

A new Eocene *Chiasmolithus* species: hypothetical reconstruction of its phyletic lineage

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Abstract *Chiasmolithus* is abundant in Southern Ocean Ocean Drilling Program Sites 689, 738 and 748, and consequently provides an opportunity to study, in detail, evolutionary lineages and investigate the biostratigraphic distribution of some of the species. In particular, in the Middle to Late Eocene, a new species, *Chiasmolithus eoaltus*, has been recognised and distinguished from *Chiasmolithus altus*. Quantitative analysis highlights a gap between the last occurrence of *C. eoaltus* in the Upper Eocene and the first occurrence of *C. altus* in the Lower Oligocene. The morphological similarity is probably the result of convergent evolution. Additionally, the evolutionary steps that mark the phylogenesis of *Chiasmolithus* species during the Middle Eocene to Late Oligocene were investigated. Biostratigraphic and morphometric data permit reconstruction of a hypothetical phylogenetic tree, delineated by speciation events: we hypothesise that *Chiasmolithus solitus* gave rise to *C. oamaruensis* and *C. eoaltus* between 40.69 and 38.34Ma (*Reticulofenestra reticulata* Nannofossil Zone), followed by the evolution of *C. altus* from *C. oamaruensis* between 33.97 and 32.49Ma (*Blackites spinosus* Nannofossil Zone).

A correlation between palaeoclimatic interpretations and the *Chiasmolithus* evolutionary tree underline that sea-surface temperature changes played a key role in the nannofossil evolutionary process, and suggest that phyletic gradualism, a recognised theoretical approach to evolutionary process, resulted from intraspecific variability subordinated to natural selection. This study represents, beyond the description of a new nannofossil species, confirmation of the neo-Darwinian concept of phyletic gradualism.

Keywords Calcareous nannofossils, *Chiasmolithus*, Eocene, Oligocene, evolution, phyletic gradualism, Southern Ocean

1. Introduction

The genus *Chiasmolithus* was erected by Hay *et al.* (1966) to include elliptical placoliths with a large central-opening, spanned by an X-shaped central-structure made of four arms. Gartner (1970) studied the species of the genus in order to determine phyletic relationships on the basis of the central-area structures. He determined the characteristics that distinguish the species: placolith size, number of elements in the distal shield, curvature of the elements, size of the central opening, shape of the cross-bars, presence/absence of accessory structures, and structure of the cross-bars. With these criteria, Gartner (1970) divided the genus into two groups: species with cross-bars made of calcite laths, and species with cross-bars composed of tabular calcite prisms. Perch-Nielsen (1985), similarly to Gartner (1970), separated the genus into two subgroups, and included *Chiasmolithus altus* in the group with cross-bars made of calcite laths.

Several quantitative evolutionary studies have been performed on the genus *Chiasmolithus* (Gartner, 1970; Romein, 1979; Perch-Nielsen, 1985), but only Firth & Wise (1992) proposed a phylogenetic lineage for *C. altus*, suggesting a link from *Chiasmolithus expansus* to *C. oamaruensis* to *C. altus*.

The evolutionary first occurrence (FO) of *C. altus* has been a matter for discussion among several authors, the age reported varying from the Middle Eocene (Firth & Wise, 1992) to the Early Oligocene (Perch-Nielsen, 1985; de

Kaenel & Villa, 1996). The different ages may arise from taxonomic problems, specifically, from the differing biostratigraphical distributions of species that have not yet been

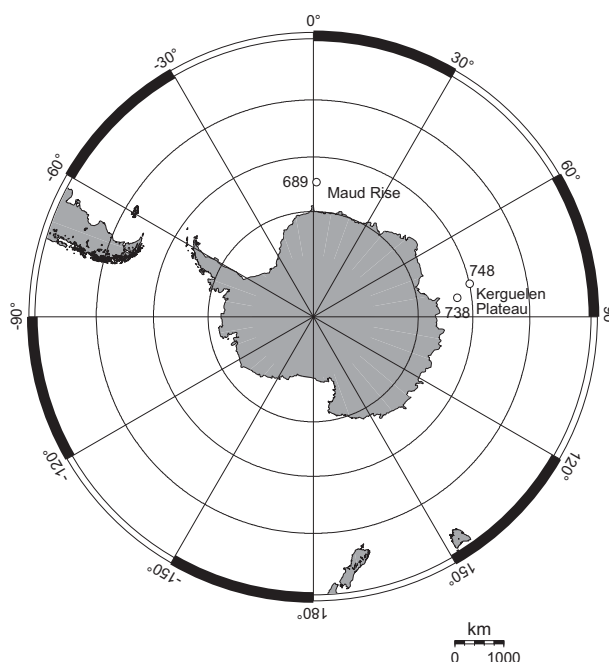


Figure 1: Location map of studied sites (modified after Villa & Persico, 2006). Leg 113, Hole 689D - 64°31.009'S/3°06.026'E; Leg 119, Hole 738B - 62°43'S/82°47'E; Leg 120, Hole 748B - 58°26.45'S/78°58.89'E

Zone (Wei & Thierstein, 1991)	Age	Studied samples	Stratigraphic ranges
<i>Reticulofenestra bisecta</i>	LATE OLIGOCENE	748B-10-2, 15-16cm 689D-7-7, 60-61cm	<i>C. altus</i>
<i>Chiasmolithus altus</i>			
<i>Reticulofenestra daviesii</i>	EARLY OLIGOCENE	748B-13-5, 20-21cm	<i>C. oamaruensis</i>
<i>Blackites spinosus</i>			
<i>Reticulofenestra oamaruensis</i>	LATE EOCENE	738B-5-6, 78-80cm	<i>C. eoaltus</i>
<i>Isthmolithus recurvus</i>			
<i>Chiasmolithus oamaruensis</i>	MIDDLE EOCENE	748B-17-4, 120-121cm 748B-17-6, 60-61cm 748B-17-6, 81-82cm	<i>C. solitus</i>
<i>Discoaster saipanensis</i>			
<i>Reticulofenestra reticulata</i>			
<i>Reticulofenestra umbilicus</i>			

Figure 2: Stratigraphic ranges of the involved species, shown against ages of sampled levels (Persico & Villa, 2004; Villa *et al.*, subm.). Nannofossil biozonation after Wei & Thierstein (1991), with basal boundaries of the *Discoaster saipanensis* and *Chiasmolithus oamaruensis* Zones modified using new biostratigraphic datums (LCO *C. solitus* and FCO *C. oamaruensis*, respectively) from Site 748 (Persico & Villa, 2004; Villa *et al.*, subm.)

identified as distinct from one another.

Biometric studies have been reported by Backman (1980), Backman & Hermelin (1986) and Pujos (1987), concerning the taxonomic and evolutionary links between species of *Coccolithus* and *Reticulofenestra*. Recent studies have used a biometric approach to highlight relationships between the abundances of some morphotypes and particular palaeoenvironmental conditions (Bauman, 1993; Bollman, 1997; Knappertsbusch *et al.*, 1997; Henderiks & Renaud, 2001). Generally, these studies have focused on species with fairly simple morphologies, that is, elliptical

placoliths with a central perforation. In this paper, we study taxa with more complex morphology, where an X-shaped central-structure is the main changing taxonomic feature.

Previous studies (Perch-Nielsen, 1985; Firth & Wise, 1992) have underlined that the variable, high evolutionary rate of the morphologically heterogeneous genus *Chiasmolithus* is represented by an elevated number of FOs, 21 in the Palaeogene, of which 15 are in the Eocene (Perch-Nielsen, 1985), recognised in northern to southern high-latitudes (Firth & Wise, 1992). These widespread geographic distributions, coupled with high intraspecific variability, suggest that ecological pressures have likely generated populations that differ slightly from each other. A population is defined as a group of specimens belonging to the same species, and distributed in a defined geographic area (Odum, 1971). A population is characterised by intraspecific variability, within which morphotypes can be recognised. If such morphotypes can be determined to have discrete stratigraphic ranges, they may be useful as biostratigraphic tools. If isolation of the population is persistent, distinct new

species can originate.

Common to abundant, moderately well-preserved specimens of *Chiasmolithus* occur in Middle Eocene-Oligocene Southern Ocean sediments recovered at Ocean Drilling Program (ODP) Sites 738 (Florindo *et al.*, subm), 748 (Villa & Persico, 2006; Villa *et al.*, subm.) and 689 (Persico & Villa, 2004; Figure 1). These sites provide a good opportunity to study, in detail, morphology, temporal distribution, and the phyletic lineage of certain *Chiasmolithus* species.

Furthermore, at ODP Sites 738, 748 and 689, in an in-

terval representing part of the Middle-Late Eocene, we detected specimens with morphological features similar to those of *C. altus*, but with subtle differences in morphology and stratigraphic range, suggesting a distinct new species. Consequently, we performed a detailed study on the biometry of the *C. solitus-oamaruensis-altus* group, to determine the real stratigraphic distribution of *C. altus*, to verify the existence of a new species, and to suggest phylogenetic relationships between *C. altus*, *C. oamaruensis*, *C. solitus* and *C. expansus*.

2. Material and methods

Sample material from ODP Sites 748, 738 and 689 (Figure 1) was used for this study. Calcareous nannofossils from these sites were originally studied by Wei & Wise (1990) and Wei & Thierstein (1991), both at low resolution. High-resolution, quantitative analyses were later performed by Persico & Villa (2004), Villa & Persico (2006) and Villa *et al.* (subm.). For this work, we used the same slides as were used for these previous studies, prepared using the settling technique described by de Kaenel & Villa (1996), at 10cm intervals from each core. All samples analysed were from a fixed quantity of sediment (2mm³). Species abundances were counted in the light microscope (LM) at 1250x magnification.

Samples were selected firstly on the basis of the abundance of *Chiasmolithus* spp., and secondly on best preservation (specimens with complete central cross-bars). The recorded poor preservation of nannofossils at the Eocene/Oligocene boundary is the reason for the lack of studied samples in this time-interval (Figure 2). To compensate for this, we used a mixture of samples from three areas in the Southern Ocean, to avoid the influence of local variability on the morphometric data.

The primary aim of this study was to apply the precise morphological values of *Chiasmolithus altus* to specimens with an *altus*-like morphology from the Middle-Late Eocene, in order to prove that certain specimens differed enough from *C. altus sensu stricto* to constitute a new species, so that we could ultimately provide a more precise age for the FO of *C. altus*. In order to achieve this, we studied two disparate stratigraphic intervals, in which the two forms were believed (from previous, non-biometric studies) not to overlap, that is, the Middle-Upper Eocene (five samples) and the Lower-Upper Oligocene (three samples; Figure 2).

Biometric data was collected on *Chiasmolithus solitus*, *C. altus* and

C. altus-like specimens, while only morphological observations were made for *C. oamaruensis*. This is because of the latter's easily recognisable morphology, despite its high intraspecific variability. These three defined taxa were chosen because of the stratigraphic continuity between their ranges, which was essential for hypothesising phylogenetic relationships. *Chiasmolithus expansus* was excluded because it has a discontinuous distribution in the studied interval.

Micrographs of 90 specimens per species were taken, using a digital video camera (Scion Fire-wire Camera, Model CFW-1612C) mounted on a Zeiss Axioscope transmitting LM. The high-quality images were then measured with Scion Image software, written by Dr. Jeremy Young (Young *et al.*, 1996).

The recorded biometric parameters (shown in Figure 3) are: size (placolith length, *L*; placolith width, *l*), morphology of the central-area (central-opening length, *D*; central-opening width, *d*), and size of the central part of the cross (length of the central part of the cross, *a*; width of the central part of the cross, *b*).

Frequency histograms of placolith length (*L*) and placolith width (*l*) are correlated with the dispersion diagrams of the same parameters (Figure 4). The dispersion diagrams of the biometric measurements were plotted, showing the distribution of groups partly overlapping (Figure 5).

3. Results and discussion

3.1 Biometric results

Biometric analysis of *Chiasmolithus solitus* has underlined the small size and easily identifiable morphology of the

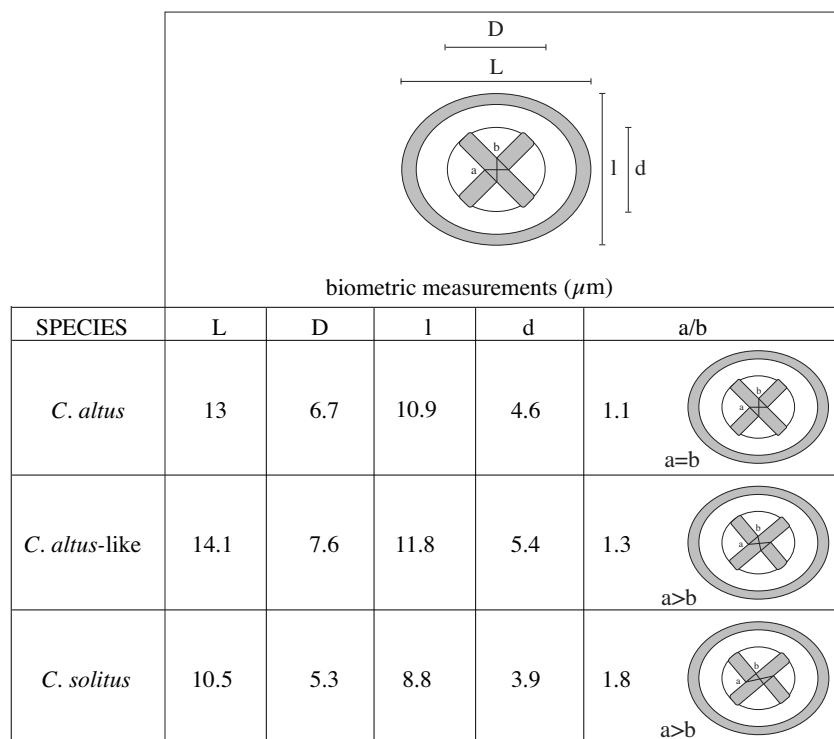


Figure 3: Biometric parameters and corresponding mean values of studied species of *Chiasmolithus*

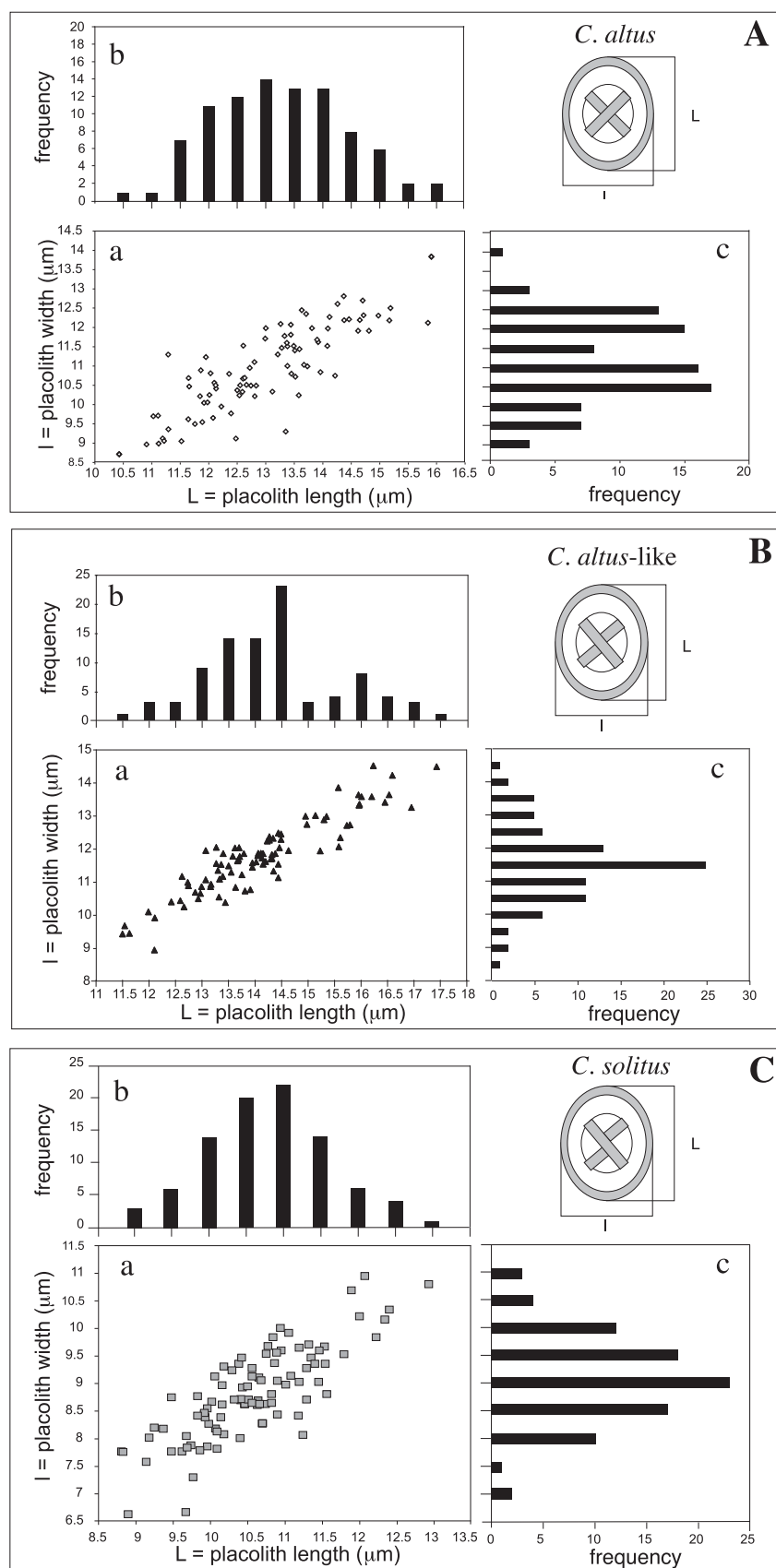


Figure 4: Distribution of placolith length and width of all *Chiasmolithus altus*, *C. altus-like* (*eoaltus*) and *C. solitus* specimens, measured from Middle to Late Oligocene samples. **A)** Placolith length vs. width. **B)** Histogram of placolith length frequency; **C)** Histogram of placolith width frequency. **Top right:** Placolith schematics illustrating morphometric measurements of length (L) and width (l)

cross-bars, which can vary from one bar being sinusoidal to two arms being non-aligned (Figure 4), as distinctive characteristics.

Figure 3 shows a comparison between the mean biometric values of the *Chiasmolithus altus*, *C. altus-like* and *C. solitus* specimens. The Middle to Upper Eocene *C. altus*-like specimens have biometric mean values of $L = 14.1\mu\text{m}$, $l = 11.8\mu\text{m}$, with $d = 5.4\mu\text{m}$ and $D = 7.6\mu\text{m}$ (Figure 3). The central cross is both thinner and larger than in the Oligocene *C. altus* specimens, within a large central-opening ($d/l = 0.46$). The central-area width (d), equivalent to half l , is an easily recognisable characteristic in the LM, therefore a distinctive taxonomical feature. Generally, the frequency histograms show a unimodal distribution of these features in the population. The L histogram of *C. altus*-like specimens highlights an imperfect unimodal distribution, which probably results from the poor preservation of some distal rims (Figure 4).

The specimens of *C. altus s.s.* from the Middle to Upper Oligocene (ODP Site 748) samples have mean values of $L = 13.00\mu\text{m}$ and $l = 10.9\mu\text{m}$, with a $d = 4.6\mu\text{m}$. The ratio $d/l = 0.42$ defines a central area proportionally smaller, with respect to the same parameter for the Middle Eocene specimens ($d/l = 0.46$). In order to facilitate comparison between the numerical data in the biometric analyses, reciprocal values (l/L , d/D and a/b) have been compared (Figure 5). The dispersion diagrams obtained show three areas, partially overlapping, the limits of which identify the morphometric characteristics of every species. In the l/L diagram (Figure 5A), the *C. solitus* group is quite separated from the other two taxa. These latter are assembled in two groups that partially overlap. This probably explains, with the overlapped distributions of the three species in the d/D diagram (Figure 5B), the reason for the lack of taxonomical separation of *C. altus* from *C. altus-like* specimens and consequent biostrati-

graphical confusion over the FO of *C. altus*. The mean values of the a/b data (Figure 5C) for the three taxa highlight the presence of three distinct groups, characterised by having different cross-bar morphology. The reciprocal comparison of the absolute measurements in the three species was made possible using the ratio a/b .

The mean value of these ratios are representative of the morphology of the central cross with $a/b = 1.1$ in *C. altus* (aligned arms), $a/b = 1.3$ in *C. altus*-like (two shifted arms), and $a/b = 1.8$ in *C. solitus* (two very shifted arms; Figure 3).

The three dispersion diagrams (Figure 5) demonstrate a morphological continuity between the three morphologies. However, the biostratigraphic distributions underline an evolutionary discontinuity between them. On the basis of the biostratigraphic discontinuity between *C. altus*-like forms and *C. altus*, and the different biometric measurements of the three species, we propose the erection of a new species, *Chiasmolithus eoaltus*, for the taxon with a distinct Middle-Upper Eocene distribution (see below).

3.2 Palaeoclimatic variations and evolution

The alternation of cold and warm climatic phases that preceded the Eocene/Oligocene boundary is reflected in nanofossil assemblage variations (Persico & Villa, 2004). Late Eocene sea-surface temperature (SST) fluctuations, triggered by palaeoceanographic changes, played a key role in speciation events that occurred relatively rapidly at different latitudes.

Particularly, SST changes, recognised on the basis of calcareous nanofossils from the Middle Eocene to the Late Oligocene (Villa *et al.*, subm.), underline the palaeoecological relationship between morphological variation within the genus *Chiasmolithus* and climatic change (Figure 6). *Chiasmolithus* has been hypothesised as a cool-water taxon (Wei & Wise, 1990; Bralower, 2002; Persico & Villa, 2004). Firth & Wise (1992) suggested that *Chiasmolithus altus* is a cold-water taxon, while *C. oamaruensis* is a cool-water taxon. At ODP Site 748, quantitative analysis allowed a more precise definition of the distribution and abundance patterns of

Chiasmolithus, and construction of a temperate-/warm-water taxa index (TWWT: Villa *et al.*, subm.). This index, plotted against this *Chiasmolithus* distribution data, suggests a link between species morphology and SST conditions.

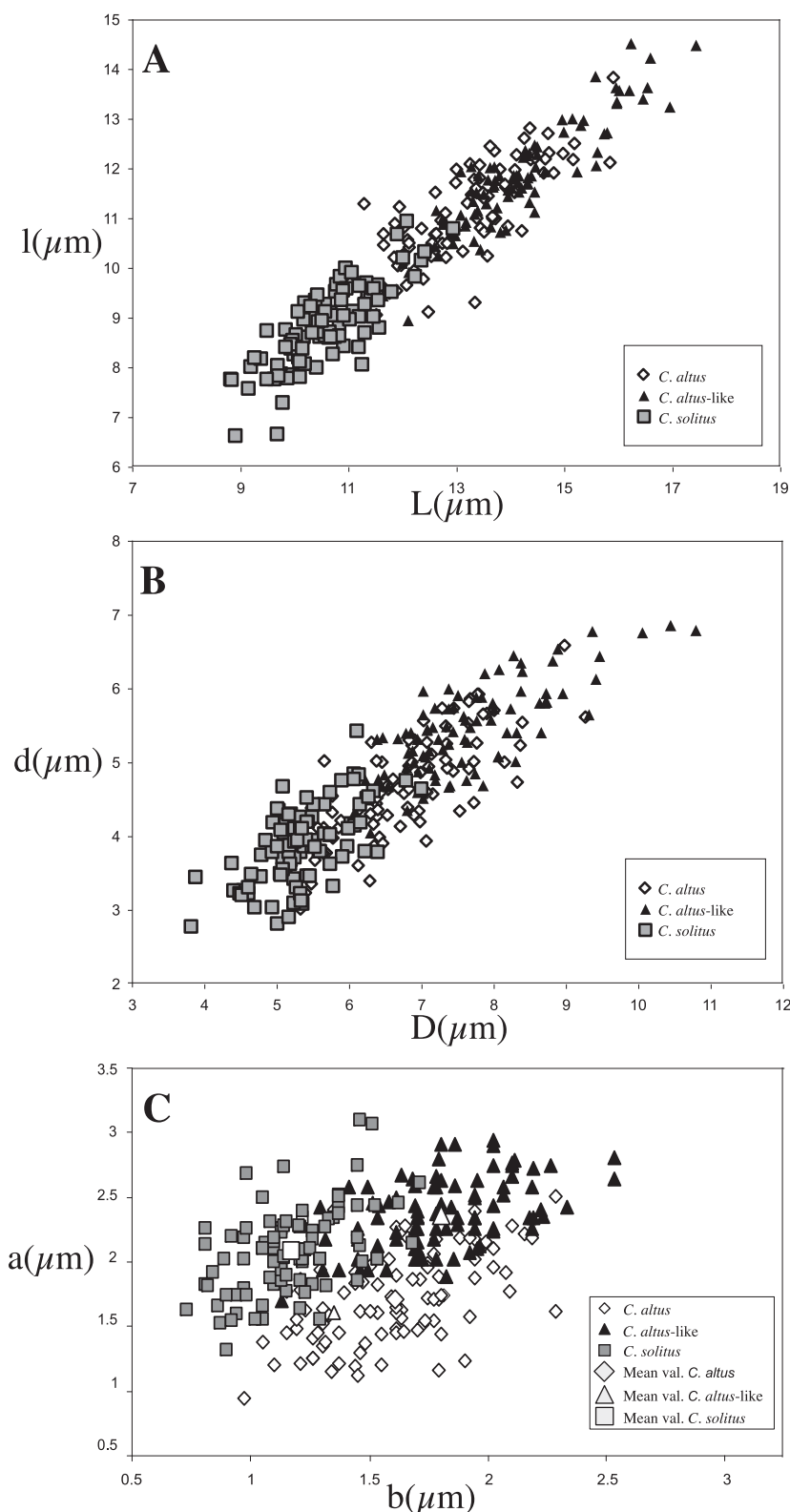


Figure 5: Distribution plots comparing the six morphological parameters measured from all specimens: **A)** l/L ; **B)** d/D ; **C)** a/b

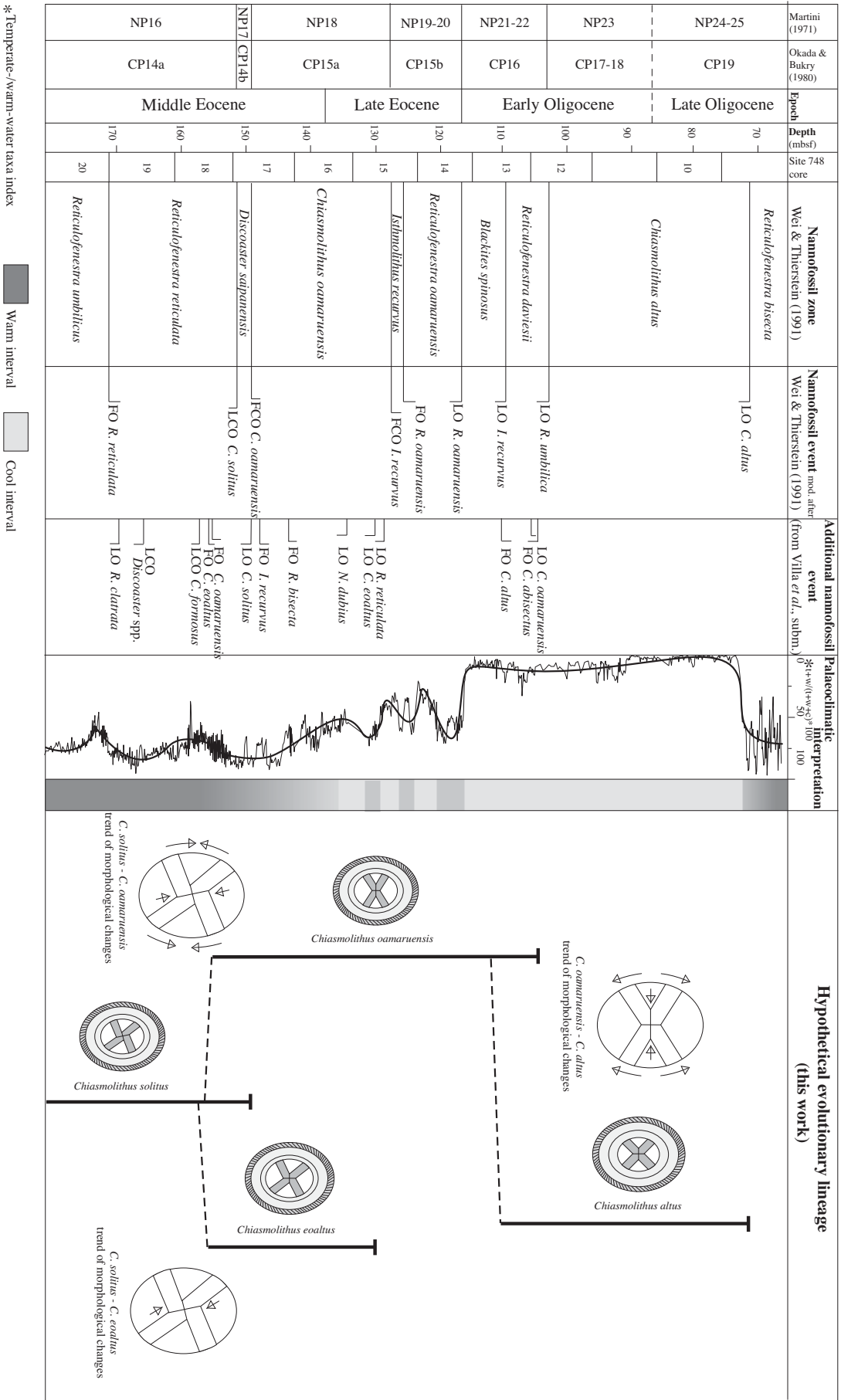


Figure 6: Biostratigraphic context and correlation between palaeoclimatic interpretations and hypothetical evolutionary lineage, incorporating hypothetical morphological changes in the cross-bars through time.
FO - first occurrence, LO - last occurrence, FCO - first common occurrence, LCO - last common occurrence

Chiasmolithus solitus goes extinct at a level of transition from warm- to cool-water conditions in the Middle Eocene, at the beginning of a cooling trend, which culminates at the Eocene/Oligocene boundary (Figure 6). Therefore, it may represent a warm-water morphology, within a cool-water genus. SST fluctuations thus may be the reason for the speciation process that resulted in the evolution of *C. oamaruensis* and *C. eoaltus* sp. nov.

C. oamaruensis lived from the late Middle Eocene to Early Oligocene. During this time, the TWWT index shows a general cooling trend, punctuated by several warming pulses. The persistence of this species through these cooling/warming episodes, and the elevated intraspecific variability occurring during its range, suggest that the morphological variability is derived from genetic recombination, linked to palaeoenvironmental changes, and thus *C. oamaruensis* may represent a transitional morphology, restricted to periods of fluctuating SSTs.

The extinction of *C. solitus* is preceded by the appearance of *C. eoaltus* sp. nov., interpreted as a cool-SST morphological adaptation, ranging from the Middle to Late Eocene, during an interval characterised by a continuous cooling trend. This trend is followed by a phase of cool/temperate alternation, with re-establishment of temperate conditions immediately before the Eocene/Oligocene boundary transition. We hypothesise that this palaeoenvironmental situation most likely caused the extinction of this species.

C. altus is interpreted as a cool-SST form. It originated in the Early Oligocene, during a phase of persisting cool-SST conditions, just after the Oi-1 event (Miller *et al.*, 1987), and went extinct at the base of the warming phase in the latest Oligocene.

There is no biostratigraphical continuity between *C. eoaltus* sp. nov. and *C. altus*. This implies that there is no direct phylogenetic relationship between the forms and, consequently, we suggest these forms are an example of evolutionary convergence, linked to cooling events that occurred at different times.

4. Conclusions

Biostratigraphic and biometric analyses have allowed the differentiation of *Chiasmolithus altus* (Early-Late Oligocene) from a new species, *C. eoaltus* sp. nov., which is characterised by a short stratigraphical range in the Middle-Late Eocene and by differences in the central cross, which is thinner and larger; the bars, which are not perfectly aligned at 90°; and the relative size of the central-opening (d/l), which is ~1/2 (0.46), compared to ~1/2.5 (0.42) in *C. altus*.

The distinction between these taxa allows us to provide more accurate FOs, and also suggests a different phylogenetic tree to those of Gartner (1970) and Firth & Wise (1992), which were based on morphological analysis and biostratigraphic data from a low-resolution sample suite. In the new tree, *Chiasmolithus solitus* gave rise to *C. oamaruensis* and *C. eoaltus* sp. nov., with *C. altus* arising

from *C. oamaruensis* (Figure 6).

We hypothesise that these evolutionary inceptions and relationships in *Chiasmolithus* are related to SST changes. *C. solitus* (Middle Eocene) represents a warm-water form, and thus last occurs at the beginning of a cooling trend. SST fluctuations most likely caused speciation from *C. solitus*, giving rise to *C. oamaruensis* and *C. eoaltus* sp. nov. We exclude, for biostratigraphic reasons, *Chiasmolithus medius* as a possible ancestor, because it goes extinct at the top of NP15 (Middle Eocene; Perch-Nielsen, 1985), while *C. eoaltus* sp. nov. and *C. oamaruensis* both have their FOs in the upper part of NP16 (Middle Eocene).

C. oamaruensis (Middle Eocene-Early Oligocene) represents a palaeoecological transitional form, characterised by high intraspecific variability, probably deriving from genetic recombination, linked to palaeoenvironmental change.

C. eoaltus sp. nov. (Middle to Late Eocene) is interpreted as a cool-SST form, representing a short phase of continuous cooling. Its extinction is linked to a phase of fluctuating SST cooling/warming and the temporary return of temperate conditions immediately preceding the Eocene/Oligocene boundary. *C. altus* (Early-Late Oligocene) is interpreted as a cool-temperature form, originating during stable, cool-SST conditions. The similar, yet distinct, morphologies of *C. eoaltus* sp. nov. and *C. altus* are thus an example of evolutionary convergence linked to cooling events.

The overlapping biometric data are a response to high intraspecific variability and underline the gradual evolutionary transition of some *Chiasmolithus* species. Stratigraphic sequences characterised by high sedimentation rates, continuous successions, and well-preserved assemblages, such as the Eocene-Oligocene records from Southern Ocean ODP sites, represent ideal conditions for evolutionary studies. Our data suggest a phyletic gradualism in the *Chiasmolithus* species, which remains indistinct in discontinuous and scarce stratigraphic records.

Taxonomical appendix

Chiasmolithus eoaltus sp. nov.

Plate 1, figs 1-12; Plate 2 Figs 1-6

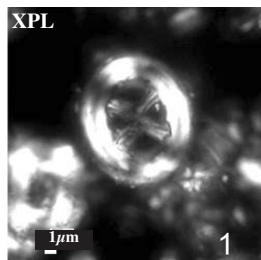
Derivation of name: From *Eocene*, referring to the distribution of the species, and *altus*, referring to the similarities in morphology to *C. altus*.

Diagnosis: Very large, elliptical species of *Chiasmolithus*, with a large central-opening surmounted by an X-shaped structure consisting of four arms. The width of the central opening is 0.5 of the coccolith's width.

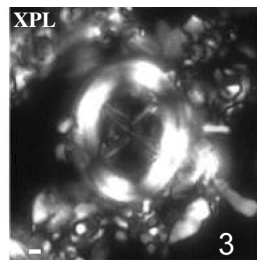
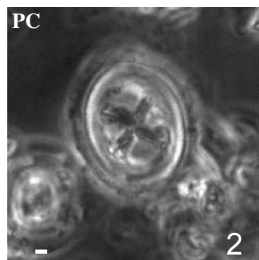
Description: Large, elliptical placolith characterised by an elliptical, and relatively large, central-opening, spanned by a delicate X-shaped structure, consisting of two straight and two curved arms, which meet about at 90°, and which form one straight and one sigmoidal bar. The length of the central part of the cross (*a* on Figure 3) varies from 1.6 to

Plate 1

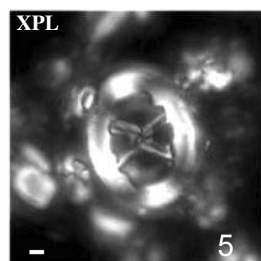
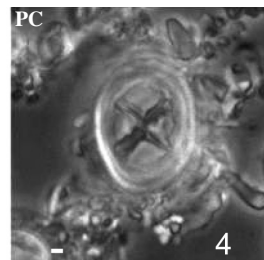
LM images of *Chiasmolithus*. XPL = cross-polarised light, PC = phase-contrast



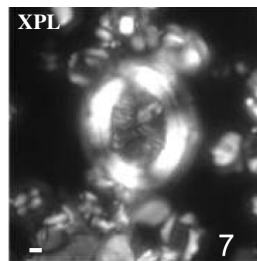
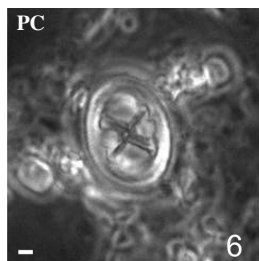
Chiasmolithus eoaltus (same specimen)
Sample ODP 748B-17-6, 60-61cm
Middle Eocene



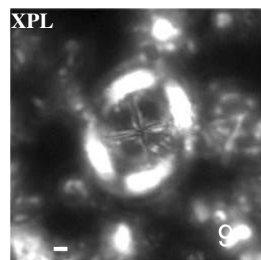
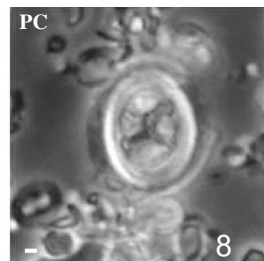
Chiasmolithus eoaltus (same specimen)
Sample ODP 748B-17-6, 60-61cm
Middle Eocene



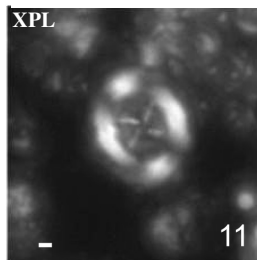
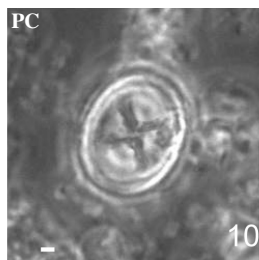
Chiasmolithus eoaltus (same specimen)
Sample ODP 748B-17-6, 81-82cm
Middle Eocene



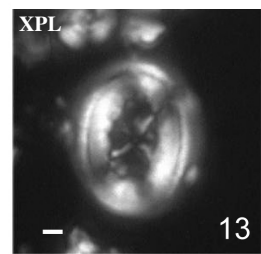
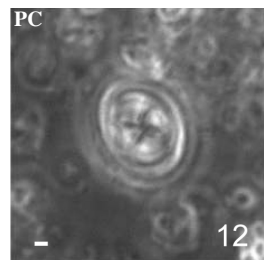
Chiasmolithus eoaltus (same specimen)
Sample ODP 738B-5-6, 78-80cm
Middle Eocene



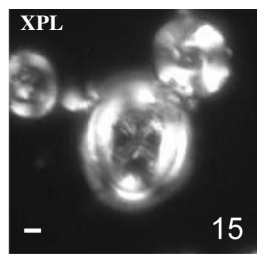
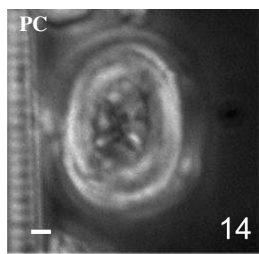
Chiasmolithus eoaltus (same specimen)
Sample ODP 748B-17-6, 81-82cm
Middle Eocene



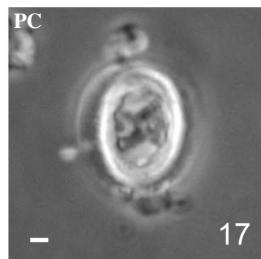
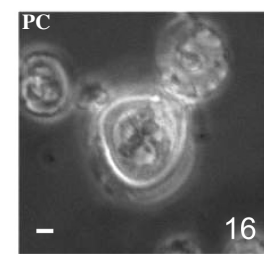
Chiasmolithus eoaltus (same specimen)
Sample ODP 748B-17-6, 81-82cm
Middle Eocene



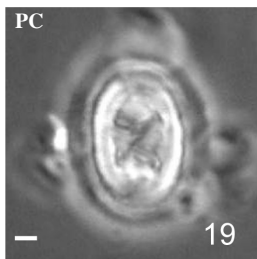
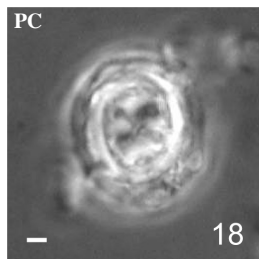
Chiasmolithus altus (same specimen)
Sample ODP 748B-10-2, 15-16cm
Upper Oligocene



Chiasmolithus altus (same specimen)
Sample ODP 748B-10-2, 15-16cm
Upper Oligocene



Chiasmolithus solitus (same specimen)
Sample ODP 748B-17-6, 60-61cm
Middle Eocene



Chiasmolithus solitus (same specimen)
Sample ODP 748B-20-3, 16-18cm
Middle Eocene

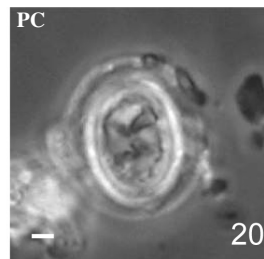
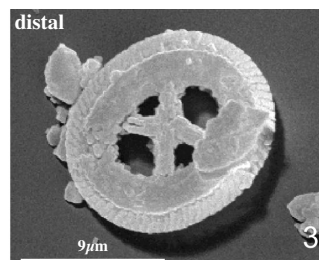
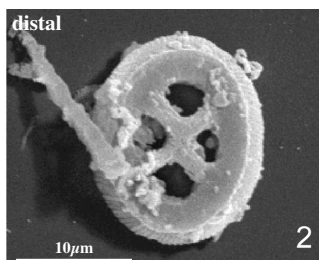
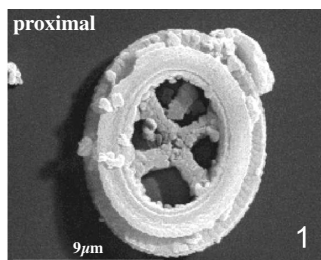
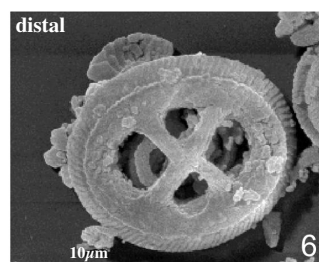
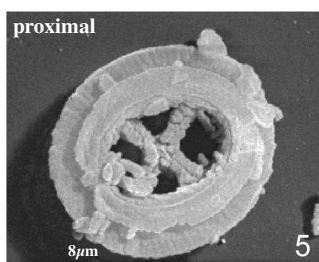
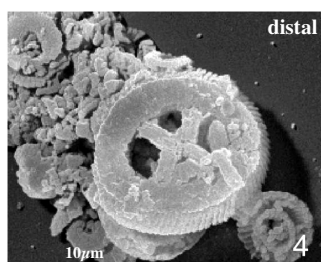


Plate 2

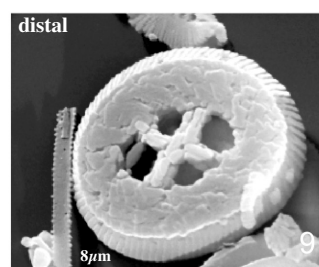
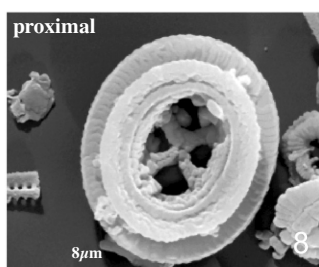
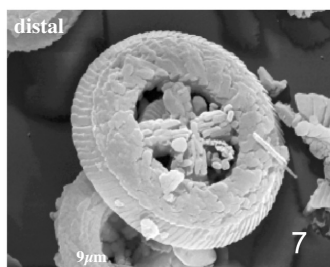
SEM images of *Chiasmolithus*



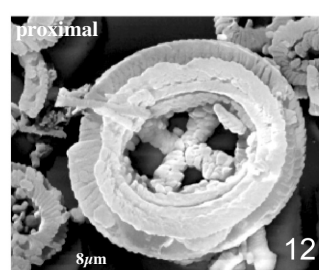
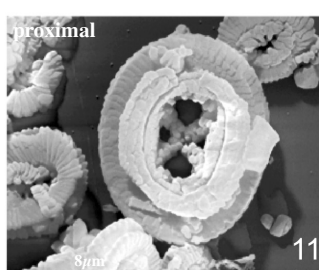
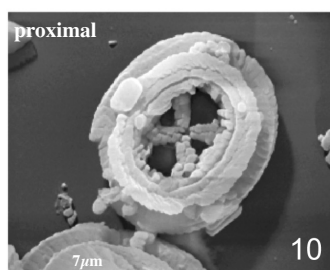
Chiasmolithus eoaltus
Sample ODP 748B-17-6, 60-61cm, Middle Eocene



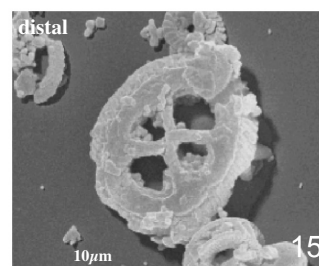
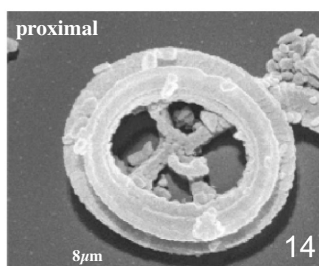
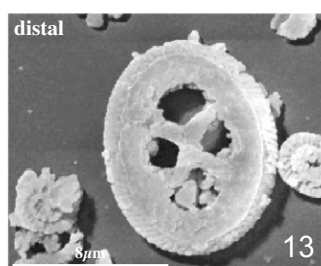
Chiasmolithus eoaltus
Sample ODP 748B-17-6, 60-61cm, Middle Eocene



Chiasmolithus altus
Sample ODP 748B-10-2, 15-16cm, Upper Oligocene



Chiasmolithus altus
Sample ODP 748B-10-2, 15-16cm, Upper Oligocene



Chiasmolithus solitus
Sample ODP 748B-20-3, 16-18cm, Middle Eocene

2.9µm. Measured along the short axis, the central-area opening is equal to one-half the total width of the coccolith. The rim is composed of about 80 elements and is faint in the outer portion in cross-polarised light.

Differentiation: *C. eoaltus* differs from *C. altus* in having a larger central-opening, a thinner rim, and a cross-bar structure not perfectly aligned (one bar is slightly sigmoidal). Compared to *C. medius* (length 7.7–8.6µm), *C. eoaltus* (11–18µm long) is larger, and the almost-symmetrical central-area structure is essentially composed of one straight bar and one slightly sigmoidal bar. The central-openings of *C. medius* and *C. solitus* are spanned by a pronounced sigmoidal bar. Also, the stratigraphic range of *C. medius* does not overlap with the range of *C. eoaltus*. *C. eoaltus* is distinguished from *C. expansus* (15–23µm) by its smaller size, and by the lack of the distal central-area crest. *C. expansus* is characterised by a large central-opening, spanned by symmetrical, hemispherical, X-shaped cross-bars (not sigmoidal).

Holotype: Pl.1, figs 1, 2 (slide and image curated in the University of Parma).

Length: 11 to 18µm.

Type level: Sample ODP Leg 120, Hole 748B-17-6, 60–61cm, Middle Eocene.

Type locality: ODP Hole 748B, Kerguelen Plateau, Southern Ocean.

Occurrence: *C. eoaltus* was recorded from Southern Ocean Middle to Upper Eocene sediments, where it co-occurs with *C. oamaruensis*.

Range: Restricted to NP16 (upper part) to NP18 (upper part), Middle to Upper Eocene.

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Elisabetta Erba and Bianca de Bernardi are thanked for the useful suggestions during the biometric analyses, and the Earth Science Department of the University of Milan for the technical support. We thank Eric de Kaenel, an anonymous reviewer and Jackie Lees for their valuable comments, which greatly improved the manuscript. In particular, Jackie Lees is acknowledged for her linguistic and editorial remarks.

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