formation should be assumed and a new geotectonic model developed for the James Ross Basin to elucidate its cause. The reasons for the discrepancies and the feasibility of the magnetostratigraphic age model performed for the LMF deserve deeper discussion in a future contribution.
- The data on the LMF offered here are useful to elucidate and support the South Atlantic Ocean circulation proposals. The LMF has a dominance of Antarctic-endemic taxa during the middle to late Eocene, as occurred with the dinoflagellate cyst assemblages from other localities in the Southern Ocean south of 45° S. The distribution of the endemic taxa reflects an ocean-circulation scheme with wide clockwise gyres surrounding Antarctica that were disrupted as a consequence of the deepening of the Tasmanian Gateway and Drake Passage. The deepening of those gateways and their definitive and final apertures occurred towards the Eocene/Oligocene transition, changing the environmental conditions producing the extinction of the endemic taxa.
- The palaeoenvironmental analyses of the LMF based on P/G and S/D ratios allowed the proposal of an overall trend through the section from marine-dominated assemblages with poor productive waters (Valle de las Focas to Acantilados II allomembers) to more terrestrially dominated assemblages, with an increase in productivity in the upper part of the unit (from Campamento to *Cucullaea* II allomembers) reflecting a shallowing trend to the top.
- This study complements the contribution of Douglas *et al.* (2014) since it confirms the age suggested by the authors and provides quantitative palynological data of the whole LMF that will enable more reliable comparisons between similar assemblages of localities around Drake Passage. The correct chronology will allow many important Palaeogene issues to be elucidated, such as biostratigraphy, phylogenies, palaeoclimatic features and Southern Ocean palaeocirculation, among others.

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- Appendix: Dinoflagellate cysts cited in the text**
- Achomosphaera crassipellis* (Deflandre & Cookson, 1955)  
Stover & Evitt, 1978
- Arachnodinium antarcticum* Wilson & Clowes, 1982
- Brigantedinium* ? spp.
- Cerebrocysta waipawaensis* (Wilson, 1988) Fensome *et al.*, 2009
- Deflandrea antarctica* Wilson, 1967
- Deflandrea cygniformis* Pöthe de Baldis, 1966
- Deflandrea oebisfeldensis* Alberti, 1959
- Deflandrea* sp. cf. *D. convexa* Wilson, 1988
- Diphyes colligerum* (Deflandre & Cookson, 1955)  
Cookson, 1965
- Enigmadinium cylindrifloriferum* Wrenn & Hart, 1988
- Enneadocysta brevistila* Fensome *et al.*, 2006
- Enneadocysta dictyostila* (Menéndez, 1965) Fensome *et al.*, 2006
- Glaphyrocysta semitecta* (Bujak in Bujak *et al.*, 1980) Lentin & Williams, 1981
- Hystrichokolpoma* sp.
- Hystrichosphaeridium salpingophorum* (Deflandre, 1935) ex Deflandre, 1937 emend. Davey & Williams, 1966
- Hystrichosphaeridium* sp. cf. *H. astartes* Sannemann, 1955
- Hystrichosphaeridium truswelliae* Wrenn & Hart, 1988
- Impagidinium parvireticulatum* Wilson, 1988
- Impagidinium* sp.
- Impletosphaeridium clavus* (Wrenn & Hart, 1988) emend. Bowman *et al.*, 2013
- Impletosphaeridium ligospinosum* Wrenn & Hart, 1988
- Lejeunecysta* spp.
- Octodinium askiniae* Wrenn & Hart, 1988
- Oligosphaeridium pulcherrimum* (Deflandre & Cookson, 1955)  
Davey & Williams, 1966
- Operculodinium centrocarpum* (Deflandre & Cookson)  
Wall, 1967
- Palaeocystodinium australinum* (Cookson, 1965) Lentin & Williams, 1976
- Phelodinium magnificum* (Stanley, 1965) Stover & Evitt, 1978
- Selenopemphix crenata* Matsuoka & Bujak, 1988
- Selenopemphix nephroides* Benedek, 1972
- Senegalinium asymmetricum* (Wilson, 1967) Stover & Evitt, 1978
- Spinidinium macmurdoense* (Wilson, 1967) Lentin & Williams, 1976
- Spiniferites ramosus* (Ehrenberg, 1838) Mantell, 1854
- Thalassiphora pelagica* (Eisenack, 1954) Eisenack & Gocht, 1960
- Turbiosphaera filosa* (Wilson, 1967) Archangelsky, 1969
- Vozzhennikovia apertura* (Wilson, 1967) Lentin & Williams, 1976