Contents lists available at ScienceDirect



Review of Palaeobotany and Palynology



journal homepage: www.elsevier.com/locate/revpalbo

Malvinia escutiana, a new biostratigraphically important Oligocene dinoflagellate cyst from the Southern Ocean

Alexander J.P. Houben^{a,}, Peter K. Bijl^a, G. Raquel Guerstein^b, Appy Sluijs^a, Henk Brinkhuis^a

^a Biomarine Sciences, Institute of Environmental Biology, Utrecht University, Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands ^b Instituto Geológico del Sur, Universidad Nacional del Sur, Departamento de Geología, San Juan 670-B8000ICN Bahía Blanca, Argentina

ARTICLE INFO

Article history: Received 22 September 2010 Received in revised form 24 February 2011 Accepted 10 March 2011 Available online 17 March 2011

Keywords: dinoflagellate cysts peridinioid Eocene Oligocene Southern Ocean Antarctic glaciation

ABSTRACT

The Eocene–Oligocene Transition (EOT, ~34 Ma) represents the culmination of Eocene cooling by the initiation of large-scale Antarctic glaciation. Recognition and correlation of the EOT in Southern Ocean sedimentary successions have been difficult as a result of the general lack of well-calibrated biostratigraphic markers. Here we describe an unusual hypnozygotic organic walled dinoflagellate cyst (dinocyst) that originated in the Southern Ocean in conjunction with the onset of major Antarctic glaciation as reflected by 'oxygen isotope event 1' (Oi-1).

We restudied samples from Deep Sea Drilling Program (DSDP) Site 511 using Light Microscopy and Scanning Electron Microscopy and found that a taxon previously known as Forma T constitutes a new protoperidinioid dinocyst genus and species that we name *Malvinia escutiana*. Published and re-evaluated data from other Southern Ocean sites show that *M. escutiana* did not occur before the Oi-1 (33.7 Ma), emphasizing its potential as a useful biostratigraphic marker for this key interval in the Southern Ocean's Cenozoic climate history.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

During the middle and late Eocene (~48-34 Ma) high latitudes experienced cooling that resulted in progressively increasing latitudinal temperature gradients (see e.g., Pearson et al., 2007; Bijl et al., 2009). This trend culminated during the Eocene–Oligocene Transition (~34 Ma, EOT) in the relatively rapid initiation of large scale Antarctic glaciation: likely a non-linear response to long term declining atmospheric carbon dioxide concentrations and favorable orbital configurations (DeConto and Pollard, 2003; Coxall et al., 2005; Liu et al., 2009; Pearson et al., 2009). The onset of Antarctic glaciation is marked globally by a distinct positive shift in deep-sea benthic for aminiferal $\delta^{18}\text{O}$ values. Recent high-resolution studies revealed that the EOT is characterized by at least two steps in increasing δ^{18} O values; a so-called 'precursor' EOT shift (EOT-1), followed by a second step that represents the onset of major Antarctic glaciation, i.e. the 'Oligocene isotope event-1' or Oi-1 (following Miller et al., 1987; Zachos et al., 1996; Katz et al., 2008; Miller et al., 2008, 2009).

The EOT and its associated stepwise shifts have been found difficult to recognize and correlate in Southern Ocean sedimentary successions. In this region, upper Eocene and lower Oligocene stratigraphies often lack carbonate fossils, suitable to identify the δ^{18} O excursions and correlate to the global ocean. Age models are hence, primarily based on organic and siliceous microfossils such as organic walled dinoflagellate cysts (dinocysts, see e.g., Kemp, 1975; Wrenn and Hart, 1988; Mohr, 1990; Brinkhuis et al., 2003a,b; Sluijs et al., 2003; Macphail and Truswell, 2004; Stickley et al., 2004a) and diatoms (see e.g., Gombos and Ciesielski, 1983; Bohaty and Harwood, 2000; Roberts et al., 2003; Stickley et al., 2004a). Well-calibrated dinocyst records in the Southern Ocean are sparse. Ocean Drilling Program (ODP) Site 1172 near Tasmania forms an exception in view of its tight biostratigraphic and magnetostratigraphic calibration (see e.g., Brinkhuis et al., 2003b; Sluijs et al., 2003; Stickley et al., 2004a).

Palynological pilot studies carried out on sediments recovered during Deep Sea Drilling Project (DSDP) Leg 71 at Site 511 in the southwest Atlantic Ocean revealed the presence of a relatively complete upper Eocene and lower Oligocene section, with rich dinocyst assemblages (Ludwig et al., 1980; Goodman and Ford, 1983, Fig. 1). We have recently generated stable oxygen- and carbon isotope, organic geochemical, and dinocyst assemblage records across the EOT at this site (Liu et al., 2009; Houben et al., submitted for publication). The first occurrence (FO) of an enigmatic dinocyst termed Forma T by Goodman and Ford (1983) was found to coincide with the Oi-1, potentially providing an important biostratigraphic marker for this isotope shift. Goodman and Ford (1983) were unable to resolve the systematic paleontology of this taxon as a result of severe folding and distortion of specimens. We have analyzed specimens of Forma T in detail by Light Microscopy (LM) and Scanning Electron Microscopy (SEM) and we find

Corresponding author. Tel.: + 31 2539318; fax: + 31 302535096. *E-mail address:* A.J.P.Houben@uu.nl (A.J.P. Houben).

^{0034-6667/\$ -} see front matter © 2011 Elsevier B.V. All rights reserved. doi:10.1016/j.revpalbo.2011.03.002

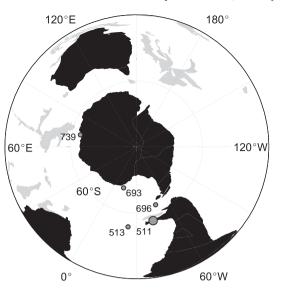


Fig. 1. Paleogeographic configuration of the southern high latitudes during the Oligocene (map obtained from http://www.odsn.de) and the localities where *Malvinia escutiana* has been recorded. The thick gray circle indicates the paleogeographic location of DSDP site 511 at 51°S in the southwest Atlantic Ocean. The other sites are DSDP Site 513 (Goodman and Ford, 1983), Argentine Basin, ODP Site 693, Maud Droning Land Basin (Mohr, 1990), ODP Site 696, South Orkney Microcontinent (Mohr, 1990) and ODP Site 739, Prydz Bay.

that it represents an unusual cyst of a peridinioid dinoflagellate. We erect the new genus *Malvinia* to accommodate the unique morphology of this taxon. We also discuss the significance of the new species *Malvinia escutiana* as a biostratigraphic marker specific for the Oi-1 isotope shift.

2. Material and methods

2.1. Material

DSDP Site 511 was drilled on the western flank of the Falkland Plateau (51°S) at a water depth of ~2600 m (Ludwig et al., 1980). The upper Eocene–lower Oligocene sequence, between 20 and 182 m below sea floor (mbsf), comprises massive gray diatomaceous- and nannofossil-diatomaceous oozes with variable carbonate content. The core recovery was poor, and therefore sample spacing was less than desirable, but performed on every section available. The age model of DSDP Site 511 (Fig. 2) is based on Houben et al. (submitted for publication); it shows a distinct increase in planktonic and bulk carbonate δ^{18} O values at 101 mbsf that was interpreted to reflect the Oi-1 (33.7 Ma, following the timescale of Gradstein et al., 2004).

2.2. Methods

Palynomorphs were extracted for analysis using standard palynological techniques. Carbonates and silicates were removed by treatment with 30% HCl and 38% HF respectively, no heavy liquid separation or oxidation was employed. After each acid step, samples were washed with water and centrifuged or settled for 24 h and decanted. Then samples were sieved over a 15 µm mesh-sieve and were given 5 min ultrasound to break up agglutinated particles of the residue. The residue was transferred to glass tubes, subsequently centrifuged (2000 rpm) and concentrated to 1 ml. Glycerin water was added to the residue, after which a droplet of homogenized residue was mounted on a slide. Glycerin jelly was added and the mixture was homogenized and sealed. All slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University. Taxonomy follows that cited in Fensome et al. (2008). LM-pictures were taken using a

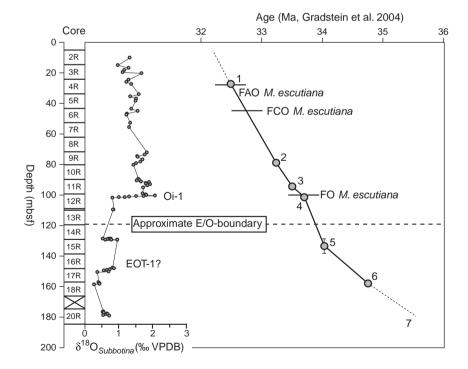


Fig. 2. Age model for DSDP Site 511, indicated are the bio- and isotope stratigraphic events applied. Identification of nannofossil events is according to Wise (1983), diatom events according to Gombos and Ciesielski (1983) and foraminifer events were identified in Houben et al. (submitted for publication). All ages are relative to the timescale of Gradstein et al. (2004). The planktonic foraminifer δ^{18} 0 (Houben et al., submitted for publication) is used to identify the Oi-1. Primary events are 1: the Last Occurrence (LO) of the calcareous nannofossil *lsthmolithus recurvus* (32.5 Ma, Villa et al., 2008), 2: mass occurrence of the nannofossil *Blackites* spp. (33.24 Ma, Marino and Flores, 2002), 3: mass occurrence of the nannofossil *Clausicoccus* spp. (33.5 Ma, Marino and Flores, 2002), 4: the 'Oligocene Isotope Event 1' (Oi-1, 33.7 Ma, Coxall and Pearson, 2007), 5: the First Occurrence (FO) of the diatom *Rhizosolenia oligocaenica* (34.0 Ma, Roberts et al., 2003), and 6: the LO of planktonic foraminifer *Globigerinatheka index* (34.8 Ma, Galeotti et al., 2002). The base of the section is defined by the presence of the nannofossil *Reticulofnestra oamaruensis* (35.5 Ma, Villa et al., 2008). The First Occurrence (FO), First Constent Occurrence (FO) and First Abundant Occurrence (FAO) for *Malvinia escutiana* are indicated. An initial step towards heavier δ^{18} O values is interpreted to represent an older EOT shift, likely EOT-1.

Leica Wild MPS52 Camera. In addition, Scanning Electron Microscope (SEM) photography was performed. For this purpose, a split of the palynological residues was sieved with warm water over a 15 μ m mesh-sieve in order to remove glycerine. The residue was transferred to a tray table and coated with 12 nm platinum using a sputter coater (Cressington 208 h) and examined using a Philips XL30S FEG device at Utrecht University.

2.3. Terminology for cyst description

Descriptive terminology for the morphology of fossil dinocysts is outlined in Evitt et al. (1977) and Evitt (1985). In this work, following Fensome et al. (1993) we refrain from using the prefix para preceding morphologic features referring to the cyst. These authors proposed the use of para terminology only in exceptional situations, such as with parasutural ridges. Furthermore, since we have encountered an unusual type of archeopyle, we here use specific terminology concerning the description of peridinioid archeopyles. Bujak and Davies (1983) introduced the term 'transverse archeopyle' for an archeopyle formed in peridinioid cysts by the opening of complete archeopyle sutures along the plate boundaries 2'/1a, 3'/1a, 1a/2a, and 4'/3a, where incomplete or complete archeopyle sutures may also be developed along the lateral margin of the (anterior) intercalary and dorsal apical plates. This implies that a transverse archeopyle represents a slit-like opening between the apical and anterior intercalary series. The term adnate was introduced by Evitt (1985) to describe an operculum that remains attached to the cyst and is not completely surrounded by an archeopyle suture. In contrast, a free operculum is completely surrounded by the archeopyle suture. Matsuoka (1988) noted that this implies that *a free operculum may* remain locally adherent to the rest of the cyst along a portion of the suture, which fails to open in a particular instance. Therefore, Matsuoka (1988) considered the transverse type identical to an adnate archeopyle. Evitt (1985) did not provide a term that allows to distinguish between archeopyles that are characterized by opercula that differ in their degree of attachment. Therefore Matsuoka (1988) proposed the use of the term theropylic (Greek, *thairos* + *pyle*; hinge of a door + gate) for opercula that are adnate in contrast to opercula that are free, but that may be adherent, for which he provided the term saphopylic (Greek, saphes + pyle; distinct +gate). In further contrast, the term chasmic simply implies that the archeopyle is slit-like and the archeopyle suture does not reflect any plate boundary.

3. Systematic paleontology

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al. 1993 Class DINOPHYCEAE Pascher 1914

Order PERIDINIALES Haeckel 1894

Family PROTOPERIDINIACEAE Bujak and Davies 1983 ex Bujak and Davies 1983 in Fensome et al. 1998, nom. cons. prop.

Genus Malvinia gen. nov.

Etymology: After the Islas Malvinas, the archipelago close to DSDP Site 511.

Type: Malvinia escutiana Plate I, 1–3

Diagnosis: Non-cavate spherical peridinioid dinocyst of intermediate size. Tabulation reflected by faint sutural ridges. *Malvinia* has a theropylic archeopyle, representing a split along the margins of the anterior intercalary- and apical series. All plates remain attached to the cyst. The cingulum consists of three plates and a small transitional plate. The anterior part of the cyst always appears distorted as a consequence of the archeopyle type.

Description: Proximate subsphaerical cyst of intermediate size. The cyst wall consists of one relatively thin layer. Tabulation is marked by faint parasutural ridges and reflects a protoperidinioid pattern (pr, 4, 3a, 7, 1t, 3c, 5, 2). The archeopyle is interpreted as a theropylic type

consisting of a straight split along the anterior margins of the anterior intercalary plates (1a, 2a and 3a), which remain attached to the cyst along their posterior margins. The split extends between the anterior intercalary plates (1a with 2a and 2a with 3a) and between the anterior intercalary- and apical plates (1a with 2 and 3, 2a with 3 and 3a with 3 and 4) as shown in Fig. 3. This type of archeopyle typically causes the anterior part of the cyst to collapse, which is therefore found strongly distorted.

Differential diagnosis:

Echinidium Zonneveld 1997 is a protoperidinioid genus with a theropylic archeopyle, it differs from Malvinia in having brown pigmentation and spinose ornamentation. Dubridinium Reid 1977 has a theropylic archeopyle but differs from Malvinia in being cavate and its tabulation reflects the cingulum only. Subtilisphaera Jain and Millepied 1973 has a transverse archeopyle and incomplete parasutures along individual anterior intercalary plates. Algidasphaeridium Matsuoka and Bujak 1988 differs from Malvinia in having a chasmic archeopyle. Malvinia differs from Islandinium Head et al. 2001, which has a saphopylic archeopyle with loss of the apical series (i.e. 2, 3 and 4). Cryodinium Esper and Zonneveld 2002 is a round brown cyst with a fully reflected tabulation on the epi- and hypocyst, it primarily differs from Malvinia since in its archeopyle type, which is a combination intercalary type involving plates 1a and 2a. Brigantedinium Reid 1977, Lejeunecysta Artzner and Dörhöfer, 1978 and Selenopemphix Benedek 1972 are fossil genera of round, brown cysts related to extant Protoperidinium species that are non tabular and have a simple archeopyle formed by the detachment of the anterior intercalary plate 2a.

Phthanoperidinium Drugg and Loeblich 1967 is a fossil peridinioid dinoflagellate genus that includes subsphaerical forms with sutural ornamentation and a closely appressed endo- and periphragm. Typically an apical projection is present. Edwards and Bebout (1981) and Islam (1982) emended the genus to include different archeopyle types; I (2a), IP (2a and 4), 3I (1a–3a), 3IP (1a, 2a, 3a and 4) and 3I3P (1a–3a, 3–5). The distinct therophylic archeopyle type is characteristic for *Malvinia*. *Phthanoperidinium* has four roughly equally sized cingular plates and is therefore not considered protoperidinioid. An apical projection has not been observed in *Malvinia*.

Species: Malvinia escutiana sp. nov.

Forma T: Goodman and Ford, plate 6, figs. 14–16.

Holotype: Sample 511–03R 01W 72–73 cm, slide #1, England Finder (EF) reference: R30-4. Plate I, 1–3. Dimension: 41–45 µm.

Paratype: Sample 511–03R 03W 75–76 cm, slide #2 , EF reference: L25. Plate I, 4–5. Dimension: $42-44 \ \mu m$.

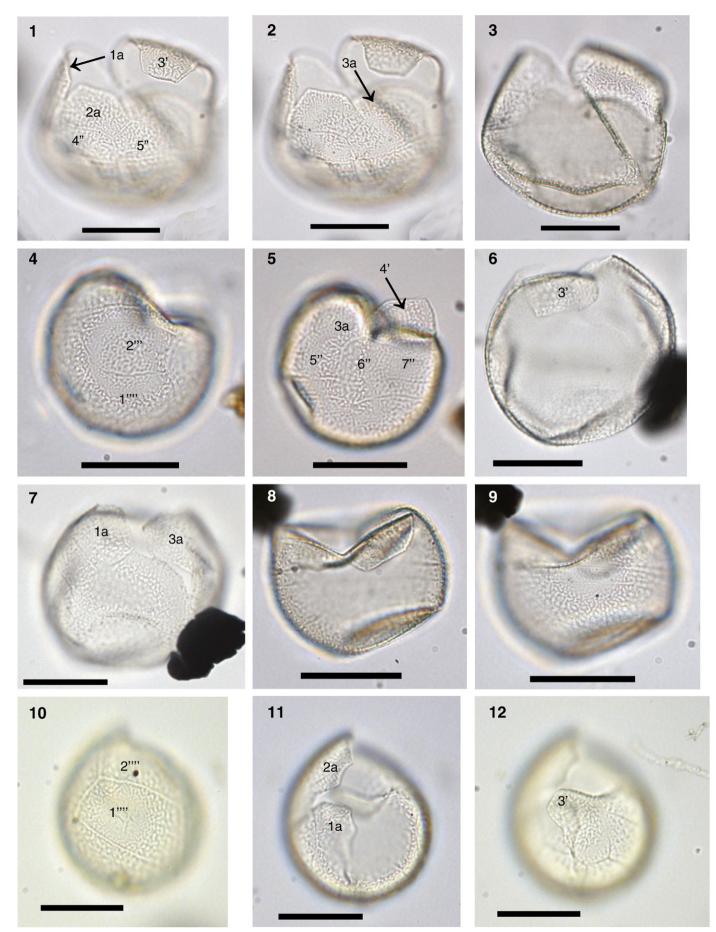
Stratum typicum: DSDP Leg 71, Site 511, Lithological Unit 2, Subunit 2a.

Derivation of name: Named in recognition of the scientific achievements of Dr. Carlota Escutia, marine geologist and geophysicist of the University of Granada (Spain), expert of the geology of the Antarctic margin.

Diagnosis: Proximate cyst of intermediate size with spherical outline, lacking horns or protrusions. The cyst wall is relatively thin, rugulate and appears to be composed of a single layer; an endo- and periphragm are not distinguishable. Tabulation is protoperidinioid (pr, 4, 3a, 7, 1t, 3c, 5, 2), indicated by low parasutural ridges. The archeopyle is theropylic between the intercalary and apical series. Typically, the dorsal-apical region displaced, generally in the direction of the empty cyst. Specimens are therefore exclusively found folded and distorted.

Dimensions: Average diameter around 45 μ m (n = 16, Holotype: 45–50 μ m).

Description: Peridinioid spherical cysts of intermediate size, lacking horns or protrusions. The outer wall surface of the cyst is rugulate, and exhibits faint parasutural ridges. These are difficult to discern under typical LM-magnification (Plate I) but reflect a protoperidinioid tabulation (pr, 4, 3a, 7, t, 3c, 5, 2) under SEM-



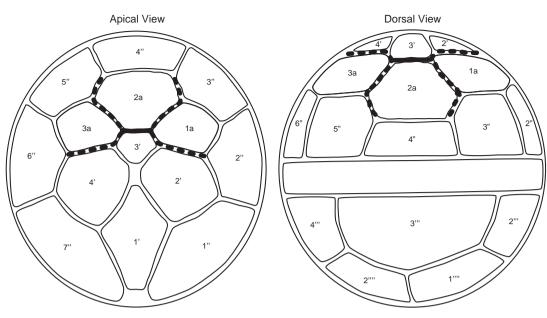


Fig. 3. Schematic representation of the anterior and dorsal side of *Malvinia escutiana*. Thick dotted lines indicate the ruptures that constitute the theropylic archeopyle. Intercalary plate 2a typically folds into the empty cyst. The apical plates 2 – 4 are generally displaced. The intercalary plates 1a and 3a remain in position.

magnification (Plate II). A small, preapical plate (pr) is clearly distinguishable on SEM images (Plate II, 1 and 3) but is not discernable on LM specimens. Plate 1 is characteristically symmetric, as is typical in peridinioid dinoflagellates. The sulcal area (Plate II, 2) consists of one anterior plate (as), a right (rs) and a left (ls) sulcal plate and a posterior (ps) plate. The cingulum is divided on the ventral face with a small sulcal-cingular transitional plate (t). The plates 1c and 3c extend only along the ventral face and the cingulum on the dorsal face consists of a single wide plate (2c) (Plate II, 2), this is characteristic for the Protoperidiniaceae family. The archeopyle is often difficult to discern as result of folding and is theropylic. Parasutural splits occur along the anterior margins of the anterior intercalary plates (1a, 2a and 3a), which remain attached to the cyst (Plate I, 1, 2, 5, 7 and 11). Such splits also occur along the parasutures between the anterior intercalary plates 1a with 2a and 2a with 3aand between apical series (1a with 2 3, 2a with 3 and 3a with 3 and 4). This generally leads to the folding of plate 2a and 3 (Plate II, 1) and displacement of the apical area (Plate I, 1–2; Plate II, 3).

Stratigraphic distribution: At Site 511, the lowest occurrence of *Malvinia* escutiana is in Sample Core 12R, Section 02 W, 115–117 cm. This level corresponds to an ~1.5 increase in foraminiferal δ^{18} O (Houben et al., submitted for publication; see also Liu et al., 2009), interpreted to represent the Oi-1 isotope shift in the earliest Oligocene (see, e.g., Coxall and Pearson, 2007). This isotopic shift is dated as 33.7 Ma following the timescale of Gradstein et al. (2004). At Site 511 *M. escutiana* initially occurs sporadically up to Core 6R to occur consistently above it and even becoming quite abundant (~20% relative abundance) in Core 4R and 3R (~32 Ma). The range top of *M. escutiana* is at least younger than 31.5 Ma at DSDP Site 511 (Fig. 2; Houben et al., submitted for publication).

Geographic distribution: Malvinia escutiana has exclusively been recorded in the Southern Ocean, that is from DSDP Sites 511 and

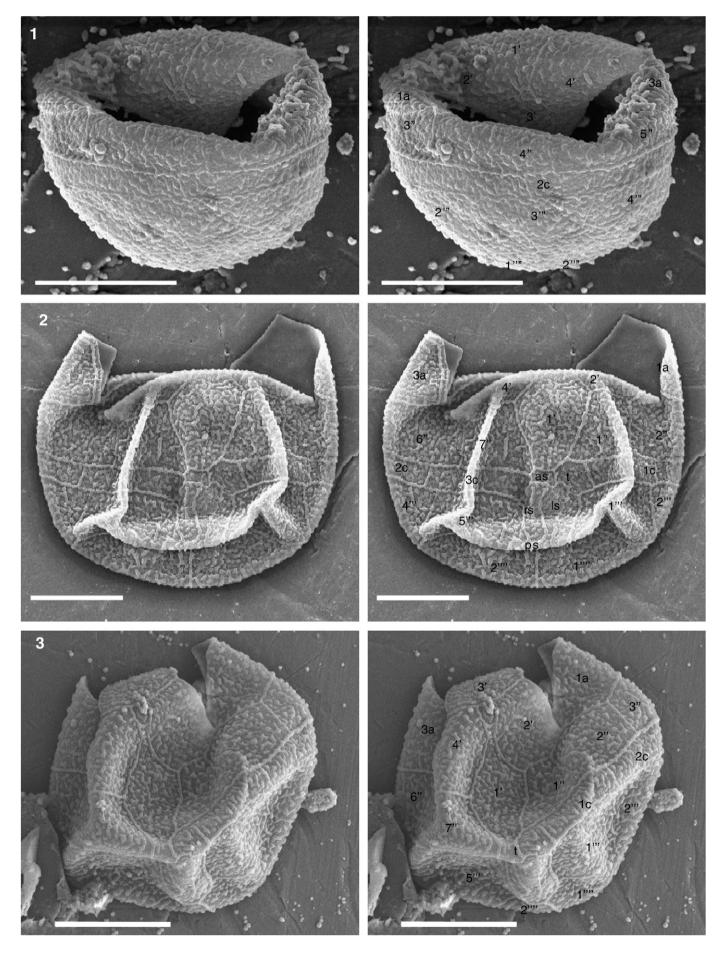
513 (Goodman and Ford, 1983, Falkland Plateau) and from ODP Sites 693 and 696 (Mohr, 1990, Weddell Sea, early Oligocene). It has also been recorded from ODP Site 739 (P.K. Bijl, 2010 pers. obs., Prydz Bay).

4. Discussion

Potential ambivalence around the chronostratigraphic position of the FO of Malvinia escutiana at DSDP Site 511 may arise from the limited core recovery. M. escutiana first appears in samples from Core 12R, which only consists of two sections of 1.5 m long. The underlying Core 13R only has one section recovered and Core 14R had no recovery (Ludwig et al., 1980). The interval between Core 15R and Core 12R straddles the critical plateau EOT phase characterized by relatively stable δ^{18} O values, between the precursor (EOT-1) and Oi-1 (Houben et al., submitted for publication). Within this interval, M. escutiana has not been recorded. Other records with a relatively complete upper Eocene such as those of the Tasman region (ODP Sites 1168 and 1172, Brinkhuis et al., 2003a,b; Sluijs et al., 2003) are devoid of *M. escutiana* (re-evaluated for this study). Chronostratigraphic calibrations of other sequences where *M. escutiana* has been recorded are based on relatively crude biostratigraphic- or preliminary considerations. For the Maud Droning Land record where M. escutiana has been recorded as Forma T of Goodman and Ford 1983 (ODP Site 693 Hole A core 40R and ODP Site 693 Hole B core 19R), an early Oligocene age was derived based on nannofossil and diatom biostratigraphy (Mohr, 1990, and references therein). At ODP Site 969, at the South Orkney Microcontinent Forma T of Goodman and Ford 1983 was recorded together with an otherwise typical Eocene dinocyst assemblage composed of classic endemic peridinioid taxa such as Vozzhennikovia apertura and Deflandrea antarctica (Mohr, 1990) and typical late Eocene taxa encountered in the Tasman region as well like



Figs. 1–3.Holotype, dorsal view (sample 511 – 03R 01W 72–73 cm, slide 1, EF Reference: R30). 1–2: Upper focus, note the *in-situ* intercalary plates 1 a and 2a and the
dislocation of apical plate 3 . 3: Lower focus, note the folding of the thin wall on the hypocyst.Figs. 4–5.Paratype, right lateral view (sample 511 – 03R 01W 72–73 cm, slide 1, EF Reference: R30–4). 4: Lower focus. 5: Upper focus.Figs. 6–7.Anterior view (sample 511 – 06R 03W 77–81, slide 1, EF Reference S20–4). 6: Upper focus, note that the apical plate 3 is dislocated arising above the anterior
part of the cyst. 7: Middle focus, note that the intercalary plates 1 a and 3a are in position, plate 2 a likely collapsed in the direction of the empty cyst.Figs. 8–9.Oblique lateral view (sample 511 – 03R 01W 72–73, slide 1, EF Reference R30-4). Note the folding of the anterior part of the cyst.Figs. 10–12.Anterior view (sample 511 – 03R 01W 72–73, slide 1 , EF Reference R20-2). 10: Upper focus. 11: Middle focus, anterior part in focus. 12: Lower focus, note that
the apical plates are splitted out from the anterior intercalary plates and plate 3 in dislocated above the dorsal anterior part of the cyst.



Turbiosphaera filosa and *Batiacasphaera compta* (Mohr, 1990, see also Sluijs et al., 2003). These may very well represent reworked late Eocene specimens that were re-deposited during the early Oligocene as a result of the initiation of glaciation and related erosion, as often seen in marginal marine Antarctic sequences (see e.g., Kemp, 1975; Guerstein et al., 2008).

Although not recognized in earlier work at ODP Site 739, Prydz Bay (e.g., Truswell, 1991), *Malvinia escutiana* occurs from Core 39R onwards (P.K. Bijl pers. obs., 2010). This part of the record at ODP Site 739 had been assigned a late Eocene to early Oligocene age (Truswell, 1991 and references therein). An exceptionally well-preserved diatom assemblage recovered from Core 30R assigned an early Oligocene age (Barron and Mahood, 1993) to that horizon, well above Core 39R. Yet, all these records together suggest that *M. escutiana* indeed first occurred in the early Oligocene, likely in conjunction with Oi-1, rather than in the late Eocene.

We have re-evaluated material from Sites 1168-1172 around Tasmania drilled during ODP Leg 189 (Brinkhuis et al., 2003a,b; Sluijs et al., 2003) and confirmed the absence of Malvinia escutiana, also in the lower Oligocene. At Sites 1170, 1171 (South Tasman Rise) and 1172 (East Tasman Plateau), the lower Oligocene is barren of palynomorphs (Sluijs et al., 2003) so the absence of M. escutiana may be due to preservation. At Site 1168, however, located west of the Tasman Gateway, a relatively complete lower Oligocene sequence is recovered. Site 1168 was under strong influence of the low-latitude derived Proto-Leeuwin current, which is reflected in fully cosmopolitan dinocyst assemblages and the absence of Antarctic endemic taxa (Brinkhuis et al., 2003a; Huber et al., 2004; Stickley et al., 2004b; Bijl et al., 2011). M. escutiana likely represents an Antarctic endemic species as it has never been recorded in any high resolution studies across the EOT elsewhere, so this may explain its absence at Site 1168. Other Antarctic records spanning the early Oligocene, such as those from Cape Roberts and the Ross Ice Shelf (Hannah et al., 1997; Hannah et al., 2001) still require reevaluation considering the range of M. escutiana. Collectively, as yet, there are no indications that *M. escutiana* occurred prior to the Oi-1.

Perhaps remarkably, the distinct theropylic archeopyle of *Malvinia* has typically been recorded in protoperidinoid genera (*Dubridinium* and *Echinidinium*, see Zonneveld, 1997; Head et al., 2001; Esper and Zonneveld, 2002 and references therein) that originated in the Quaternary. Nonetheless, the appearance of *Malvinia escutiana* in conjunction with the onset of Antarctic glaciation in the early Oligocene leads us to speculate that the appearance of this morphology relates to specific conditions arising from glaciation; i.e. sea ice and/or increased (seasonal) upwelling. Apart from a few upper Miocene specimens of *Dubridinium* spp. (Guler, 2003), dinocysts with a theropylic archeopyle are not known from the remainder of the Oligocene and Neogene, although it should be noted that Antarctic dinocyst records are sparse for this time period.

Acknowledgements

The authors thank Statoil (A.J.P.H.), the Netherlands Organisation for Scientific Research (NWO), the LPP Foundation and Utrecht University (P.K.B.) for funding. The research leading to these results has received funding from the European Research Council under the European Community's Seventh Framework Program (FP7/2007-2013)/ERC Grant agreement no. 259627 to A.S. This study used samples provided by the Deep Sea Drilling Project (DSDP). DSDP was sponsored by the US National Science Foundation (NSF). We thank Natasja Welters, Leonard Bik and Jan van Tongeren for technical support. Steven M. Bohaty, Rob Fensome and Andrés Boltovskoy are thanked for helpful suggestions. We are grateful to Jörg Pross for his constructive review, which significantly improved this manuscript.

References

- Artzner, D.G., Dörhöfer, G., 1978. Taxonomic note: Lejeunecysta nom. nov. pro Lejeunia Gerlach 1961 emend. Lentin and Williams 1978 dinoflagellate cyst genus. Canadian Journal of Botany 56, 1381–1382.
- Barron, J.A., Mahood, A.D., 1993. Exceptionally well-preserved early Oligocene diatoms from glacial sediments of Prydz Bay, East Antarctica. Micropaleontology 39, 29–45.
- Benedek, P.N., 1972. Phytoplanktonten aus dem Mittel- und Oberoligozän von Tonisberg (Niederrheingebiet). Paleontographica, Abteilung B 137, 1–71.
- Bijl, P.K., Schouten, S., Sluijs, A., Reichart, G.-J., Zachos, J.C., Brinkhuis, H., 2009. Early Palaeogene temperature evolution of the southwest Pacific Ocean. Nature 461, 776–779.
- Bijl, P.K., Pross, J., Warnaar, J., Stickley, C.E., Huber, M., Guerstein, R., Houben, A.J.P., Sluijs, A., Visscher, H., Brinkhuis, H., 2011. Environmental forcings of Paleogene Southern Ocean dinoflagellate biogeography. Paleoceanography 26, PA1202. doi:10.1029/2009PA001905.
- Bohaty, S., Harwood, D.M., 2000. Ebridian and silicoflagellate biostratigraphy from Eocene McMurdo erratics and the Southern Ocean. In: Stillwell, J.D., Feldmann, R.M. (Eds.), Paleobiology and Paleoenvironments of Eocene rocks, McMurdo Sound East Antarctica, AGU Ant. Res. Ser., 76, pp. 99–159.
- Brinkhuis, H., Munsterman, D.K., Sengers, S., Sluijs, A., Warnaar, J., Williams, G.L., 2003a. Late Eocene-Quaternary dinoflagellate cysts from ODP Site 1168, off Western Tasmania. In: Exon, N.F., Kennett, J.P., Malone, M.J. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results Volume, 189. Available at http://www-odp. tamu.edu/publications/189_SR/105/105.htm.
- Brinkhuis, H., Sengers, S., Sluijs, A., Warnaar, J., Williams, G.L., 2003b. Latest Cretaceous– Earliest Oligocene and Quaternary Dinoflagellate cysts, ODP Site 1172, East Tasman Plateau. In: Exon, N.F., Kennett, J.P., Malone, M.J. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, Volume 189. Available at http://www-odp. tamu.edu/publications/189_SR/106/106.htm.
- Bujak, J.P., Davies, E.H., 1983. Modern and Fossil Peridiniineae. American Association of Stratigraphic Palynologists contributions Series, # 13: 203 pp.
- Bütschli, O., 1885. Erster Band. Protozoa. Dr. H.G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. C.F. Winter'sche Verlagsbuchhandlung, Leipzig und Heidelberg, pp. 865–1088.
- Coxall, H.K., Pearson, P.N., 2007. The Eocene–Oligocene Transition. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep-time perspectives on climate change: Marrying the signal from computer models and biological proxies: The Micropalaeontological Society Special Publication, 2, pp. 287–351.
- Coxall, H.K., Wilson, P.A., Pälike, H., Lear, C.H., Backman, J., 2005. Rapid stepwise onset of Antarctic glaciation and deeper calcite compensation in the Pacific Ocean. Nature 433, 53–57.
- DeConto, R.M., Pollard, D., 2003. Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO₂. Nature 421, 245–249.
- Drugg, W.S., Loeblich Jr., A.R., 1967. Some Eocene and Oligocene phytoplankton from the Gulf Coast, U.S.A. Tulane Studies in Geology 5 (4), 191–194.
- Edwards, L.E., Bebout, J.W., 1981. Emendation of *Phthanoperidinium* Drugg & Loeblich 1967, and a Description of *P. brooksii* sp. nov. from the Eocene of the Mid-Atlantic Outer Continental Shelf. Palynology 5, 29–41.
- Esper, O., Zonneveld, K.A.F., 2002. Distribution of organic-walled dinoflagellate cysts in surface sediments of the Southern Ocean (eastern Atlantic sector) between the subtropical front and the Weddell Gyre. Marine Micropaleontology 46, 177–208.
- Evitt, W.R., 1985. Sporopollenin dinoflagellate cysts: their morphology and interpretation. American Association of Stratigraphic Palynologists Foundation Monograph Series, 1, p. 333.
- Evitt, W.R., Lentin, J.K., Millioud, M.E., Stover, L.E., Williams, G.L., 1977. Dinoflagellate cyst terminology. Geological Survey Canada paper, pp. 24–76.
- Fensome, R.A., Taylor, F.J.R., Norris, G., Sarjeant, W.A.S., Wharton, D.I., Williams, G.L., 1993. A classification of modern and fossil dinoflagellates. Special papers in Paleontology, 7. Micropaleontology Press, p. 351.
- Fensome, R.A., Jansonius, J., Skog, J.E., 1998. Proposals to amend provisions regarding typification of the names of fossil plants. Taxon 47, 489–490.
- Fensome, R.A., MacRae, R.A., Williams, G.L., 2008. DINOFLAJ2, Version 1. American Association of Stratigraphic Palynologists Foundation, Data Series # 1. Available online: http://dinoflaj.smu.ca/wiki/Main_Page.

Plate II. Scanning Electron Microscope (SEM) pictures of Malvinia escutiana with interpretation of the tabulation (rightmost pictures). The scale bar is 20 µm.

Fig. 1. Dorsal view (sample 511 - 03R 02W 73-76 cm). Note the theropylic archeopyle leading to folding and collapse of plate 2a and the apical plates (2 - 4) into the empty cyst. Note the single cingular plate (2c) extending along the dorsal side of the cyst.

Fig. 2. Ventral view (sample 511 – 03R 02W 73–76 cm). The sulcal tabulation is clearly defined in this specimen. Note the antapical plates 1 and 2 . The intercalary plates 1a and 3a are *in-situ*. Note the small transitional (t) cingular plate on the ventral face of the cyst.

Fig. 3. Ventral anterior view (sample 511 – 03R 02W 73–76 cm) elucidating the apical plate arrangement, note the preapical plate and the theropylic archeopyle margin, keeping intercalary plates 1a and 3a *in-situ* and showing the collapse of the apical series.

- Galeotti, S., Coccioni, R., Gersonde, R., 2002, Middle Eocene–Early Pliocene subantarctic planktic foraminiferal biostratigraphy of Site 1090, Agulhas Ridge. Marine Micropaleontology 45, 357–381.
- Gombos, A.M., Ciesielski, P.F., 1983. Late Eocene to early Miocene diatoms from the southwest Atlantic. In: Ludwig, W.J., Krasheninnikov, V.A., et al. (Eds.), Init. Repts. DSDP, 71. U.S. Govt. Printing Office, Washington, pp. 583–634.
- Goodman, D.K., Ford, L.N.J., 1983. Preliminary dinoflagellate biostratigraphy for the middle Eocene to Lower Oligocene from the Southwest Altantic Ocean. In: Ludwig, W.J., Krasheninnikov, V.A., et al. (Eds.), Init. Repts. DSDP, 71. U.S. Govt. Printing Office, Washington, pp. 859-977.
- Gradstein, F.M., Ogg, J.G., Smith, A.G., 2004. A Geologic Time Scale. Cambridge
- University Press, Cambridge, UK. 589 pp. Guerstein, R., Guler, M.V., Williams, G.L., Fensome, R.A., Chiesa, J.O., 2008. Middle Palaeogene dinoflagellate cysts from Tierra del Fuego, Argentina: biostratigraphy and palaeoenvironments. Journal of Micropaleontology 27, 75-94.
- Guler, M.V., 2003. Quistes de dinoflagelados de la familia Protoperidiniaceae del Neogeno de la cuenca del Colorado, Argentina. Ameghiniana 40, 457-467.
- Haeckel, 1894. Systematische Phylogenie, Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammegeschichte, I. Systematische Phylogenie der Protisten und Pflanzen. Reimer, Berlin: XV: 400 pp.
- Hannah, M.J., Cita, M.B., Coccioni, R., Monechi, S., 1997. The Eocene/Oligocene boundary at 70° South, McMurdo Sound, Antarctica. Terra Antartica 4, 79-87.
- Hannah, M.J., Wrenn, J.H., Wilson, G.J., 2001. Preliminary report on early Oligocene and latest Eocene marine palynomorphs from the CRP-3 drillhole, Victoria Land Basin, Antarctica. Terra Antartica 8. 383–388.
- Head, M.J., Harland, R., Matthiessen, J., 2001. Cold marine indicators of the late Quaternary: the new dinoflagellate cyst genus Islandinium and related morphotypes. Journal of Quaternary Science 17, 621-636.
- Houben, A.J.P., Schouten, S., Bohaty, S., Sluijs, A. and Brinkhuis, H., submitted for publication. Stepwise temperature and environmental change associated with the Eocene-Oligocene Transition in the southwest Atlantic Ocean.
- Huber, M., Brinkhuis, H., Stickley, C.E., Doos, K., Sluijs, A., Warnaar, J., Schellenberg, S.A., Williams, G.L., 2004. Eocene circulation of the Southern Ocean: was Antarctica kept warm by subtropical waters? Paleoceanography 19, PA4026. doi:10.1029/ 2004PA001014.
- Islam, M.A., 1982. Archeopyle structure in the fossil dinoflagellate Phthanoperidinium. Review of Palaeobotany and Palynology 36, 305-316.
- Jain, K.P., Millepied, P., 1973. Cretaceous microplankton from Senegal Basin, NW Africa. 1. Some new genera, species and combinations of dinoflagellates. The Palaeobotanist 20, 22-32.
- Katz, M.E., Miller, K.G., Wright, J.D., Wade, B.S., Browning, J.V., Cramer, B.S., Rosenthal, Y., 2008. Stepwise transition from the Eocene greenhouse to the Oligocene icehouse. Nature Geoscience 1, 329-334.
- Kemp, E.M., 1975. Palynology of Leg 28 drill sites, Deep Sea Drilling Project. Initial Reports of the Deep Sea Drilling Project, 28, pp. 599-623.
- Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M., Pearson, A., 2009. Global cooling during the Eocene-Oligocene climate transition. Science 323, 1187-1190.
- Ludwig, W.J., Krasheninnikov, V., Basov, I.A., Bayer, U.L.F., Bloemendal, J.A.N., Bornhold, B., Ciesielski, P., Goldstein, E.H., Robert, C., Salloway, J.C., 1980. Tertiary and Cretaceous paleoenvironments in the southwest Atlantic Ocean: preliminary results of Deep Sea Drilling Project Leg 71. Bulletin of the Geological Society of America 91, 655-664.
- Macphail, M.K., Truswell, E.M., 2004. Palynology of Site 1166, Prydz Bay, East Antarctica. In: Cooper, A.K., O'Brien, P.E., Richter, C. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, 188. Available at http://www-odp.tamu.edu/publications/188_SR/ 013/013.htm.
- Marino, M., Flores, J.-A., 2002. Middle Eocene to early Oligocene calcareous nannofossil stratigraphy at Leg 177 Site 1090. Marine Micropaleontology 383-398.
- Matsuoka, K., 1988. Cyst-theca relationships in the diplopsalid group (Peridiniales, Dinophyceae). Review of Palaeobotany and Palynology 46, 95-122.

- Matsuoka, K., Bujak, J.P., 1988, Cenozoic dinoflagellate cysts from the Navarin Basin. Norton Sound and St. George Basin, Bering Sea: Bull. Fac. Lib. Arts, Nagasaki Univ., Nat. Sci. 29. pp. 1-147.
- Miller, K.G., Fairbanks, R.G., Mountain, G.S., 1987, Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Paleoceanography 2, 1-19.
- Miller, K.G., Browning, J.V., Aubry, M.P., Wade, B.S., Katz, M.E., Kulpecz, A.A., Wright, J.D., 2008. Eocene-Oligocene global climate and sea-level changes: St. Stephens Quarry, Alabama, GSA Bulletin 120, 34-53.
- Miller, K.G., Wright, J.D., Katz, M.E., Wade, B.S., Browning, J.V., Cramer, B.S., Rosenthal, Y., 2009. Climate threshold at the Eocene-Oligocene Transition: Antarctic ice sheet influence on ocean circulation. Geological Society of America Special Papers 452, 169-178.
- Mohr, B.A.R., 1990. Eocene and Oligocene sporomorphs and dinoflagellate cysts from Leg 113 drill sites, Weddell Sea, Antarctica. In: Barker, P.F., Kennett, J.R., et al. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, 113, pp. 595-612.
- Pascher, A., 1914. Über Flagellaten und Algen. Deutsche Botanische Gesellschaft, Berichte 32 136-160
- Pearson, P.N., Van Dongen, B., Nicholas, C.J., Pancost, R.D., Schouten, S., Singano, J.M., Wade, B.S., 2007. Stable warm tropical climate through the Eocene Epoch. Geology 35. 211-214.
- Pearson, P.N., Foster, G.L., Wade, B.S., 2009. Atmospheric carbon dioxide through the Eocene-Oligocene climate transition. Nature 461, 1110-1113.
- Reid, P.C., 1977. Peridiniacean and glenodiniacean dinoflagellate cysts from the British Isles. Nova Hedwigia 29, 429-463.
- Roberts, A.P., Bicknell, S.J., Byatt, J., Bohaty, S., Florindo, F., Harwood, D.M., 2003. Magnetostratigraphic calibration of Southern Ocean diatom datums from the Eocene/Oligocene of Kerguelen Plateau (Ocean Drilling Program sites 744 and 748).
- Palaeogeography, Palaeoclimatology, Palaeoecology 198, 145–168. Sluijs, A., Brinkhuis, H., Stickley, C.E., Warnaar, J., Williams, G.L., Fuller, M., 2003. Dinoflagellate cysts from the Eocene-Oligocene Transition in the Southern Ocean: Results from ODP Leg 189. In: Exon, N., Kennett, J.P. (Eds.), Proceedings of the Ocean Drilling Program, Scientific Results, Volume 189. Available at http://wwwodp.tamu.edu/publications/189_SR/104/104.htm.
- Stickley, C.E., Brinkhuis, H., McGonigal, K.L., Chaproniere, G.C.H., Fuller, M., Kelly, D.C., Nurnberg, D., Pfuhl, H.A., Schellenberg, S.A., Schoenfeld, J., Suzuki, N., Touchard, Y., Wei, W., Williams, G.L., Lara, J., Stant, S.A., 2004a. Late Cretaceous Quaternary biomagnetostratigraphy of ODP site 1168, 1170, 1171 & 1172, Tasmanian Gateway. In: Exon, N.F., Kennett, J.P., Malone, M.J. (Eds.), Proceedings of the Ocean Drilling Program, Volume 189. Available at http://www-odp.tamu.edu/publications/ 189_SR/volume/chapters/111.pdf.
- Stickley, C.E., Brinkhuis, H., Schellenberg, S.A., Sluijs, A., Röhl, U., Fuller, M., Grauert, M., Huber, M., Warnaar, J., Williams, G.L., 2004b. Timing and nature of the deepening of the Tasmanian Gateway. Paleoceonography 19, PA4027. doi:10.1029/ 2004PA001022
- Truswell, E.M., 1991. Palynology of sediments from Leg 119 drill sites in Prydz Bay, East Antarctica. In: Barron, J., Larsen, B., et al. (Eds.), Proceedings of the Ocean Drilling Program Scientific Results, 119. Ocean Drilling Program, College Station, TX, pp. 941-948.
- Villa, G., Fioroni, C., Pea, L., Bohaty, S., Persico, D., 2008. Middle Eocene-late Oligocene climate variability: calcareous nannofossil response at Kerguelen Plateau, Site 748. Marine Micropaleontology 69, 171-192.
- Wise Jr., S.W., 1983. Mesozoic and Cenozoic calcareous nannofossils recovered by Deep Sea Drilling Project Leg 71 in the Falkland Plateau Region, Southwest Atlantic Ocean. In: Ludwig, W.J., Krasheninnikov, V.A., et al. (Eds.), Init. Repts. DSDP, 71. U.S. Govt. Printing Office, Washington, pp. 481-550.
- Wrenn, J.H., Hart, G.F., 1988. Paleogene dinoflagellate cyst biostratigraphy of Seymour Island, Antarctica. Geol. Soc. America Memoires, 169, pp. 321-447.
- Zachos, J.C., Quinn, T.M., Salamy, K.A., 1996. High-resolution (104 years) deep-sea foraminiferal stable isotope records of the Eocene-Oligocene climate transition. Paleoceanography 11, 251–266.
- Zonneveld, K.A.F., 1997. New species of organic-walled dinoflagellate cysts from modern sediments of the Arabian Sea (Indian Ocean). Review of Palaeobotany and Palynology 97, 319-337.