

The Oligocene nannolith *Sphenolithus* evolutionary lineage: morphometrical insights from the palaeo-equatorial Pacific Ocean

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ABSTRACT – Changes in morphology within the biostratigraphically important Oligocene nannofossil lineage, *Sphenolithus predistentus*, *S. distentus* and *S. ciproensis* were investigated in carbonate sediments from the palaeo-equatorial Pacific Ocean Site 1218 in order to determine the nature of this evolutionary lineage. Using differences in their morphology and stratigraphical ranges, the aim of this study was to determine whether these taxa represent an anagenetic evolutionary lineage or a set of discrete species with overlapping stratigraphical ranges. A total of 1215 specimens from 12 samples were analysed morphometrically and the basal ratio, i.e. the ratio between the basal width and proximal cycle height, was identified as a key parameter for the study of this lineage. We conclude that *S. distentus* and *S. predistentus* are intergradational species forming an anagenetic lineage but that *S. ciproensis* is a discrete species which evolved relatively abruptly in the Late Oligocene. *J. Micropalaeontol.* 29(1): 17–35, May 2010.

KEYWORDS: *Sphenolithus*, evolutionary lineage, Oligocene, morphometry, ODP Leg 199 Site 1218

INTRODUCTION

A continuous Oligocene carbonate section was recovered at Ocean Drilling Program (ODP) Site 1218 (8° 53.38' N; 135° 22.00' W; water depth 4826 m) from the palaeo-equatorial Pacific Ocean (Lyle *et al.*, 2002; Wilson *et al.*, 2006). A well-constrained magnetostratigraphy and a high-resolution astronomically calibrated cyclostratigraphy have been established and integrated to provide an excellent age model for this Oligocene section (Lanci *et al.*, 2005; Pälike *et al.*, 2006). This age model was used for calibration of calcareous nannofossil bioevents (Blaj *et al.*, 2009). During this study problems emerged in the identification of sphenolith species used as biostratigraphical markers and so a morphometrical study was undertaken to resolve these issues. The main difficulty to investigate was to clearly distinguish between the transitional forms and the end-member morphotypes of the lineage.

The diversity of Oligocene calcareous nannofossil assemblages is relatively low (Bown *et al.*, 2004) (Fig. 1a), and the zonal marker events in the classical biostratigraphical zonations of Martini (1971) and Bukry (1978) are wider spaced than in other Cenozoic series (Fig. 1b). Hence, it is particularly important that Oligocene nannofossil events are clearly defined and well calibrated.

The genus *Sphenolithus* is particularly important for the subdivision of Oligocene time (Roth *et al.*, 1970). Index species belong to *S. predistentus*–*distentus*–*ciproensis* and transitional forms between these taxa (Huang, 1977; Olafsson & Villa, 1992). This group is well represented in the assemblage through the Late Oligocene of Site 1218 and thus is suitable for study of evolutionary changes and phenotypic variations of this lineage.

The main aim of this study is to clarify taxonomic concepts of these biostratigraphically important Oligocene sphenoliths by studying their evolutionary patterns in order to understand how phenotypic variations could be used for identifying end-members within this lineage. Previous authors (e.g. Bramlette &

Wilcoxon, 1967; Roth *et al.*, 1970; Haq, 1971) have agreed that three successive species can be distinguished, *S. predistentus*, *S. distentus* and *S. ciproensis*, and that they are directly related. However, there is no consensus whether this sphenolith lineage is a set of discrete species resulting from a sequence of cladogenetic events or whether it represents an anagenetic sequence of intergradational morphotypes (Fig. 2a).

An evolutionary lineage is a sequence of species that form a line of descent, in which each new species is the direct result of speciation from an immediate ancestral species. In this context, an intergrading (anagenetic) lineage refers to a series of species that grade into each other and have some overlap in their stratigraphical ranges (Fig. 2a (I)), i.e. at any one time only one biospecies is present but the continuous morphological change allows a set of chronospecies to be arbitrarily defined, each of which has a discrete stratigraphical range. The alternative possibility is that morphological variation has arisen as a result of a sequence of cladogenetic events and so there is a series of separate species that have distinct morphologies, no transitional forms and distinct stratigraphic ranges (Fig. 2a (II)).

MATERIAL AND METHODS

Morphometric measurements of *S. predistentus*, *S. distentus* and *S. ciproensis* specimens were carried out on a total of 12 samples (Table 1) containing abundant and well-preserved sphenoliths from different Oligocene stratigraphical intervals between 29.86 and 26.76 Ma at Site 1218 (Fig. 3; ten samples). This time interval was chosen as the morphologically similar sphenoliths, identified as *S. predistentus* and *S. distentus*, co-occurred within this interval and because of the presence of *S. ciproensis* in the upper part of the investigated interval. Two additional samples were selected below this interval to investigate the characteristics of 'transitional' forms within *S. predistentus*-dominated assemblages at 31.60 and 33.02 Ma,

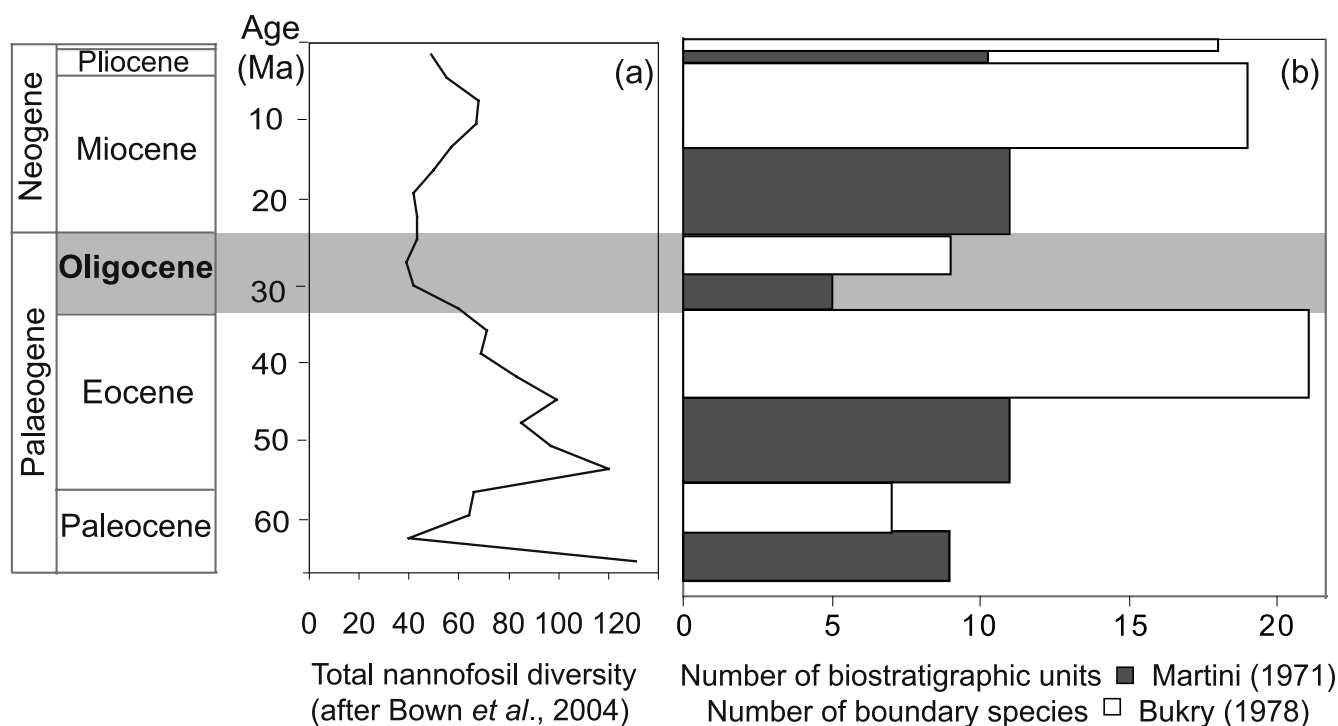


Fig. 1. Cenozoic nannofossil diversity data: (a) total nannofossil diversity (after Bown *et al.*, 2004); (b) the number of biostratigraphical units (Martini, 1971) and boundary species (Bukry, 1978) used in the standard Cenozoic zonation schemes. Note the low diversity and low number of biostratigraphic events/boundary species in the Oligocene (shaded interval).

which will be discussed separately (Fig. 3; see also Blaj *et al.*, 2009). Thus, our study focused on the problematic interval during which a range of morphotypes co-occur, as opposed to the earlier interval during which *S. predistentus* predominates or the subsequent interval when only *S. ciproensis* occurs.

All nannofossil analyses were performed on smear-slides prepared from raw sediment samples using standard techniques (Haq & Lohmann, 1976; Perch-Nielsen, 1985). Light microscope (LM) images were captured using a Zeiss Axioplan microscope equipped with a Leica DFC 280 digital camera, at 1600 \times magnification. The images were taken of sphenolith specimens viewed at 45 $^{\circ}$ to the polarizers; in this orientation the extinction line between the apical cycle and proximal cycle is clearly distinguishable. One hundred randomly selected specimens were imaged from each of the ten samples of the *S. predistentus*–*distentus*–*ciproensis* group (Appendix A) and measured. We have chosen to focus on measurements of the proximal cycle height and basal width (Fig. 2b), because the optical behaviour of the proximal elements cycle in polarized light provides the main criterion by which the *S. predistentus*–*distentus*–*ciproensis* lineage is taxonomically separated (Roth *et al.*, 1970), and also because the apical spine was often broken and/or missing.

Measurements of sphenolith proximal cycle height and basal width were made on calibrated digital images (1 pixel corresponds to 0.054 μ m) using the public domain program ImageJ (<http://rsb.info.nih.gov/ij/>). In order to increase the accuracy of the measurements, the statistical mean (Appendix A) of two measurements was used. Selected sphenolith samples were also studied by scanning electron microscopy using a Phillips XL30 Field Emission Scanning Electron Microscope (SEM) at the

Natural History Museum, London in order to investigate in more detail their morphological features.

TAXONOMIC REMARKS

Oligocene sphenolith evolutionary lineage

Sphenolithus is an extinct genus of nannoliths, having a long stratigraphical range (Paleocene–Pliocene) and commonly used in Cenozoic biostratigraphy and especially for the subdivision of the Oligocene (Bramlette & Wilcoxon, 1967; Roth *et al.*, 1970; Haq, 1971; Martini, 1971; Bukry, 1975; Okada & Bukry, 1980). The sphenoliths are conical nannofossils with a concave base, formed from cycles of elements radiating from a common centre. The species of the studied *Sphenolithus* lineage, i.e. *S. predistentus*, *S. distentus* and *S. ciproensis*, have a distinctive structure with an apical cone formed of two sub-parallel elements separated by a median suture and a single proximal cycle of radiating elements. In well-preserved specimens a long spine often extends from the tip of each apical cone element (e.g. Plate 1B, figs 21, 26). The apical cycle formed of two elements, the pair of apical spines, and the presence of only a single cycle of basal elements distinguish this set of species from other sphenoliths. Variation within these *Sphenolithus* species lead to them being one of the first calcareous nannofossil genera in which an evolutionary lineage was documented (Bramlette & Wilcoxon, 1967). The *S. predistentus*, *S. distentus* and *S. ciproensis* lineage evolved through the late Eocene and Oligocene. Most observations of this lineage are based on qualitative separation of the morphotypes, using their appearance in cross-polarized light. In this study, the criteria used to separate these morphologically

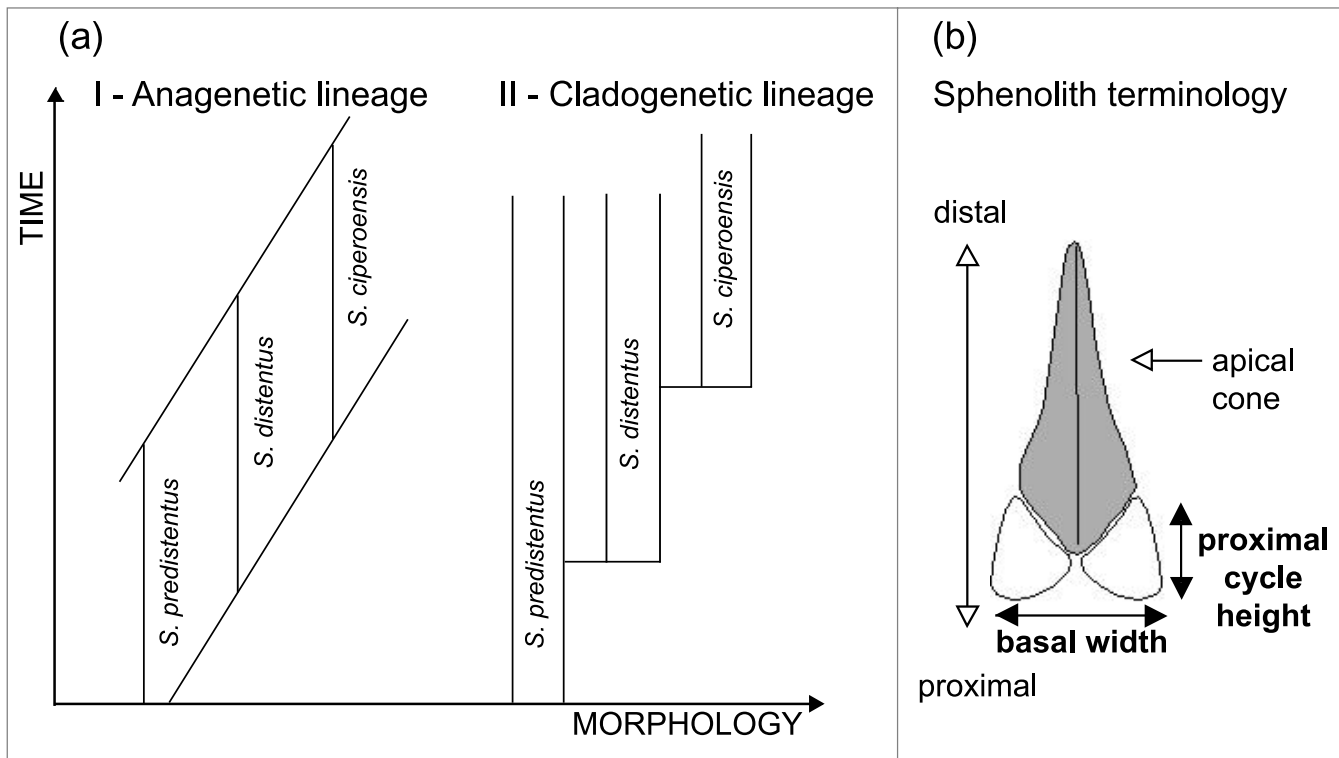


Fig. 2. (a) The Oligocene sphenolith lineage and two end-member hypotheses on the evolutionary nature of this lineage: (I) anagenetic lineage of intergradational chronospecies; (II) cladogenetic lineage with branching of discrete species. (b) Drawing of *Sphenolithus distentus* (from Young, 1998) showing morphological features investigated in this study (i.e. basal width and proximal cycle height). Shading indicates the portion of the sphenolith which is dark in cross polars in this orientation.

Sample #	Leg	Site	Hole	Core	T	Sc	Interval	rmdc	Age (P06)
1	199	1218	A	14	H	3	45	141.07	26.76
2	199	1218	B	15	H	1	135	146.57	27.08
3	199	1218	A	15	H	3	115	152.07	27.43
4	199	1218	B	16	H	1	145	157.47	27.84
5	199	1218	B	16	H	5	115	163.07	28.24
6	199	1218	B	17	H	2	15	167.83	28.54
7	199	1218	B	17	H	5	125	173.43	28.89
8	199	1218	C	11	H	5	65	179.17	29.20
9	199	1218	A	18	H	3	105	184.81	29.51
10	199	1218	C	12	X	5	65	189.93	29.86
11	199	1218	B	21	X	4	143	213.25	31.60
12	199	1218	A	23	X	3	65	232.39	33.02

Age is from Pälke *et al.* (2006; P06).

T, type; Sc, section; rmdc, revised meter composite depth.

Table 1. Samples used for the morphometric study of the Oligocene sphenoliths.

similar and most probably phylogenetically related species follow Roth *et al.* (1970) and Perch-Nielsen (1985).

Discrimination of the species is conventionally made with the sphenolith orientated at 45° to the polarization direction. In this orientation the apical cycle shows maximum birefringence and is clearly separated from the proximal cycle by dark extinction lines (Plate 1A). The great variability in this feature provides the main morphological criterion for distinguishing different taxa. In *S. predistentus* the extinction lines run straight across the specimen. In *S. distentus* the extinction lines are inclined, giving

a V-shaped appearance. In *S. ciproensis* the proximal elements are larger and separated from the spine by curved extinction lines, giving an X-shaped extinction figure (Perch-Nielsen, 1985).

While investigating Oligocene nannofossil biostratigraphy, several nannofossil workers (e.g. Roth *et al.*, 1970; Haq, 1971; Moran & Watkins, 1988; Okada, 1990; Olafsson & Villa, 1992) noticed difficulties in identifying the transitional forms from the end-members of the *S. predistentus*, *S. distentus* and *S. ciproensis* lineage. Transitional forms between *S. predistentus* and *S.*

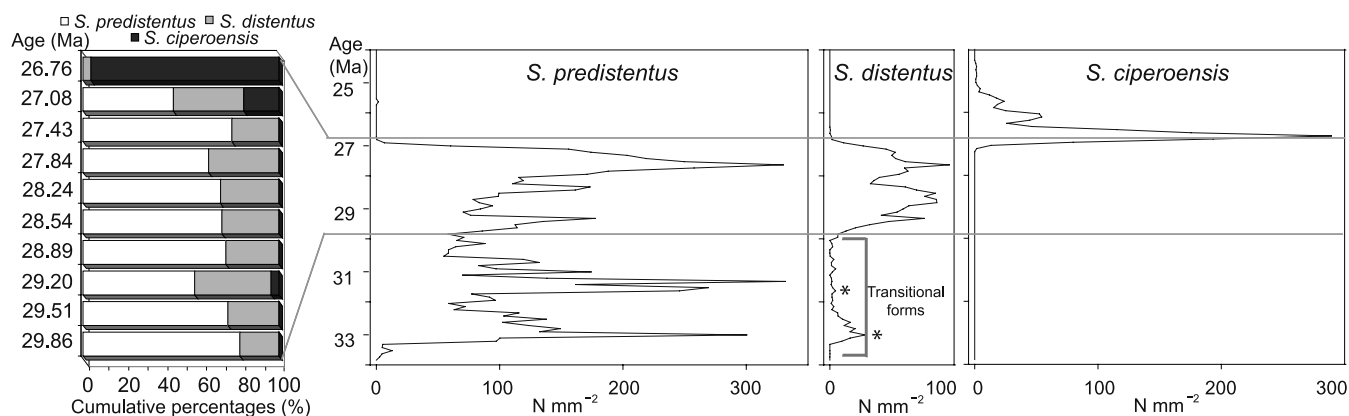


Fig. 3. Left panel: Abundance pattern as cumulative % of the 100 investigated sphenoliths in each of the ten Oligocene samples used for morphological measurements. Right panels: Abundances (as number of specimens per mm^2 of slide surface, N mm^{-2}) of *S. predistentus*, *S. distentus* and *S. ciproensis* as identified at Site 1218 (from Blaj *et al.*, 2009). Two additional samples investigated for ‘transitional’ forms of *S. predistentus* are indicated with asterisks.

distentus were also observed at Site 1218 (Fig. 3) (Blaj *et al.*, 2009). In these transitional forms, the extinction line between the apical and proximal cycle of the sphenolith varies: it is neither nearly straight, as in *S. predistentus*, nor clearly V-shaped, as in *S. distentus*, when viewed at 45° to the polarizers. *Sphenolithus predistentus* apparently grades into *S. distentus*. These intergrading forms between *S. predistentus* and *S. distentus* made placement of the lowest occurrence (LO) of *S. distentus* problematic (Blaj *et al.*, 2009). By contrast, the LO of *S. ciproensis* was easy to locate as specimens of *S. ciproensis* could be clearly distinguished from *S. distentus*, and no transitional forms between the two were observed at Site 1218 (Blaj *et al.*, 2009).

RESULTS AND DISCUSSION

Sphenolith morphological features in LM and SEM investigation

The sphenoliths were observed using both LM and SEM. The LM observations (Pl. 1A) confirmed that the majority of specimens could be consistently assigned to species based on their extinction pattern in polarized light: the extinction line between the apical and proximal cycle is straight in *S. predistentus* (Pl. 1A, figs 1–5), V-shaped in *S. distentus* (Pl. 1A, figs 6–10) and X-shaped in *S. ciproensis* (Pl. 1A, figs 11–15).

For SEM observations we used samples dominated by *Sphenolithus* and from each sample a suite of specimens was imaged (75 in total) in order to determine if additional structural differences between the species could be identified. The sphenoliths vary in shape and preservation; most observed specimens appear overgrown and to some extent broken; the apical spines are preserved in only a few specimens. The SEM investigation shows that the proximal cycle forms an open cone, which consists of 9 to 12 individual crystal elements in all investigated species, thus preventing the use of this criterion for taxonomic purposes, whereas the height of the proximal cycle elements varies between different species (Pl. 1B). In *S. predistentus* the individual elements are short, lie under the apical cone and have similar height around the entire proximal cycle (Pl. 1B, figs 16–20). This results in a straight extinction line between the

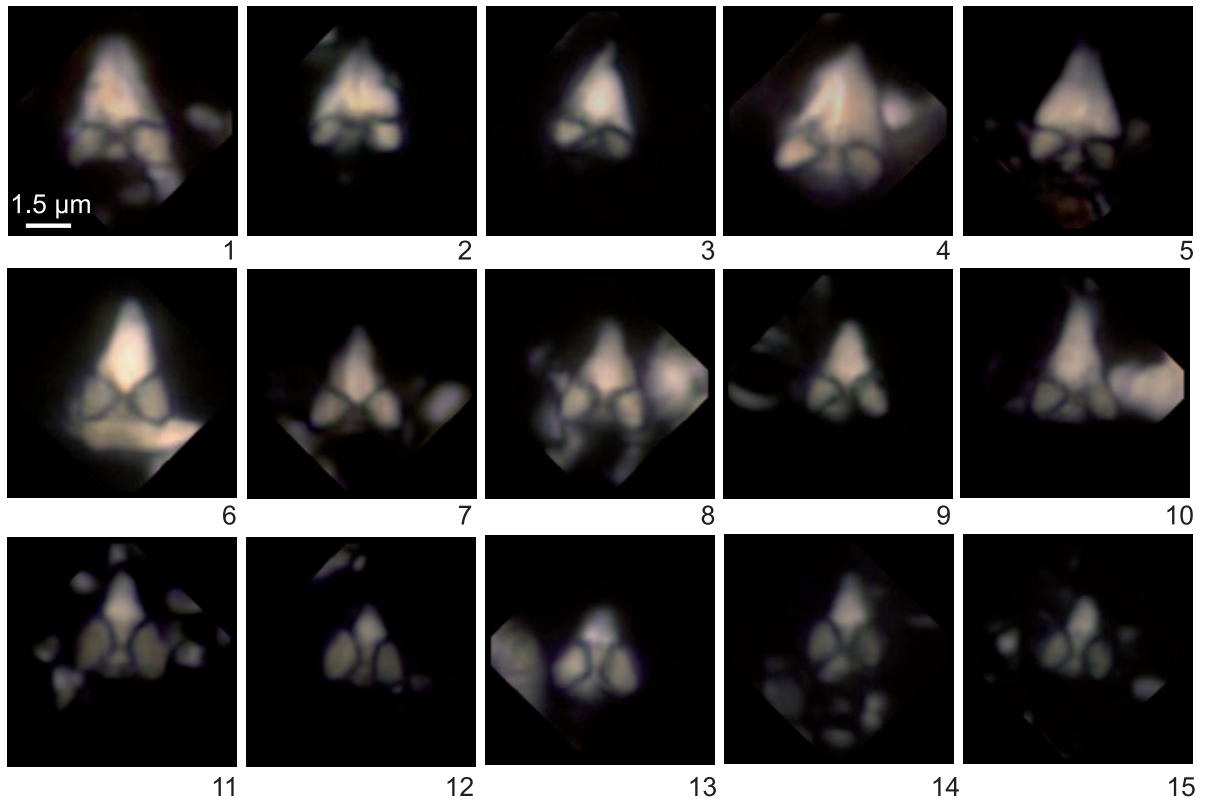
apical cycle and proximal column in LM. In *S. distentus* the height of the proximal cycle elements varies, typically with some higher elements (Pl. 1B, figs 21–28); this results in a V-shaped extinction line in LM. In *S. ciproensis* (Pl. 1B, figs 29–30) the proximal cycle shows even higher lateral elements, which results in an X-shaped extinction line of this species. The SEM investigations confirm that there are no additional morphological features to distinguish different species; indeed, they are harder to discriminate using the SEM than a LM.

Abundance patterns

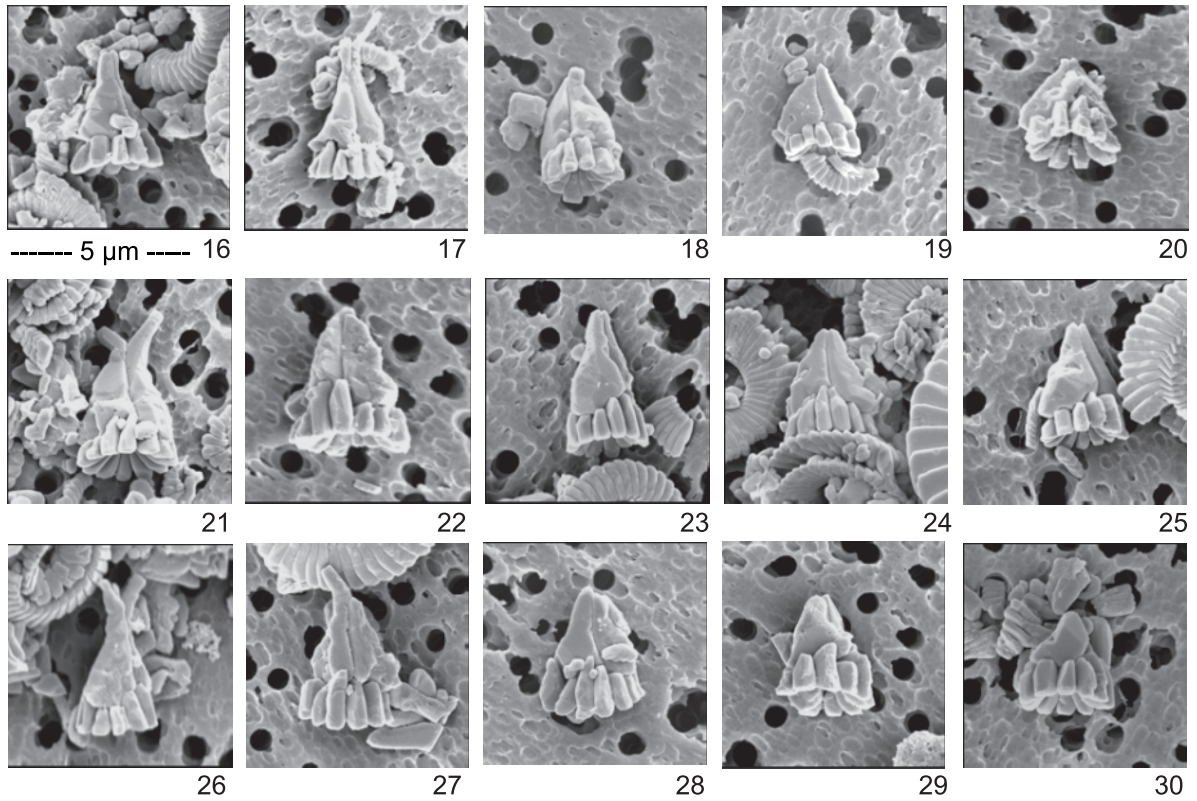
The abundance patterns (expressed as number of specimens per mm^2) and the sphenolith bioevents (i.e. the LO of *S. distentus* and *S. ciproensis* and highest occurrence (HO) of *S. predistentus*, *S. distentus* and *S. ciproensis*) were determined in a previous study at Site 1218 (Blaj *et al.*, 2009), based on LM identification of specimens using conventional criteria. The investigated sphenolith taxa are present throughout the succession but show strong abundance fluctuations throughout their ranges (Fig. 3, right panels). *Sphenolithus predistentus* dominates the assemblages through most of the analysed core and co-occurs with *S. distentus* in the higher part of its range. The LO of *Sphenolithus ciproensis*, as determined at Site 1218 is very close to the HO of *S. predistentus* and *S. distentus* (Fig. 3, right panels).

Ten samples with mixed populations of the two or three sphenolith species taken in consideration were chosen for morphometric analysis; from each of these, 100 specimens were selected at random in the LM and imaged. Counts of the abundances of *S. predistentus*, *S. distentus* and *S. ciproensis* in the ten analysed samples are presented as cumulative frequencies of the 100 specimens measured in each sample and plotted against age (Fig. 3, left panel). The sphenolith assemblages are clearly dominated by *S. predistentus*, which may contribute some bias to the morphometric data since the three sphenolith taxa are not equally represented. *Sphenolithus predistentus* constitutes about 70% of the sphenolith assemblage, at least in the first eight samples, but decreases in abundance to around 40% towards the upper part of the interval where *S. ciproensis* enters

A LM Zeiss Axioplan, Magnification 1600x



B Phillips XL 30 Field Emission SEM, Magnification 5000x



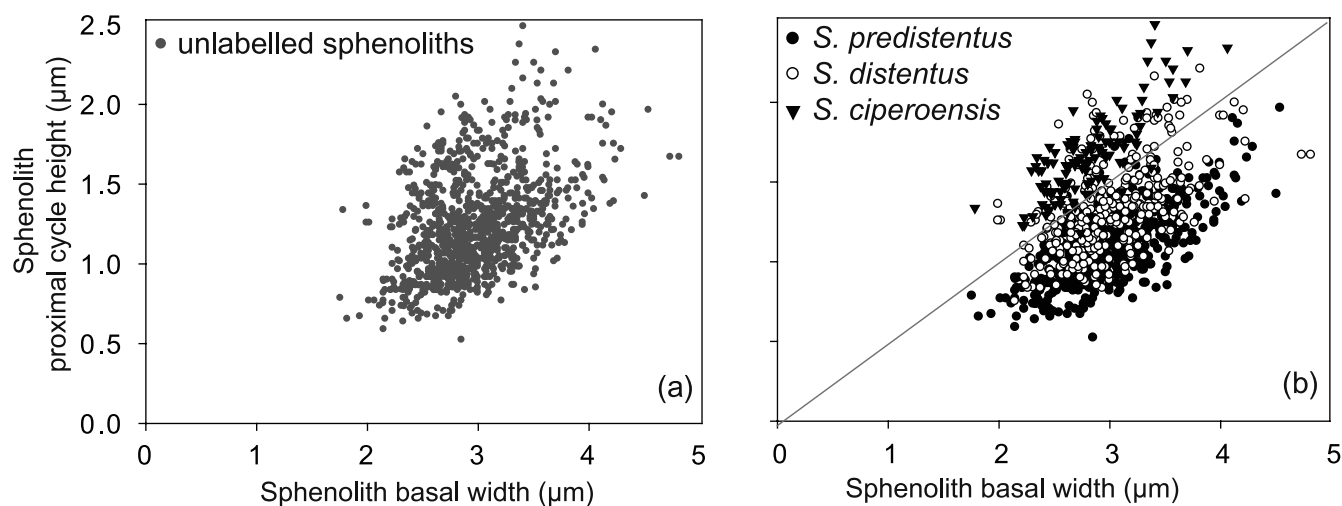


Fig. 4. (a) Relationship between proximal cycle height and basal width in the ten investigated samples of 1000 unlabelled sphenoliths taxa. (b) Scatter plot of proximal cycle height and basal width of the 1000 sphenoliths taxa identified as *S. predistentus*, *S. distentus* and *S. ciproensis*.

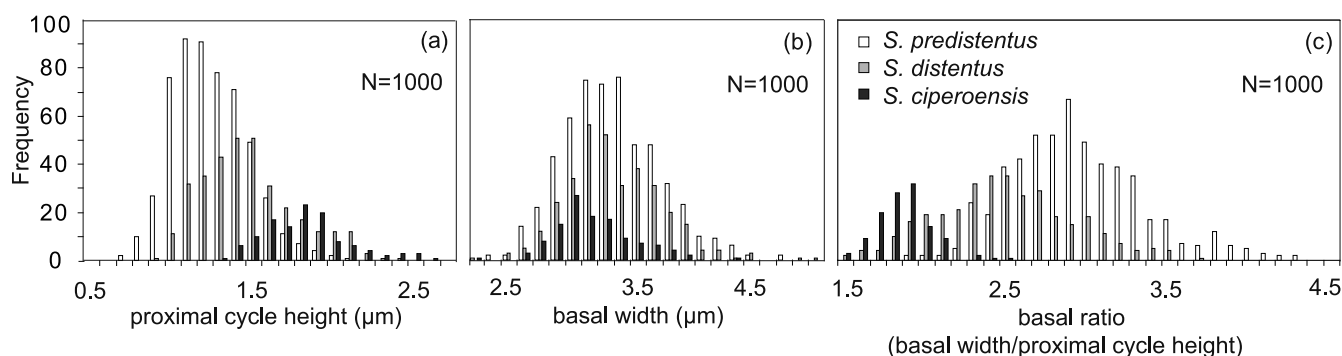


Fig. 5. Histograms of (a) sphenolith proximal cycle height, (b) basal width and (c) basal ratio (between basal width and proximal cycle height).

the stratigraphic record. The two additional samples investigated below this interval are dominated by *S. predistentus*, but contain 17–26% ‘transitional’ forms (Appendix A).

Sphenolith morphometry

Sphenolith basal width and proximal cycle height Since the morphological features, which enable us to distinguish the different species, are based primarily on development of the proximal cycle, the basal width and proximal cycle length were measured on each of the 1000 (plus 215) imaged sphenoliths (Appendix A). In a first analysis the relationship between sphenolith basal width and proximal cycle height was investi-

gated. The basal width ranges from 1.76 μm to 4.81 μm, while the proximal cycle height varies from 0.52 μm to 2.49 μm (Fig. 4a). The two parameters show only very weak correlation ($r^2 = 0.2$). The scatter diagram of basal width versus proximal cycle height from all samples (Fig. 4a) shows a single large cluster with weak evidence of a frequency minimum around length equals half width. The frequency histograms for the total sphenolith assemblages indicate unimodal distributions of both proximal cycle height (Fig. 5a) and basal width (Fig. 5b), with peaks centred at around 1.1 μm and 3 μm, respectively.

Based on their optical behaviour (i.e. the different shape of the extinction line), the sphenoliths measured in each sample were identified as *S. distentus*, *S. predistentus* and *S. ciproensis*.

Explanation of Plate 1.

Light and electron micrographs of the three species of *Sphenolithus* considered here. As discussed, the main difference between the three species is in the height of the proximal cycle relative to the sphenolith width. This affects the shape of the contact between the apical spine and the proximal surface, a feature which is much more obvious in LM than in SEM. (A) LM micrographs. **figs 1–5.** *S. predistentus*: **1**, sample 1218C 11H-5, 65 cm; **2–3**, sample 1218C 12H-5, 65 cm; **4**, sample 1218C 11H-5, 65 cm; **5**, sample 1218B 16H-1, 145 cm. **figs 6–10.** *S. distentus*: **6**, sample 1218B 17H-5, 125 cm; **7**, sample 1218A 18H-3, 105 cm; **8**, sample 1218C 12H-5, 65 cm; **9**, sample 1218 B 17H-2, 15 cm; **10**, sample 1218 B 16H-1, 145 cm. **figs 11–15.** *S. ciproensis*: sample 1218A 14H-1, 45 cm. (B) SEM micrographs. **figs 16–20.** *S. predistentus*: **16**, sample 1218A 14H-3, 45 cm; **17**, sample 1218A 15H-1, 135 cm; **18–19**, sample 1218B 16H-1, 145 cm; **20**, sample 1218A 18H-3, 105 cm. **figs 21–28.** *S. distentus*: **21**, sample 1218A 14H-6, 15 cm; **22**, sample 1218A 18H-3, 105 cm; **23**, sample 1218A 14H-6, 15 cm; **24**, sample 1218B 16H-5, 115 cm; **25–26**, sample 1218A 15H-3, 115 cm; **27**, sample 1218B 16H-1, 145 cm; **28**, sample 1218A 14H-3, 45 cm. **figs 29–30.** *S. ciproensis*: **29**, sample 1218B 18H-3, 105 cm; **30**, sample 1218A 15H-3, 115 cm.

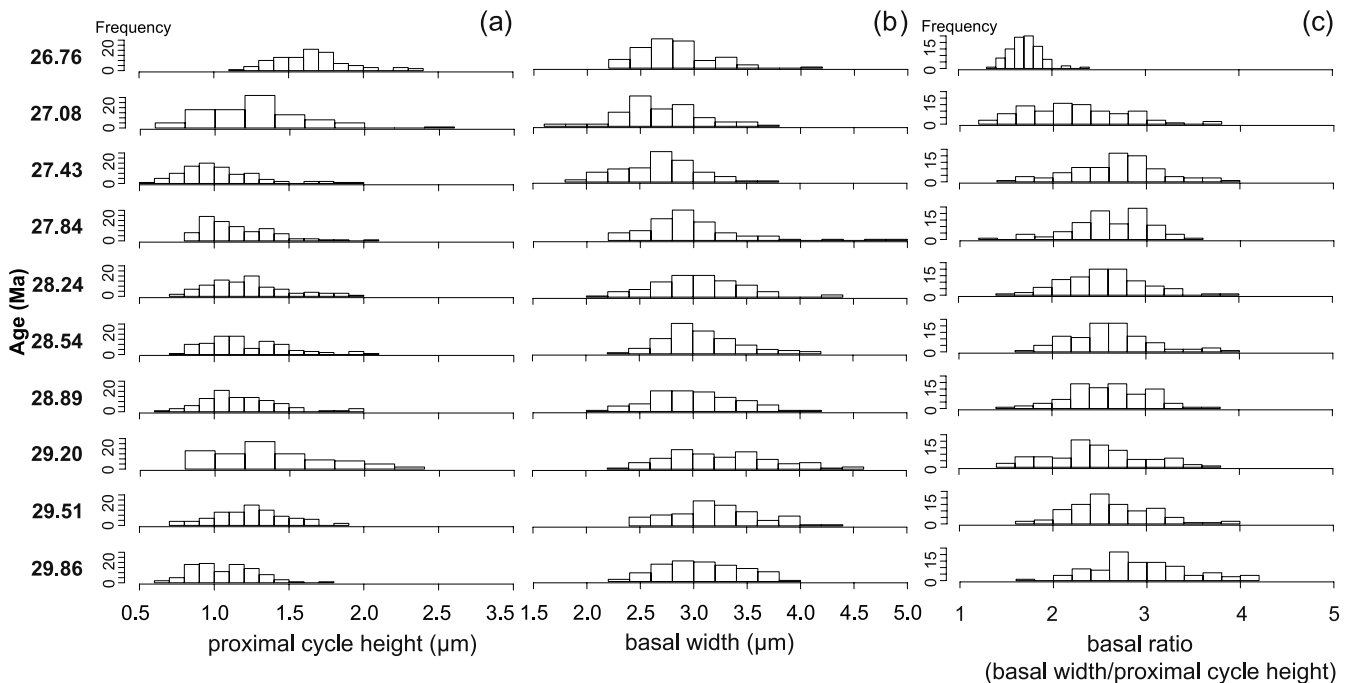


Fig. 6. Histograms of (a) proximal cycle height, (b) basal width and (c) basal ratio in ten different samples arranged in chronological order, i.e. from oldest (bottom) to youngest (top).

When the data points are labelled by species (Fig. 4b), the scatter diagram of all measurements divides into three partially overlapping clusters. The *S. predistentus* and *S. distentus* clusters overlap considerably. *Sphenolithus ciproensis*, on the other hand, is rather well separated from the other two taxa at the frequency minimum noted in the labelled plot (oblique line in Fig. 4b). The frequency histograms for the single sphenolith taxa show unimodal distributions of both proximal cycle height (Fig. 5a) and basal width (Fig. 5b) with great overlap between the three species.

The ratio between sphenolith width and proximal height The three data clusters representative of the different sphenolith species (i.e. *S. predistentus*, *S. distentus* and *S. ciproensis*) have different slopes and positions within the width versus proximal cycle height plot (Fig. 4b), suggesting that the ratio between basal width and proximal cycle height varies between the different taxa. Therefore, in a second analysis the ratio between basal width and proximal cycle height, termed the basal ratio, was investigated within each sphenolith species and sample.

The mean value of the basal ratio (in all samples taken together) is highest in *S. predistentus* (2.79), followed by *S. distentus* (2.23) and is lowest in *S. ciproensis* (1.70). The frequency histogram of the basal ratio shows a bimodal distribution, with a frequency minimum at 2.0 (Fig. 5c). This frequency minimum likely corresponds to the separation of *S. ciproensis* from *S. distentus* and *S. predistentus*, as already pointed out in the scatter diagram (Fig. 4b). Moreover, the specimens assigned to *S. distentus* show lower basal ratio values than those assigned to *S. predistentus*, but with extensive overlap.

Unimodal distributions of sphenolith proximal cycle height, basal width and basal ratio are found in each of the top ten

investigated samples (Fig. 6). Proximal cycle height and basal width histograms show changing trends with time; in particular, changes in basal width are less distinguishable. Therefore, the basal ratio is mostly influenced by changes in the proximal cycle height (Fig. 6c). The ‘transitional’ forms within the *S. predistentus*-dominated assemblages from lower stratigraphic levels tend to have smaller basal ratios (Fig. 7).

The basal ratio decreases with time. This decrease is evident both within the sphenolith lineage (Fig. 6c) but also within different sphenolith species (Fig. 8). Notably, *S. predistentus* and *S. distentus* show very similar patterns of morphological variability over time, and their basal ratios are consistently separated from each other by a relatively constant ~ 0.5 difference in the ratio (Fig. 8). This differentiation would not be as obvious when analysing either basal width or proximal cycle height, as the two taxa largely overlap (Fig. 4b). Since the basal ratio varies through time (Table 2), basal width and proximal cycle height must change independently, causing a change in the sphenolith shape.

Changes in the basal ratio values suggest that the *S. predistentus*, *S. distentus* and *S. ciproensis* lineage is composed of three different morphospecies. However, it is important to note that the groups are not distinct in terms of bimodality. Our results reveal time-progressive changes in the basal ratio within the investigated species towards morphospecies with larger proximal cycle height and smaller basal ratios (Fig. 8). These changes are interpreted as indicating evolution within the lineage. If such temporal trends and changes in morphology prove to be globally consistent, the *S. predistentus*, *S. distentus* and *S. ciproensis* lineage could serve as a valuable example for understanding the evolutionary mechanisms that underlie size and morphology changes in calcareous nannofossils (e.g. Young, 1990; Knappertsbusch, 2000; Henderiks & Pagani, 2008). In

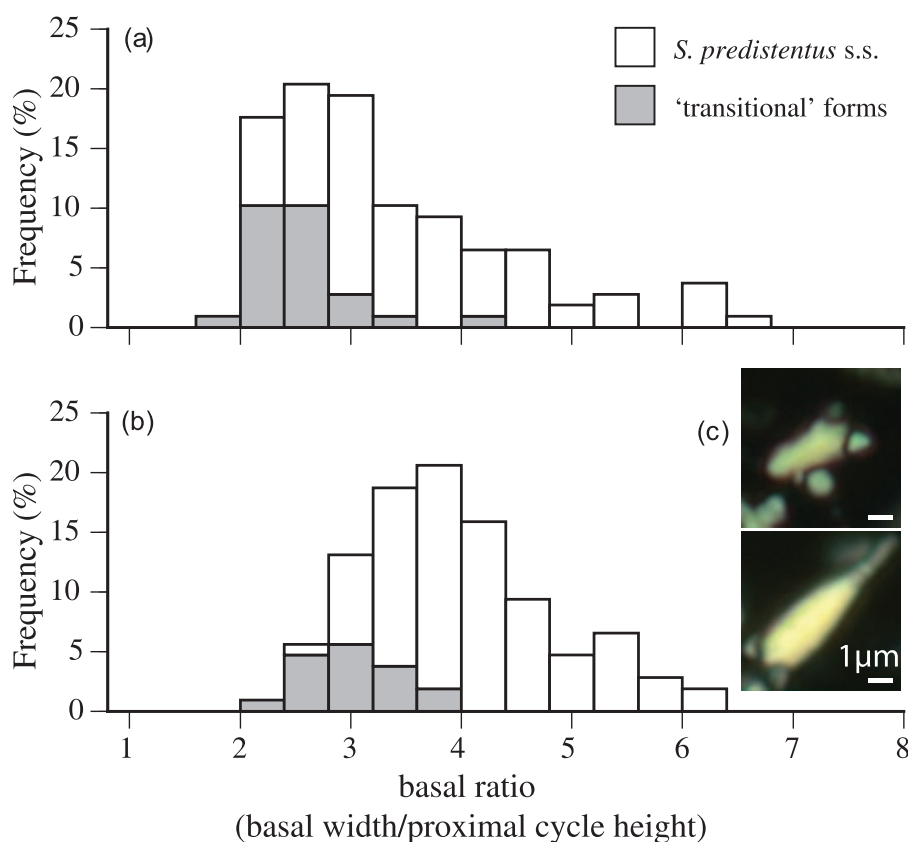


Fig. 7. Histograms of basal ratio in two selected samples containing ‘transitional’ forms (in grey) and *S. predistentus* s.s. (in white). (a) Sample 1218B 21X 04 143 cm, 31.60 Ma; (b) Sample 1218A 23X 03 65 cm, 33.02 Ma; (c) LM micrographs of transitional forms encountered in (a), taken at 2500 × magnification (scale bar = 1 µm). Note that the extinction line in LM is not straight, as in *S. predistentus* s.s., but slightly curved, although not fully developed in a V-shaped extinction line, which is typical of *S. distentus*.

order to investigate this issue further, additional investigations of *Sphenolithus* assemblages from different locations and

extended stratigraphic range – and especially from different latitudes – are needed.

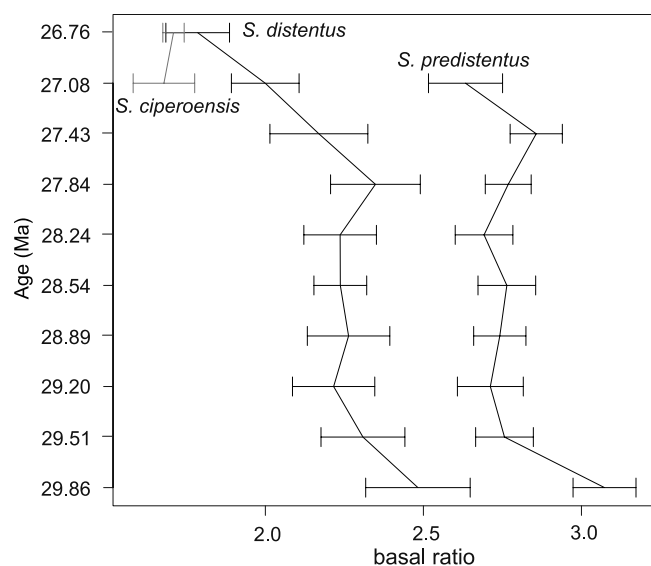


Fig. 8. Plot of changes in time of the basal ratio of *S. predistentus*, *S. distentus* and *S. ciproensis*; bars represent standard error of the mean; grey shading indicates specimens intergradational between *S. distentus* and *S. predistentus*.

Anagenetic or cladogenetic evolutionary lineage? The main aim of this study was to determine the evolutionary patterns of the Oligocene sphenolith lineage. Based on the stratigraphical range observations (Fig. 3) and the results of morphometric analyses (Figs 4, 5) of the investigated sphenolith taxa, we propose a combined model for the evolutionary nature of this lineage. The first two members of this lineage (*S. predistentus* and *S. distentus*) are difficult to consistently separate either qualitatively or morphometrically and have extensively overlapping stratigraphical ranges, as exemplified by transitional forms between both morphospecies (Fig. 7). These features are characteristic of what we defined as an anagenetic evolutionary model of the lineage. *Sphenolithus ciproensis*, on the other hand, is relatively easy to distinguish from the other two species using either qualitative morphological criteria or morphometrics and has a clearly discrete stratigraphical range. In addition, *S. ciproensis* has only a very narrow interval of co-occurrence with the other two species; this is a characteristic of a cladogenetic lineage. It would appear obvious that all members of this lineage evolved from each other; however, no transitional forms between *S. distentus* and *S. ciproensis* were observed at Site 1218 (Fig. 3, last panel).

Species/samples #	1	2	3	4	5	6	7	8	9	10
<i>S. predistentus</i>	NA	2.63	2.86	2.77	2.7	2.76	2.74	2.71	2.76	3.07
<i>S. distentus</i>	1.79	2.00	2.17	2.34	2.23	2.23	2.26	2.21	2.31	2.48
<i>S. ciperoensis</i>	1.71	1.68	NA	NA	NA	NA	NA	1.64	NA	NA
All sphenoliths	1.71	2.23	2.69	2.62	2.56	2.61	2.61	2.47	2.64	2.95

NA, not available

Table 2. Changes in the ratio between sphenolith width and proximal cycle height; units (in μm) represent the mean value of the different species measurements in each sample.

CONCLUSIONS

The evolutionary pattern of sphenoliths, as observed in the sedimentary record at Site 1218 in a 3 Ma interval during the Oligocene (29.86–26.76 Ma), indicates that the lineage resulted from successive gradual evolutionary transitions through time.

For the first time, this study provides detailed morphometric evidence for the distinction between three morphospecies, *S. predistentus*, *S. distentus* and *S. ciperoensis*. Our data reveal that the basal ratio (between basal width and proximal cycle height) is distinct between the different morphospecies and can be used to consistently distinguish between the different sphenolith species. The highest basal ratios were found in *S. predistentus*, lower basal ratios in *S. distentus* and lowest basal ratios in *S. ciperoensis*. Indeed, basal ratios in ‘transitional’ forms of *S. predistentus* tend to be smaller than *S. predistentus* s.s. found in the same assemblages.

Through the time period of co-occurrence of the *S. distentus* and *S. predistentus* species, this basal ratio shows parallel changes in the two species, with an overall trend to lower values, supporting the inference that the two species represent an artificial subdivision of a single anagenetic lineage.

The straightforward morphometric measurements adopted here provide an effective tool for studying evolution within this widespread and biostratigraphically useful lineage and should encourage further exploration by including additional and multiple deep-sea locations.

Based on the stratigraphical range observations and results of the morphometric analyses, we propose a combined model for the evolutionary nature of this lineage: with an anagenetic transition between *S. predistentus* and *S. distentus* and a cladogenetic origin for *S. ciperoensis*. The LO of *S. distentus* appears to represent a shift in morphology within a single phylogenetic lineage without any cladogenesis occurring, whilst the LO of *S. ciperoensis* marks a much more abrupt shift of morphology and probably a cladogenetic event shortly followed by extinction of the ancestral species.

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APPENDIX A: MEASUREMENTS OF SPECIMENS FROM THE *S. PREDISTENTUS*–*DISTENTUS*–*CIPEROENSIS* GROUP

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
1	26.76	2.51	1.38	1.82	<i>S. distentus</i>
1	26.76	2.88	1.56	1.85	<i>S. distentus</i>
1	26.76	2.95	1.60	1.84	<i>S. distentus</i>
1	26.76	2.91	1.78	1.63	<i>S. distentus</i>
1	26.76	2.80	1.49	1.88	<i>S. ciperoensis</i>
1	26.76	2.55	1.39	1.84	<i>S. ciperoensis</i>
1	26.76	2.69	1.75	1.53	<i>S. ciperoensis</i>
1	26.76	2.67	1.70	1.57	<i>S. ciperoensis</i>
1	26.76	2.78	1.57	1.77	<i>S. ciperoensis</i>
1	26.76	2.67	1.95	1.37	<i>S. ciperoensis</i>
1	26.76	2.57	1.49	1.73	<i>S. ciperoensis</i>
1	26.76	2.69	1.77	1.52	<i>S. ciperoensis</i>
1	26.76	2.82	1.42	1.98	<i>S. ciperoensis</i>
1	26.76	2.69	1.46	1.84	<i>S. ciperoensis</i>
1	26.76	2.90	1.52	1.90	<i>S. ciperoensis</i>
1	26.76	2.83	1.70	1.66	<i>S. ciperoensis</i>
1	26.76	2.44	1.62	1.51	<i>S. ciperoensis</i>
1	26.76	2.34	1.65	1.42	<i>S. ciperoensis</i>
1	26.76	2.88	1.88	1.53	<i>S. ciperoensis</i>
1	26.76	2.67	1.72	1.55	<i>S. ciperoensis</i>
1	26.76	3.50	2.26	1.55	<i>S. ciperoensis</i>
1	26.76	3.01	1.83	1.64	<i>S. ciperoensis</i>
1	26.76	2.49	1.62	1.54	<i>S. ciperoensis</i>
1	26.76	3.37	1.59	2.12	<i>S. ciperoensis</i>
1	26.76	3.57	2.03	1.76	<i>S. ciperoensis</i>
1	26.76	2.90	1.72	1.69	<i>S. ciperoensis</i>
1	26.76	2.77	1.62	1.71	<i>S. ciperoensis</i>
1	26.76	3.00	1.83	1.63	<i>S. ciperoensis</i>
1	26.76	2.67	1.74	1.54	<i>S. ciperoensis</i>
1	26.76	2.23	1.28	1.74	<i>S. ciperoensis</i>
1	26.76	2.80	1.62	1.73	<i>S. ciperoensis</i>
1	26.76	3.13	1.75	1.79	<i>S. ciperoensis</i>
1	26.76	2.39	1.36	1.76	<i>S. ciperoensis</i>
1	26.76	2.78	1.60	1.73	<i>S. ciperoensis</i>
1	26.76	2.59	1.49	1.74	<i>S. ciperoensis</i>
1	26.76	3.11	1.44	2.16	<i>S. ciperoensis</i>
1	26.76	2.42	1.29	1.87	<i>S. ciperoensis</i>
1	26.76	2.83	1.51	1.88	<i>S. ciperoensis</i>
1	26.76	3.11	1.97	1.58	<i>S. ciperoensis</i>
1	26.76	2.46	1.72	1.43	<i>S. ciperoensis</i>
1	26.76	3.00	1.75	1.71	<i>S. ciperoensis</i>

Table A1. Measurements of 100 randomly selected from 10 samples of the *S. predistentus*–*distentus*–*ciperoensis* group.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID	Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
1	26.76	2.82	1.64	1.72	<i>S. ciperoensis</i>	2	27.08	2.41	1.10	2.19	<i>S. predistentus</i>
1	26.76	2.60	1.60	1.62	<i>S. ciperoensis</i>	2	27.08	3.30	1.05	3.15	<i>S. predistentus</i>
1	26.76	2.60	1.56	1.67	<i>S. ciperoensis</i>	2	27.08	2.72	0.92	2.97	<i>S. predistentus</i>
1	26.76	3.34	2.26	1.48	<i>S. ciperoensis</i>	2	27.08	2.59	1.23	2.11	<i>S. predistentus</i>
1	26.76	2.62	1.60	1.63	<i>S. ciperoensis</i>	2	27.08	2.38	0.84	2.84	<i>S. predistentus</i>
1	26.76	2.62	1.74	1.51	<i>S. ciperoensis</i>	2	27.08	3.07	0.92	3.34	<i>S. predistentus</i>
1	26.76	2.36	1.57	1.50	<i>S. ciperoensis</i>	2	27.08	2.38	1.00	2.39	<i>S. predistentus</i>
1	26.76	2.73	1.65	1.65	<i>S. ciperoensis</i>	2	27.08	3.07	1.07	2.85	<i>S. predistentus</i>
1	26.76	2.46	1.33	1.85	<i>S. ciperoensis</i>	2	27.08	2.93	1.15	2.55	<i>S. predistentus</i>
1	26.76	2.62	1.31	2.00	<i>S. ciperoensis</i>	2	27.08	3.35	1.55	2.17	<i>S. predistentus</i>
1	26.76	3.24	1.74	1.87	<i>S. ciperoensis</i>	2	27.08	1.76	0.79	2.23	<i>S. predistentus</i>
1	26.76	2.91	1.92	1.52	<i>S. ciperoensis</i>	2	27.08	2.54	1.10	2.31	<i>S. predistentus</i>
1	26.76	2.21	1.23	1.80	<i>S. ciperoensis</i>	2	27.08	2.36	0.76	3.10	<i>S. predistentus</i>
1	26.76	2.51	1.69	1.49	<i>S. ciperoensis</i>	2	27.08	2.28	1.02	2.23	<i>S. predistentus</i>
1	26.76	3.28	1.93	1.69	<i>S. ciperoensis</i>	2	27.08	2.41	0.86	2.79	<i>S. predistentus</i>
1	26.76	3.24	1.92	1.69	<i>S. ciperoensis</i>	2	27.08	2.33	0.73	3.18	<i>S. predistentus</i>
1	26.76	2.47	1.42	1.74	<i>S. ciperoensis</i>	2	27.08	2.91	0.97	3.00	<i>S. predistentus</i>
1	26.76	2.95	1.52	1.94	<i>S. ciperoensis</i>	2	27.08	3.25	1.15	2.82	<i>S. predistentus</i>
1	26.76	2.62	1.60	1.63	<i>S. ciperoensis</i>	2	27.08	2.91	1.26	2.31	<i>S. predistentus</i>
1	26.76	2.23	1.23	1.81	<i>S. ciperoensis</i>	2	27.08	2.46	0.66	3.76	<i>S. predistentus</i>
1	26.76	2.49	1.44	1.73	<i>S. ciperoensis</i>	2	27.08	3.07	1.21	2.54	<i>S. predistentus</i>
1	26.76	2.96	1.65	1.79	<i>S. ciperoensis</i>	2	27.08	3.07	1.26	2.44	<i>S. predistentus</i>
1	26.76	2.42	1.49	1.63	<i>S. ciperoensis</i>	2	27.08	2.80	1.07	2.61	<i>S. predistentus</i>
1	26.76	2.73	1.18	2.32	<i>S. ciperoensis</i>	2	27.08	2.96	1.36	2.17	<i>S. predistentus</i>
1	26.76	2.55	1.36	1.88	<i>S. ciperoensis</i>	2	27.08	2.59	0.94	2.75	<i>S. predistentus</i>
1	26.76	2.51	1.36	1.84	<i>S. ciperoensis</i>	2	27.08	2.52	0.84	3.00	<i>S. predistentus</i>
1	26.76	2.96	1.75	1.69	<i>S. ciperoensis</i>	2	27.08	2.57	1.21	2.13	<i>S. predistentus</i>
1	26.76	3.00	1.67	1.79	<i>S. ciperoensis</i>	2	27.08	2.78	1.31	2.12	<i>S. predistentus</i>
1	26.76	2.62	1.59	1.65	<i>S. ciperoensis</i>	2	27.08	3.41	1.34	2.55	<i>S. predistentus</i>
1	26.76	2.93	1.69	1.74	<i>S. ciperoensis</i>	2	27.08	2.54	0.92	2.77	<i>S. predistentus</i>
1	26.76	3.06	2.01	1.52	<i>S. ciperoensis</i>	2	27.08	2.80	1.21	2.33	<i>S. predistentus</i>
1	26.76	2.93	1.90	1.54	<i>S. ciperoensis</i>	2	27.08	2.65	0.94	2.81	<i>S. predistentus</i>
1	26.76	2.96	1.87	1.59	<i>S. ciperoensis</i>	2	27.08	2.38	0.89	2.68	<i>S. predistentus</i>
1	26.76	2.42	1.34	1.80	<i>S. ciperoensis</i>	2	27.08	2.86	1.21	2.37	<i>S. predistentus</i>
1	26.76	2.37	1.47	1.61	<i>S. ciperoensis</i>	2	27.08	2.93	1.36	2.15	<i>S. predistentus</i>
1	26.76	3.13	1.72	1.82	<i>S. ciperoensis</i>	2	27.08	2.67	1.15	2.32	<i>S. predistentus</i>
1	26.76	2.41	1.64	1.47	<i>S. ciperoensis</i>	2	27.08	2.49	1.05	2.38	<i>S. predistentus</i>
1	26.76	2.69	1.60	1.67	<i>S. ciperoensis</i>	2	27.08	2.54	0.92	2.77	<i>S. predistentus</i>
1	26.76	2.55	1.44	1.77	<i>S. ciperoensis</i>	2	27.08	2.59	1.18	2.20	<i>S. predistentus</i>
1	26.76	3.08	1.75	1.76	<i>S. ciperoensis</i>	2	27.08	2.88	1.15	2.50	<i>S. predistentus</i>
1	26.76	2.78	1.42	1.95	<i>S. ciperoensis</i>	2	27.08	2.15	0.89	2.41	<i>S. predistentus</i>
1	26.76	4.06	2.34	1.73	<i>S. ciperoensis</i>	2	27.08	2.54	0.68	3.73	<i>S. predistentus</i>
1	26.76	2.72	1.64	1.66	<i>S. ciperoensis</i>	2	27.08	2.46	0.94	2.61	<i>S. distentus</i>
1	26.76	3.57	2.21	1.61	<i>S. ciperoensis</i>	2	27.08	3.56	1.81	1.97	<i>S. distentus</i>
1	26.76	3.24	1.80	1.80	<i>S. ciperoensis</i>	2	27.08	2.93	1.68	1.75	<i>S. distentus</i>
1	26.76	3.23	1.75	1.84	<i>S. ciperoensis</i>	2	27.08	2.83	1.60	1.77	<i>S. distentus</i>
1	26.76	2.29	1.57	1.46	<i>S. ciperoensis</i>	2	27.08	2.83	1.52	1.86	<i>S. distentus</i>
1	26.76	2.67	1.38	1.94	<i>S. ciperoensis</i>	2	27.08	2.31	0.84	2.75	<i>S. distentus</i>
1	26.76	2.90	1.78	1.62	<i>S. ciperoensis</i>	2	27.08	2.44	1.47	1.66	<i>S. distentus</i>
1	26.76	2.62	1.59	1.65	<i>S. ciperoensis</i>	2	27.08	2.52	1.18	2.13	<i>S. distentus</i>
1	26.76	2.78	1.69	1.65	<i>S. ciperoensis</i>	2	27.08	2.70	1.31	2.06	<i>S. distentus</i>
1	26.76	3.29	2.01	1.63	<i>S. ciperoensis</i>	2	27.08	1.99	1.36	1.46	<i>S. distentus</i>
1	26.76	2.75	1.59	1.73	<i>S. ciperoensis</i>	2	27.08	2.23	1.10	2.02	<i>S. distentus</i>
1	26.76	2.87	1.65	1.73	<i>S. ciperoensis</i>	2	27.08	2.02	1.26	1.60	<i>S. distentus</i>
1	26.76	3.28	1.85	1.77	<i>S. ciperoensis</i>	2	27.08	2.62	1.31	2.00	<i>S. distentus</i>
1	26.76	2.80	1.49	1.88	<i>S. ciperoensis</i>	2	27.08	2.78	1.44	1.93	<i>S. distentus</i>
1	26.76	2.54	1.51	1.68	<i>S. ciperoensis</i>	2	27.08	2.41	1.15	2.09	<i>S. distentus</i>
1	26.76	2.69	1.34	2.00	<i>S. ciperoensis</i>	2	27.08	2.54	1.86	1.37	<i>S. distentus</i>
1	26.76	3.37	2.37	1.42	<i>S. ciperoensis</i>	2	27.08	2.44	1.21	2.02	<i>S. distentus</i>
2	27.08	3.17	1.23	2.57	<i>S. predistentus</i>	2	27.08	3.35	1.36	2.46	<i>S. distentus</i>
2	27.08	2.44	0.86	2.82	<i>S. predistentus</i>	2	27.08	2.57	1.26	2.04	<i>S. distentus</i>
2	27.08	2.46	0.86	2.85	<i>S. predistentus</i>	2	27.08	2.59	1.36	1.90	<i>S. distentus</i>
2	27.08	2.78	0.97	2.86	<i>S. predistentus</i>	2	27.08	3.04	1.34	2.27	<i>S. distentus</i>

Table A1. Continued.

Table A1. Continued.

Oligocene *Sphenolithus* evolutionary lineage

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
2	27.08	2.54	1.21	2.11	<i>S. distentus</i>
2	27.08	2.65	1.23	2.15	<i>S. distentus</i>
2	27.08	3.64	1.49	2.44	<i>S. distentus</i>
2	27.08	2.72	1.21	2.26	<i>S. distentus</i>
2	27.08	2.36	1.31	1.80	<i>S. distentus</i>
2	27.08	2.46	1.10	2.24	<i>S. distentus</i>
2	27.08	2.65	1.34	1.98	<i>S. distentus</i>
2	27.08	2.33	1.26	1.85	<i>S. distentus</i>
2	27.08	2.86	1.91	1.49	<i>S. distentus</i>
2	27.08	2.83	1.28	2.20	<i>S. distentus</i>
2	27.08	2.80	1.52	1.84	<i>S. distentus</i>
2	27.08	1.99	1.26	1.58	<i>S. distentus</i>
2	27.08	2.65	1.70	1.55	<i>S. distentus</i>
2	27.08	2.88	1.18	2.44	<i>S. distentus</i>
2	27.08	2.70	1.18	2.29	<i>S. distentus</i>
2	27.08	2.65	1.76	1.51	<i>S. ciperoensis</i>
2	27.08	2.88	1.83	1.57	<i>S. ciperoensis</i>
2	27.08	2.91	1.70	1.71	<i>S. ciperoensis</i>
2	27.08	2.62	1.49	1.75	<i>S. ciperoensis</i>
2	27.08	1.78	1.34	1.33	<i>S. ciperoensis</i>
2	27.08	2.83	1.73	1.64	<i>S. ciperoensis</i>
2	27.08	3.09	1.62	1.90	<i>S. ciperoensis</i>
2	27.08	2.38	1.57	1.52	<i>S. ciperoensis</i>
2	27.08	2.67	1.62	1.65	<i>S. ciperoensis</i>
2	27.08	2.41	1.44	1.67	<i>S. ciperoensis</i>
2	27.08	2.33	1.60	1.46	<i>S. ciperoensis</i>
2	27.08	2.31	1.28	1.80	<i>S. ciperoensis</i>
2	27.08	3.43	1.94	1.77	<i>S. ciperoensis</i>
2	27.08	3.12	1.62	1.92	<i>S. ciperoensis</i>
2	27.08	2.83	1.28	2.20	<i>S. ciperoensis</i>
2	27.08	2.44	1.44	1.69	<i>S. ciperoensis</i>
2	27.08	3.41	2.49	1.37	<i>S. ciperoensis</i>
2	27.08	2.59	1.47	1.77	<i>S. ciperoensis</i>
3	27.43	2.36	0.84	2.82	<i>S. predistentus</i>
3	27.43	2.62	0.88	2.96	<i>S. predistentus</i>
3	27.43	2.36	0.98	2.40	<i>S. predistentus</i>
3	27.43	2.96	1.16	2.55	<i>S. predistentus</i>
3	27.43	3.05	1.72	1.77	<i>S. predistentus</i>
3	27.43	2.70	0.92	2.95	<i>S. predistentus</i>
3	27.43	2.55	0.85	3.00	<i>S. predistentus</i>
3	27.43	2.18	0.90	2.42	<i>S. predistentus</i>
3	27.43	2.87	0.98	2.92	<i>S. predistentus</i>
3	27.43	3.11	1.06	2.92	<i>S. predistentus</i>
3	27.43	2.75	1.05	2.63	<i>S. predistentus</i>
3	27.43	2.75	1.15	2.40	<i>S. predistentus</i>
3	27.43	2.46	0.70	3.49	<i>S. predistentus</i>
3	27.43	2.34	0.79	2.98	<i>S. predistentus</i>
3	27.43	2.36	0.85	2.77	<i>S. predistentus</i>
3	27.43	2.52	0.82	3.08	<i>S. predistentus</i>
3	27.43	2.16	0.66	3.30	<i>S. predistentus</i>
3	27.43	3.31	0.95	3.48	<i>S. predistentus</i>
3	27.43	2.15	0.77	2.79	<i>S. predistentus</i>
3	27.43	2.23	0.70	3.16	<i>S. predistentus</i>
3	27.43	2.06	0.77	2.68	<i>S. predistentus</i>
3	27.43	2.62	0.67	3.90	<i>S. predistentus</i>
3	27.43	2.15	0.59	3.64	<i>S. predistentus</i>
3	27.43	2.49	0.69	3.62	<i>S. predistentus</i>
3	27.43	2.77	1.02	2.73	<i>S. predistentus</i>
3	27.43	2.64	0.72	3.66	<i>S. predistentus</i>
3	27.43	2.39	0.87	2.75	<i>S. predistentus</i>
3	27.43	2.60	0.95	2.74	<i>S. predistentus</i>
3	27.43	2.65	0.90	2.95	<i>S. predistentus</i>
3	27.43	1.93	0.67	2.88	<i>S. predistentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
3	27.43	2.54	1.08	2.35	<i>S. predistentus</i>
3	27.43	2.69	1.06	2.52	<i>S. predistentus</i>
3	27.43	3.37	1.41	2.40	<i>S. predistentus</i>
3	27.43	2.98	1.00	2.98	<i>S. predistentus</i>
3	27.43	2.16	0.84	2.59	<i>S. predistentus</i>
3	27.43	3.14	1.21	2.59	<i>S. predistentus</i>
3	27.43	2.64	1.03	2.56	<i>S. predistentus</i>
3	27.43	2.65	0.92	2.89	<i>S. predistentus</i>
3	27.43	2.42	0.88	2.74	<i>S. predistentus</i>
3	27.43	2.64	0.88	2.98	<i>S. predistentus</i>
3	27.43	2.77	0.92	3.02	<i>S. predistentus</i>
3	27.43	2.33	0.84	2.78	<i>S. predistentus</i>
3	27.43	2.73	0.87	3.15	<i>S. predistentus</i>
3	27.43	2.21	0.84	2.65	<i>S. predistentus</i>
3	27.43	2.33	0.87	2.68	<i>S. predistentus</i>
3	27.43	1.82	0.66	2.78	<i>S. predistentus</i>
3	27.43	2.01	0.77	2.62	<i>S. predistentus</i>
3	27.43	2.82	0.84	3.37	<i>S. predistentus</i>
3	27.43	2.44	0.75	3.24	<i>S. predistentus</i>
3	27.43	3.06	1.06	2.88	<i>S. predistentus</i>
3	27.43	3.34	1.16	2.87	<i>S. predistentus</i>
3	27.43	3.09	1.08	2.86	<i>S. predistentus</i>
3	27.43	2.83	0.90	3.15	<i>S. predistentus</i>
3	27.43	2.33	0.79	2.96	<i>S. predistentus</i>
3	27.43	2.67	1.02	2.63	<i>S. predistentus</i>
3	27.43	2.98	0.93	3.19	<i>S. predistentus</i>
3	27.43	2.78	0.87	3.21	<i>S. predistentus</i>
3	27.43	2.15	0.82	2.62	<i>S. predistentus</i>
3	27.43	2.82	1.13	2.49	<i>S. predistentus</i>
3	27.43	2.87	1.06	2.69	<i>S. predistentus</i>
3	27.43	3.00	0.98	3.05	<i>S. predistentus</i>
3	27.43	3.49	1.28	2.73	<i>S. predistentus</i>
3	27.43	2.88	1.16	2.48	<i>S. predistentus</i>
3	27.43	3.18	1.03	3.08	<i>S. predistentus</i>
3	27.43	2.37	1.03	2.30	<i>S. predistentus</i>
3	27.43	2.44	1.02	2.40	<i>S. predistentus</i>
3	27.43	2.72	1.21	2.24	<i>S. predistentus</i>
3	27.43	2.90	0.93	3.11	<i>S. predistentus</i>
3	27.43	2.64	0.87	3.04	<i>S. predistentus</i>
3	27.43	2.88	0.97	2.98	<i>S. predistentus</i>
3	27.43	2.54	1.02	2.50	<i>S. predistentus</i>
3	27.43	3.18	1.13	2.81	<i>S. predistentus</i>
3	27.43	2.67	0.98	2.72	<i>S. predistentus</i>
3	27.43	2.11	0.74	2.87	<i>S. predistentus</i>
3	27.43	2.46	0.95	2.59	<i>S. predistentus</i>
3	27.43	3.29	0.95	3.47	<i>S. predistentus</i>
3	27.43	2.85	1.46	1.96	<i>S. distentus</i>
3	27.43	2.87	1.03	2.78	<i>S. distentus</i>
3	27.43	2.77	1.34	2.06	<i>S. distentus</i>
3	27.43	2.77	0.98	2.82	<i>S. distentus</i>
3	27.43	3.62	1.69	2.15	<i>S. distentus</i>
3	27.43	2.44	1.21	2.01	<i>S. distentus</i>
3	27.43	2.72	1.60	1.69	<i>S. distentus</i>
3	27.43	2.83	1.77	1.60	<i>S. distentus</i>
3	27.43	2.65	1.15	2.31	<i>S. distentus</i>
3	27.43	2.34	1.29	1.81	<i>S. distentus</i>
3	27.43	2.87	1.21	2.36	<i>S. distentus</i>
3	27.43	2.70	0.98	2.75	<i>S. distentus</i>
3	27.43	2.42	1.02	2.39	<i>S. distentus</i>
3	27.43	3.19	1.15	2.79	<i>S. distentus</i>
3	27.43	2.88	1.29	2.23	<i>S. distentus</i>
3	27.43	2.65	1.26	2.10	<i>S. distentus</i>
3	27.43	2.51	1.23	2.04	<i>S. distentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID	Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
3	27.43	3.18	1.18	2.69	<i>S. distentus</i>	4	27.84	2.62	0.92	2.86	<i>S. predistentus</i>
3	27.43	2.60	1.39	1.87	<i>S. distentus</i>	4	27.84	2.33	0.92	2.54	<i>S. predistentus</i>
3	27.43	2.83	1.39	2.04	<i>S. distentus</i>	4	27.84	2.88	0.85	3.38	<i>S. predistentus</i>
3	27.43	2.88	1.93	1.49	<i>S. distentus</i>	4	27.84	2.73	0.90	3.04	<i>S. predistentus</i>
3	27.43	3.26	1.90	1.72	<i>S. distentus</i>	4	27.84	3.95	1.38	2.87	<i>S. predistentus</i>
3	27.43	2.75	1.24	2.21	<i>S. distentus</i>	4	27.84	3.34	1.15	2.91	<i>S. predistentus</i>
3	27.43	2.91	1.33	2.20	<i>S. distentus</i>	4	27.84	2.52	1.13	2.23	<i>S. predistentus</i>
4	27.84	3.24	1.34	2.41	<i>S. predistentus</i>	4	27.84	2.91	1.39	2.09	<i>S. predistentus</i>
4	27.84	2.82	1.00	2.82	<i>S. predistentus</i>	4	27.84	3.03	1.36	2.23	<i>S. distentus</i>
4	27.84	4.73	1.67	2.83	<i>S. predistentus</i>	4	27.84	2.29	1.24	1.84	<i>S. distentus</i>
4	27.84	2.96	0.97	3.07	<i>S. predistentus</i>	4	27.84	3.77	1.24	3.03	<i>S. distentus</i>
4	27.84	3.28	1.26	2.60	<i>S. predistentus</i>	4	27.84	2.72	1.06	2.55	<i>S. distentus</i>
4	27.84	2.87	0.97	2.97	<i>S. predistentus</i>	4	27.84	3.55	1.20	2.97	<i>S. distentus</i>
4	27.84	4.22	1.39	3.04	<i>S. predistentus</i>	4	27.84	2.87	1.26	2.27	<i>S. distentus</i>
4	27.84	2.93	0.84	3.51	<i>S. predistentus</i>	4	27.84	2.88	1.15	2.51	<i>S. distentus</i>
4	27.84	3.67	1.28	2.87	<i>S. predistentus</i>	4	27.84	3.14	0.93	3.37	<i>S. distentus</i>
4	27.84	2.55	1.05	2.44	<i>S. predistentus</i>	4	27.84	3.19	1.39	2.29	<i>S. distentus</i>
4	27.84	4.81	1.67	2.88	<i>S. predistentus</i>	4	27.84	2.65	1.49	1.78	<i>S. distentus</i>
4	27.84	2.26	0.84	2.71	<i>S. predistentus</i>	4	27.84	3.44	1.47	2.33	<i>S. distentus</i>
4	27.84	3.19	1.03	3.10	<i>S. predistentus</i>	4	27.84	2.70	1.16	2.32	<i>S. distentus</i>
4	27.84	2.55	0.97	2.64	<i>S. predistentus</i>	4	27.84	2.82	1.28	2.21	<i>S. distentus</i>
4	27.84	2.87	0.90	3.18	<i>S. predistentus</i>	4	27.84	2.87	1.16	2.46	<i>S. distentus</i>
4	27.84	2.77	0.95	2.91	<i>S. predistentus</i>	4	27.84	2.80	1.11	2.51	<i>S. distentus</i>
4	27.84	2.52	0.85	2.96	<i>S. predistentus</i>	4	27.84	2.90	1.10	2.64	<i>S. distentus</i>
4	27.84	2.83	1.06	2.66	<i>S. predistentus</i>	4	27.84	2.59	1.42	1.82	<i>S. distentus</i>
4	27.84	3.73	1.46	2.56	<i>S. predistentus</i>	4	27.84	2.83	1.33	2.14	<i>S. distentus</i>
4	27.84	2.72	0.95	2.86	<i>S. predistentus</i>	4	27.84	3.41	1.33	2.57	<i>S. distentus</i>
4	27.84	2.47	0.92	2.70	<i>S. predistentus</i>	4	27.84	3.19	1.05	3.05	<i>S. distentus</i>
4	27.84	2.70	1.06	2.54	<i>S. predistentus</i>	4	27.84	2.83	1.70	1.66	<i>S. distentus</i>
4	27.84	3.00	1.02	2.95	<i>S. predistentus</i>	4	27.84	2.80	2.05	1.37	<i>S. distentus</i>
4	27.84	3.72	1.44	2.58	<i>S. predistentus</i>	4	27.84	3.13	1.88	1.66	<i>S. distentus</i>
4	27.84	3.06	1.23	2.49	<i>S. predistentus</i>	4	27.84	3.09	1.23	2.52	<i>S. distentus</i>
4	27.84	2.88	1.15	2.51	<i>S. predistentus</i>	4	27.84	3.26	1.36	2.40	<i>S. distentus</i>
4	27.84	3.09	1.34	2.30	<i>S. predistentus</i>	4	27.84	2.90	1.18	2.46	<i>S. distentus</i>
4	27.84	3.18	1.10	2.90	<i>S. predistentus</i>	4	27.84	3.18	1.13	2.81	<i>S. distentus</i>
4	27.84	2.85	1.11	2.56	<i>S. predistentus</i>	4	27.84	2.29	1.02	2.26	<i>S. distentus</i>
4	27.84	2.75	1.06	2.58	<i>S. predistentus</i>	4	27.84	3.27	1.54	2.12	<i>S. distentus</i>
4	27.84	3.47	1.20	2.90	<i>S. predistentus</i>	4	27.84	3.03	1.36	2.23	<i>S. distentus</i>
4	27.84	2.77	1.11	2.49	<i>S. predistentus</i>	4	27.84	2.72	0.97	2.81	<i>S. distentus</i>
4	27.84	2.59	0.98	2.63	<i>S. predistentus</i>	4	27.84	2.65	1.18	2.25	<i>S. distentus</i>
4	27.84	2.70	1.02	2.66	<i>S. predistentus</i>	4	27.84	2.75	1.28	2.15	<i>S. distentus</i>
4	27.84	2.78	0.87	3.21	<i>S. predistentus</i>	4	27.84	2.60	1.46	1.79	<i>S. distentus</i>
4	27.84	3.08	1.10	2.81	<i>S. predistentus</i>	4	27.84	2.77	0.98	2.82	<i>S. distentus</i>
4	27.84	2.85	1.08	2.64	<i>S. predistentus</i>	4	27.84	3.16	1.36	2.33	<i>S. distentus</i>
4	27.84	3.01	1.44	2.09	<i>S. predistentus</i>	5	28.24	3.49	1.24	2.80	<i>S. predistentus</i>
4	27.84	3.18	1.08	2.94	<i>S. predistentus</i>	5	28.24	2.75	1.00	2.75	<i>S. predistentus</i>
4	27.84	2.59	1.00	2.59	<i>S. predistentus</i>	5	28.24	2.67	0.87	3.08	<i>S. predistentus</i>
4	27.84	2.83	1.10	2.58	<i>S. predistentus</i>	5	28.24	2.60	1.24	2.09	<i>S. predistentus</i>
4	27.84	3.26	1.51	2.16	<i>S. predistentus</i>	5	28.24	3.32	0.87	3.83	<i>S. predistentus</i>
4	27.84	2.23	0.90	2.47	<i>S. predistentus</i>	5	28.24	2.75	0.93	2.95	<i>S. predistentus</i>
4	27.84	2.93	0.97	3.03	<i>S. predistentus</i>	5	28.24	2.91	1.36	2.14	<i>S. predistentus</i>
4	27.84	2.88	0.92	3.14	<i>S. predistentus</i>	5	28.24	3.39	1.23	2.76	<i>S. predistentus</i>
4	27.84	2.57	0.92	2.80	<i>S. predistentus</i>	5	28.24	3.32	1.21	2.74	<i>S. predistentus</i>
4	27.84	2.24	0.85	2.63	<i>S. predistentus</i>	5	28.24	2.87	0.87	3.30	<i>S. predistentus</i>
4	27.84	3.13	0.98	3.18	<i>S. predistentus</i>	5	28.24	2.98	1.00	2.98	<i>S. predistentus</i>
4	27.84	3.00	0.92	3.27	<i>S. predistentus</i>	5	28.24	3.18	1.15	2.77	<i>S. predistentus</i>
4	27.84	2.91	1.06	2.74	<i>S. predistentus</i>	5	28.24	3.64	1.28	2.85	<i>S. predistentus</i>
4	27.84	2.64	0.95	2.78	<i>S. predistentus</i>	5	28.24	2.51	0.84	3.00	<i>S. predistentus</i>
4	27.84	2.37	0.84	2.84	<i>S. predistentus</i>	5	28.24	3.52	1.39	2.53	<i>S. predistentus</i>
4	27.84	2.77	0.88	3.13	<i>S. predistentus</i>	5	28.24	2.39	0.72	3.32	<i>S. predistentus</i>
4	27.84	3.26	1.10	2.97	<i>S. predistentus</i>	5	28.24	2.90	0.92	3.16	<i>S. predistentus</i>
4	27.84	2.82	1.08	2.61	<i>S. predistentus</i>	5	28.24	2.72	0.97	2.81	<i>S. predistentus</i>
4	27.84	2.67	0.95	2.81	<i>S. predistentus</i>	5	28.24	3.39	1.60	2.11	<i>S. predistentus</i>

Table A1. Continued.

Table A1. Continued.

Oligocene *Sphenolithus* evolutionary lineage

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
5	28.24	2.80	1.13	2.48	<i>S. predistentus</i>
5	28.24	3.68	1.21	3.04	<i>S. predistentus</i>
5	28.24	3.41	1.24	2.74	<i>S. predistentus</i>
5	28.24	2.82	1.05	2.69	<i>S. predistentus</i>
5	28.24	3.06	1.34	2.28	<i>S. predistentus</i>
5	28.24	3.08	1.02	3.03	<i>S. predistentus</i>
5	28.24	3.47	1.33	2.62	<i>S. predistentus</i>
5	28.24	2.47	0.92	2.70	<i>S. predistentus</i>
5	28.24	3.32	1.29	2.57	<i>S. predistentus</i>
5	28.24	3.18	1.20	2.66	<i>S. predistentus</i>
5	28.24	3.23	1.31	2.46	<i>S. predistentus</i>
5	28.24	2.90	1.02	2.85	<i>S. predistentus</i>
5	28.24	3.46	1.20	2.89	<i>S. predistentus</i>
5	28.24	2.44	1.02	2.40	<i>S. predistentus</i>
5	28.24	2.65	0.85	3.12	<i>S. predistentus</i>
5	28.24	2.85	1.05	2.72	<i>S. predistentus</i>
5	28.24	2.15	0.90	2.38	<i>S. predistentus</i>
5	28.24	3.64	1.42	2.55	<i>S. predistentus</i>
5	28.24	2.78	0.85	3.27	<i>S. predistentus</i>
5	28.24	3.09	1.26	2.45	<i>S. predistentus</i>
5	28.24	3.24	1.05	3.09	<i>S. predistentus</i>
5	28.24	2.65	1.20	2.22	<i>S. predistentus</i>
5	28.24	3.14	1.62	1.94	<i>S. predistentus</i>
5	28.24	3.14	1.26	2.49	<i>S. predistentus</i>
5	28.24	2.85	1.10	2.60	<i>S. predistentus</i>
5	28.24	3.00	1.00	3.00	<i>S. predistentus</i>
5	28.24	3.09	1.31	2.36	<i>S. predistentus</i>
5	28.24	3.59	1.11	3.22	<i>S. predistentus</i>
5	28.24	3.36	1.34	2.50	<i>S. predistentus</i>
5	28.24	2.91	1.02	2.87	<i>S. predistentus</i>
5	28.24	2.85	1.15	2.49	<i>S. predistentus</i>
5	28.24	3.34	1.41	2.37	<i>S. predistentus</i>
5	28.24	2.77	1.26	2.19	<i>S. predistentus</i>
5	28.24	2.51	1.05	2.39	<i>S. predistentus</i>
5	28.24	3.18	1.21	2.63	<i>S. predistentus</i>
5	28.24	3.42	1.57	2.18	<i>S. predistentus</i>
5	28.24	2.21	0.84	2.65	<i>S. predistentus</i>
5	28.24	3.47	1.29	2.68	<i>S. predistentus</i>
5	28.24	2.44	1.03	2.37	<i>S. predistentus</i>
5	28.24	2.54	1.15	2.21	<i>S. predistentus</i>
5	28.24	3.13	1.08	2.89	<i>S. predistentus</i>
5	28.24	3.29	0.98	3.35	<i>S. predistentus</i>
5	28.24	2.62	1.41	1.86	<i>S. predistentus</i>
5	28.24	3.05	1.16	2.62	<i>S. predistentus</i>
5	28.24	2.57	1.18	2.18	<i>S. predistentus</i>
5	28.24	2.85	0.77	3.70	<i>S. predistentus</i>
5	28.24	3.28	1.18	2.78	<i>S. predistentus</i>
5	28.24	2.96	1.10	2.70	<i>S. predistentus</i>
5	28.24	3.18	1.31	2.43	<i>S. predistentus</i>
5	28.24	3.09	1.23	2.52	<i>S. predistentus</i>
5	28.24	3.31	1.08	3.06	<i>S. predistentus</i>
5	28.24	4.21	1.95	2.16	<i>S. distentus</i>
5	28.24	3.01	1.24	2.42	<i>S. distentus</i>
5	28.24	4.22	1.75	2.41	<i>S. distentus</i>
5	28.24	2.85	1.13	2.52	<i>S. distentus</i>
5	28.24	3.39	1.56	2.18	<i>S. distentus</i>
5	28.24	3.36	1.29	2.59	<i>S. distentus</i>
5	28.24	3.13	1.13	2.77	<i>S. distentus</i>
5	28.24	3.36	1.47	2.28	<i>S. distentus</i>
5	28.24	3.11	1.44	2.16	<i>S. distentus</i>
5	28.24	3.42	1.41	2.43	<i>S. distentus</i>
5	28.24	2.91	1.28	2.28	<i>S. distentus</i>
5	28.24	3.55	1.83	1.94	<i>S. distentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
5	28.24	3.62	1.62	2.23	<i>S. distentus</i>
5	28.24	3.13	1.15	2.73	<i>S. distentus</i>
5	28.24	2.23	1.00	2.23	<i>S. distentus</i>
5	28.24	3.19	1.64	1.95	<i>S. distentus</i>
5	28.24	3.08	1.41	2.19	<i>S. distentus</i>
5	28.24	3.06	1.24	2.46	<i>S. distentus</i>
5	28.24	2.75	1.70	1.62	<i>S. distentus</i>
5	28.24	2.37	0.97	2.46	<i>S. distentus</i>
5	28.24	3.44	1.90	1.81	<i>S. distentus</i>
5	28.24	2.28	1.08	2.11	<i>S. distentus</i>
5	28.24	2.87	1.08	2.65	<i>S. distentus</i>
5	28.24	2.85	1.70	1.67	<i>S. distentus</i>
5	28.24	2.62	1.38	1.90	<i>S. distentus</i>
5	28.24	2.87	1.82	1.58	<i>S. distentus</i>
5	28.24	3.72	1.60	2.33	<i>S. distentus</i>
5	28.24	2.77	1.03	2.68	<i>S. distentus</i>
5	28.24	2.65	1.28	2.08	<i>S. distentus</i>
5	28.24	2.88	1.26	2.29	<i>S. distentus</i>
6	28.54	2.85	0.93	3.05	<i>S. predistentus</i>
6	28.54	2.59	0.85	3.04	<i>S. predistentus</i>
6	28.54	3.11	1.15	2.71	<i>S. predistentus</i>
6	28.54	3.59	1.34	2.67	<i>S. predistentus</i>
6	28.54	2.39	0.87	2.75	<i>S. predistentus</i>
6	28.54	2.80	1.05	2.67	<i>S. predistentus</i>
6	28.54	3.01	1.03	2.92	<i>S. predistentus</i>
6	28.54	3.08	1.31	2.35	<i>S. predistentus</i>
6	28.54	3.82	1.41	2.71	<i>S. predistentus</i>
6	28.54	2.72	1.11	2.44	<i>S. predistentus</i>
6	28.54	3.36	1.26	2.66	<i>S. predistentus</i>
6	28.54	2.93	1.02	2.89	<i>S. predistentus</i>
6	28.54	2.70	0.98	2.75	<i>S. predistentus</i>
6	28.54	3.54	1.11	3.18	<i>S. predistentus</i>
6	28.54	2.83	1.02	2.79	<i>S. predistentus</i>
6	28.54	2.98	1.03	2.89	<i>S. predistentus</i>
6	28.54	3.52	0.97	3.64	<i>S. predistentus</i>
6	28.54	3.37	0.98	3.43	<i>S. predistentus</i>
6	28.54	3.24	1.00	3.25	<i>S. predistentus</i>
6	28.54	2.88	0.92	3.14	<i>S. predistentus</i>
6	28.54	3.62	1.18	3.07	<i>S. predistentus</i>
6	28.54	3.03	1.11	2.72	<i>S. predistentus</i>
6	28.54	2.69	1.20	2.25	<i>S. predistentus</i>
6	28.54	3.24	1.10	2.96	<i>S. predistentus</i>
6	28.54	3.21	1.46	2.20	<i>S. predistentus</i>
6	28.54	2.91	1.11	2.62	<i>S. predistentus</i>
6	28.54	2.87	0.80	3.57	<i>S. predistentus</i>
6	28.54	2.65	0.84	3.18	<i>S. predistentus</i>
6	28.54	2.85	1.08	2.64	<i>S. predistentus</i>
6	28.54	3.14	1.28	2.46	<i>S. predistentus</i>
6	28.54	2.67	0.82	3.26	<i>S. predistentus</i>
6	28.54	3.06	1.23	2.49	<i>S. predistentus</i>
6	28.54	2.80	1.10	2.55	<i>S. predistentus</i>
6	28.54	2.60	0.87	3.00	<i>S. predistentus</i>
6	28.54	3.01	1.42	2.11	<i>S. predistentus</i>
6	28.54	2.64	1.08	2.44	<i>S. predistentus</i>
6	28.54	3.18	1.77	1.80	<i>S. predistentus</i>
6	28.54	2.85	1.08	2.64	<i>S. predistentus</i>
6	28.54	2.49	1.03	2.41	<i>S. predistentus</i>
6	28.54	2.93	1.20	2.45	<i>S. predistentus</i>
6	28.54	2.75	1.06	2.58	<i>S. predistentus</i>
6	28.54	2.98	1.21	2.46	<i>S. predistentus</i>
6	28.54	2.67	1.25	2.12	<i>S. predistentus</i>
6	28.54	2.82	0.98	2.87	<i>S. predistentus</i>
6	28.54	2.88	1.10	2.63	<i>S. predistentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID	Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
6	28.54	2.90	0.93	3.11	<i>S. predistentus</i>	7	28.89	2.70	0.98	2.75	<i>S. predistentus</i>
6	28.54	2.95	1.02	2.90	<i>S. predistentus</i>	7	28.89	3.16	1.13	2.80	<i>S. predistentus</i>
6	28.54	2.44	0.87	2.81	<i>S. predistentus</i>	7	28.89	3.27	1.28	2.56	<i>S. predistentus</i>
6	28.54	2.69	0.70	3.81	<i>S. predistentus</i>	7	28.89	2.88	0.93	3.09	<i>S. predistentus</i>
6	28.54	2.83	1.03	2.75	<i>S. predistentus</i>	7	28.89	3.32	1.21	2.74	<i>S. predistentus</i>
6	28.54	2.95	1.36	2.17	<i>S. predistentus</i>	7	28.89	2.60	0.83	3.12	<i>S. predistentus</i>
6	28.54	3.06	1.15	2.67	<i>S. predistentus</i>	7	28.89	3.44	1.08	3.18	<i>S. predistentus</i>
6	28.54	3.05	1.18	2.58	<i>S. predistentus</i>	7	28.89	3.08	1.10	2.81	<i>S. predistentus</i>
6	28.54	3.39	1.34	2.52	<i>S. predistentus</i>	7	28.89	4.16	1.87	2.23	<i>S. predistentus</i>
6	28.54	3.16	1.20	2.64	<i>S. predistentus</i>	7	28.89	2.45	0.79	3.12	<i>S. predistentus</i>
6	28.54	2.78	0.93	2.98	<i>S. predistentus</i>	7	28.89	3.11	0.92	3.39	<i>S. predistentus</i>
6	28.54	3.19	1.18	2.71	<i>S. predistentus</i>	7	28.89	3.11	1.33	2.35	<i>S. predistentus</i>
6	28.54	3.90	1.62	2.40	<i>S. predistentus</i>	7	28.89	2.78	0.92	3.04	<i>S. predistentus</i>
6	28.54	3.18	1.34	2.37	<i>S. predistentus</i>	7	28.89	3.22	1.16	2.77	<i>S. predistentus</i>
6	28.54	3.09	1.10	2.82	<i>S. predistentus</i>	7	28.89	3.70	1.36	2.72	<i>S. predistentus</i>
6	28.54	3.31	1.34	2.46	<i>S. predistentus</i>	7	28.89	3.58	1.46	2.46	<i>S. predistentus</i>
6	28.54	3.80	1.46	2.61	<i>S. predistentus</i>	7	28.89	3.08	1.03	2.98	<i>S. predistentus</i>
6	28.54	3.03	1.20	2.53	<i>S. predistentus</i>	7	28.89	3.40	1.31	2.60	<i>S. predistentus</i>
6	28.54	3.13	0.87	3.60	<i>S. predistentus</i>	7	28.89	2.88	1.06	2.71	<i>S. predistentus</i>
6	28.54	2.54	0.87	2.92	<i>S. predistentus</i>	7	28.89	2.93	1.01	2.89	<i>S. predistentus</i>
6	28.54	3.16	1.13	2.80	<i>S. predistentus</i>	7	28.89	3.32	1.26	2.64	<i>S. predistentus</i>
6	28.54	2.41	1.00	2.41	<i>S. predistentus</i>	7	28.89	3.35	1.03	3.25	<i>S. predistentus</i>
6	28.54	3.09	0.82	3.78	<i>S. predistentus</i>	7	28.89	2.63	1.06	2.48	<i>S. predistentus</i>
6	28.54	3.31	1.15	2.89	<i>S. predistentus</i>	7	28.89	3.34	1.41	2.37	<i>S. predistentus</i>
6	28.54	2.85	1.03	2.76	<i>S. predistentus</i>	7	28.89	2.88	1.13	2.55	<i>S. predistentus</i>
6	28.54	2.75	0.98	2.80	<i>S. predistentus</i>	7	28.89	3.65	1.42	2.56	<i>S. predistentus</i>
6	28.54	3.23	1.51	2.14	<i>S. distentus</i>	7	28.89	3.45	1.47	2.34	<i>S. predistentus</i>
6	28.54	3.31	1.34	2.46	<i>S. distentus</i>	7	28.89	2.95	1.03	2.86	<i>S. predistentus</i>
6	28.54	2.93	1.24	2.36	<i>S. distentus</i>	7	28.89	2.32	0.64	3.64	<i>S. predistentus</i>
6	28.54	2.75	1.13	2.43	<i>S. distentus</i>	7	28.89	3.04	1.10	2.78	<i>S. predistentus</i>
6	28.54	2.90	1.10	2.64	<i>S. distentus</i>	7	28.89	2.83	0.93	3.04	<i>S. predistentus</i>
6	28.54	3.14	1.31	2.40	<i>S. distentus</i>	7	28.89	2.63	0.97	2.73	<i>S. predistentus</i>
6	28.54	2.88	1.57	1.83	<i>S. distentus</i>	7	28.89	3.11	1.23	2.53	<i>S. predistentus</i>
6	28.54	3.34	1.70	1.96	<i>S. distentus</i>	7	28.89	3.11	1.03	3.02	<i>S. predistentus</i>
6	28.54	3.49	1.47	2.37	<i>S. distentus</i>	7	28.89	2.73	1.08	2.53	<i>S. predistentus</i>
6	28.54	4.13	2.00	2.07	<i>S. distentus</i>	7	28.89	3.70	1.39	2.66	<i>S. predistentus</i>
6	28.54	4.00	1.92	2.09	<i>S. distentus</i>	7	28.89	2.59	0.95	2.72	<i>S. predistentus</i>
6	28.54	3.24	1.65	1.96	<i>S. distentus</i>	7	28.89	2.72	0.93	2.91	<i>S. predistentus</i>
6	28.54	3.70	2.01	1.84	<i>S. distentus</i>	7	28.89	3.14	1.36	2.31	<i>S. predistentus</i>
6	28.54	3.00	1.38	2.18	<i>S. distentus</i>	7	28.89	3.40	1.11	3.06	<i>S. predistentus</i>
6	28.54	3.44	1.34	2.56	<i>S. distentus</i>	7	28.89	2.42	1.08	2.24	<i>S. predistentus</i>
6	28.54	3.37	1.60	2.10	<i>S. distentus</i>	7	28.89	3.03	1.10	2.76	<i>S. predistentus</i>
6	28.54	3.65	1.52	2.40	<i>S. distentus</i>	7	28.89	2.78	0.92	3.04	<i>S. predistentus</i>
6	28.54	3.50	1.49	2.35	<i>S. distentus</i>	7	28.89	2.68	1.21	2.22	<i>S. predistentus</i>
6	28.54	3.23	1.39	2.32	<i>S. distentus</i>	7	28.89	2.59	1.11	2.32	<i>S. predistentus</i>
6	28.54	2.78	1.47	1.89	<i>S. distentus</i>	7	28.89	2.83	1.18	2.40	<i>S. predistentus</i>
6	28.54	3.47	1.39	2.49	<i>S. distentus</i>	7	28.89	2.91	0.97	3.02	<i>S. predistentus</i>
6	28.54	3.06	1.41	2.17	<i>S. distentus</i>	7	28.89	2.63	0.83	3.16	<i>S. predistentus</i>
6	28.54	3.44	1.41	2.44	<i>S. distentus</i>	7	28.89	2.24	0.88	2.54	<i>S. predistentus</i>
6	28.54	2.82	1.15	2.46	<i>S. distentus</i>	7	28.89	2.83	1.23	2.31	<i>S. predistentus</i>
6	28.54	4.03	1.92	2.10	<i>S. distentus</i>	7	28.89	3.06	1.06	2.88	<i>S. predistentus</i>
6	28.54	2.96	1.34	2.21	<i>S. distentus</i>	7	28.89	3.62	1.55	2.33	<i>S. predistentus</i>
6	28.54	2.95	1.16	2.54	<i>S. distentus</i>	7	28.89	2.99	0.83	3.59	<i>S. predistentus</i>
6	28.54	3.14	1.51	2.09	<i>S. distentus</i>	7	28.89	3.35	1.44	2.33	<i>S. predistentus</i>
6	28.54	2.93	1.44	2.03	<i>S. distentus</i>	7	28.89	2.65	1.31	2.02	<i>S. predistentus</i>
7	28.89	3.08	0.95	3.24	<i>S. predistentus</i>	7	28.89	3.13	1.10	2.85	<i>S. predistentus</i>
7	28.89	3.75	1.18	3.18	<i>S. predistentus</i>	7	28.89	3.45	1.21	2.85	<i>S. predistentus</i>
7	28.89	2.37	0.82	2.90	<i>S. predistentus</i>	7	28.89	2.83	0.88	3.20	<i>S. predistentus</i>
7	28.89	3.03	1.18	2.57	<i>S. predistentus</i>	7	28.89	2.75	1.28	2.15	<i>S. predistentus</i>
7	28.89	2.31	0.74	3.13	<i>S. predistentus</i>	7	28.89	3.48	1.15	3.04	<i>S. predistentus</i>
7	28.89	3.52	1.39	2.53	<i>S. predistentus</i>	7	28.89	2.91	1.06	2.74	<i>S. predistentus</i>
7	28.89	3.32	1.10	3.03	<i>S. predistentus</i>	7	28.89	2.83	1.00	2.84	<i>S. predistentus</i>
7	28.89	2.83	1.29	2.19	<i>S. predistentus</i>	7	28.89	2.91	1.55	1.87	<i>S. predistentus</i>

Table A1. Continued.

Table A1. Continued.

Oligocene *Sphenolithus* evolutionary lineage

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
7	28.89	2.99	1.11	2.69	<i>S. predistentus</i>
7	28.89	2.95	1.10	2.69	<i>S. predistentus</i>
7	28.89	3.48	1.31	2.66	<i>S. distentus</i>
7	28.89	3.81	1.47	2.59	<i>S. distentus</i>
7	28.89	2.99	1.49	2.01	<i>S. distentus</i>
7	28.89	2.85	2.00	1.43	<i>S. distentus</i>
7	28.89	2.80	1.26	2.22	<i>S. distentus</i>
7	28.89	2.80	1.18	2.37	<i>S. distentus</i>
7	28.89	2.80	1.31	2.14	<i>S. distentus</i>
7	28.89	3.22	1.34	2.40	<i>S. distentus</i>
7	28.89	2.67	0.98	2.72	<i>S. distentus</i>
7	28.89	3.03	1.28	2.37	<i>S. distentus</i>
7	28.89	2.49	1.06	2.34	<i>S. distentus</i>
7	28.89	2.14	0.75	2.85	<i>S. distentus</i>
7	28.89	2.47	1.28	1.94	<i>S. distentus</i>
7	28.89	2.39	1.15	2.09	<i>S. distentus</i>
7	28.89	3.65	2.00	1.83	<i>S. distentus</i>
7	28.89	2.52	1.11	2.26	<i>S. distentus</i>
7	28.89	2.67	1.06	2.51	<i>S. distentus</i>
7	28.89	3.04	1.78	1.71	<i>S. distentus</i>
7	28.89	3.24	1.42	2.28	<i>S. distentus</i>
7	28.89	2.62	1.10	2.39	<i>S. distentus</i>
7	28.89	3.14	1.26	2.49	<i>S. distentus</i>
7	28.89	2.65	1.23	2.16	<i>S. distentus</i>
7	28.89	3.24	1.16	2.79	<i>S. distentus</i>
7	28.89	3.17	1.59	2.00	<i>S. distentus</i>
7	28.89	3.34	1.93	1.73	<i>S. distentus</i>
7	28.89	3.34	1.34	2.49	<i>S. distentus</i>
7	28.89	3.55	1.51	2.36	<i>S. distentus</i>
8	29.20	2.55	0.95	2.69	<i>S. predistentus</i>
8	29.20	4.13	1.54	2.68	<i>S. predistentus</i>
8	29.20	3.19	1.47	2.17	<i>S. predistentus</i>
8	29.20	4.13	1.75	2.36	<i>S. predistentus</i>
8	29.20	4.19	1.38	3.05	<i>S. predistentus</i>
8	29.20	3.19	1.36	2.35	<i>S. predistentus</i>
8	29.20	2.91	1.23	2.37	<i>S. predistentus</i>
8	29.20	4.11	1.90	2.16	<i>S. predistentus</i>
8	29.20	3.75	1.15	3.27	<i>S. predistentus</i>
8	29.20	3.03	1.21	2.50	<i>S. predistentus</i>
8	29.20	2.85	0.52	5.44	<i>S. predistentus</i>
8	29.20	2.54	0.92	2.77	<i>S. predistentus</i>
8	29.20	2.77	0.85	3.25	<i>S. predistentus</i>
8	29.20	3.13	1.39	2.25	<i>S. predistentus</i>
8	29.20	3.18	1.23	2.59	<i>S. predistentus</i>
8	29.20	2.60	0.87	3.00	<i>S. predistentus</i>
8	29.20	2.95	0.97	3.05	<i>S. predistentus</i>
8	29.20	2.65	0.97	2.75	<i>S. predistentus</i>
8	29.20	4.04	1.34	3.01	<i>S. predistentus</i>
8	29.20	2.78	1.31	2.13	<i>S. predistentus</i>
8	29.20	2.62	0.88	2.96	<i>S. predistentus</i>
8	29.20	3.18	1.16	2.73	<i>S. predistentus</i>
8	29.20	3.36	1.21	2.77	<i>S. predistentus</i>
8	29.20	3.88	1.52	2.55	<i>S. predistentus</i>
8	29.20	4.03	1.41	2.86	<i>S. predistentus</i>
8	29.20	3.55	1.33	2.68	<i>S. predistentus</i>
8	29.20	3.31	1.44	2.30	<i>S. predistentus</i>
8	29.20	2.41	1.05	2.30	<i>S. predistentus</i>
8	29.20	3.01	1.24	2.42	<i>S. predistentus</i>
8	29.20	2.98	1.16	2.56	<i>S. predistentus</i>
8	29.20	4.29	1.72	2.50	<i>S. predistentus</i>
8	29.20	3.96	1.31	3.03	<i>S. predistentus</i>
8	29.20	2.52	0.85	2.96	<i>S. predistentus</i>
8	29.20	3.05	1.29	2.35	<i>S. predistentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
8	29.20	2.87	1.05	2.73	<i>S. predistentus</i>
8	29.20	3.72	1.52	2.44	<i>S. predistentus</i>
8	29.20	2.83	0.97	2.93	<i>S. predistentus</i>
8	29.20	2.34	0.88	2.65	<i>S. predistentus</i>
8	29.20	3.19	1.39	2.29	<i>S. predistentus</i>
8	29.20	3.08	0.92	3.36	<i>S. predistentus</i>
8	29.20	3.05	1.20	2.55	<i>S. predistentus</i>
8	29.20	3.36	0.98	3.42	<i>S. predistentus</i>
8	29.20	3.01	1.26	2.39	<i>S. predistentus</i>
8	29.20	3.50	0.93	3.75	<i>S. predistentus</i>
8	29.20	3.60	1.38	2.62	<i>S. predistentus</i>
8	29.20	2.83	0.85	3.33	<i>S. predistentus</i>
8	29.20	3.42	1.64	2.09	<i>S. predistentus</i>
8	29.20	2.62	0.84	3.14	<i>S. predistentus</i>
8	29.20	4.50	1.42	3.16	<i>S. predistentus</i>
8	29.20	3.50	1.03	3.40	<i>S. predistentus</i>
8	29.20	2.91	1.10	2.66	<i>S. predistentus</i>
8	29.20	4.54	1.97	2.31	<i>S. predistentus</i>
8	29.20	3.95	1.56	2.54	<i>S. predistentus</i>
8	29.20	3.65	1.46	2.51	<i>S. predistentus</i>
8	29.20	3.03	1.23	2.47	<i>S. predistentus</i>
8	29.20	3.16	1.39	2.27	<i>S. predistentus</i>
8	29.20	3.00	0.85	3.52	<i>S. predistentus</i>
8	29.20	3.47	1.47	2.36	<i>S. distentus</i>
8	29.20	2.83	1.16	2.44	<i>S. distentus</i>
8	29.20	3.28	1.36	2.41	<i>S. distentus</i>
8	29.20	2.64	1.64	1.61	<i>S. distentus</i>
8	29.20	3.37	1.65	2.04	<i>S. distentus</i>
8	29.20	2.47	1.11	2.22	<i>S. distentus</i>
8	29.20	2.80	1.28	2.19	<i>S. distentus</i>
8	29.20	3.70	1.72	2.15	<i>S. distentus</i>
8	29.20	3.32	1.31	2.54	<i>S. distentus</i>
8	29.20	2.95	1.10	2.69	<i>S. distentus</i>
8	29.20	2.88	1.56	1.85	<i>S. distentus</i>
8	29.20	3.34	1.42	2.34	<i>S. distentus</i>
8	29.20	3.00	1.36	2.20	<i>S. distentus</i>
8	29.20	3.47	1.38	2.52	<i>S. distentus</i>
8	29.20	2.96	1.29	2.29	<i>S. distentus</i>
8	29.20	3.21	1.67	1.92	<i>S. distentus</i>
8	29.20	2.55	1.13	2.26	<i>S. distentus</i>
8	29.20	2.96	1.10	2.70	<i>S. distentus</i>
8	29.20	3.23	1.83	1.76	<i>S. distentus</i>
8	29.20	3.42	1.92	1.79	<i>S. distentus</i>
8	29.20	2.65	1.18	2.25	<i>S. distentus</i>
8	29.20	3.41	1.88	1.81	<i>S. distentus</i>
8	29.20	3.21	0.98	3.27	<i>S. distentus</i>
8	29.20	2.98	1.24	2.39	<i>S. distentus</i>
8	29.20	3.52	1.97	1.79	<i>S. distentus</i>
8	29.20	3.82	2.21	1.73	<i>S. distentus</i>
8	29.20	2.67	1.34	1.99	<i>S. distentus</i>
8	29.20	3.54	1.85	1.91	<i>S. distentus</i>
8	29.20	3.64	1.24	2.92	<i>S. distentus</i>
8	29.20	3.41	1.72	1.98	<i>S. distentus</i>
8	29.20	2.70	1.10	2.46	<i>S. distentus</i>
8	29.20	3.59	2.01	1.78	<i>S. distentus</i>
8	29.20	3.57	1.52	2.34	<i>S. distentus</i>
8	29.20	4.00	1.60	2.49	<i>S. distentus</i>
8	29.20	3.00	0.88	3.39	<i>S. distentus</i>
8	29.20	3.41	2.16	1.58	<i>S. distentus</i>
8	29.20	3.64	1.92	1.90	<i>S. distentus</i>
8	29.20	2.87	1.49	1.92	<i>S. distentus</i>
8	29.20	3.41	1.52	2.24	<i>S. distentus</i>
8	29.20	3.54	2.13	1.66	<i>S. ciperoensis?</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID	Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
8	29.20	3.70	2.33	1.59	<i>S. ciperoensis?</i>	9	29.51	4.14	1.52	2.72	<i>S. predistentus</i>
8	29.20	3.68	2.13	1.73	<i>S. ciperoensis?</i>	9	29.51	4.24	1.65	2.56	<i>S. predistentus</i>
8	29.20	3.31	2.10	1.58	<i>S. ciperoensis?</i>	9	29.51	3.73	1.13	3.30	<i>S. predistentus</i>
9	29.51	3.57	1.23	2.91	<i>S. predistentus</i>	9	29.51	2.90	1.11	2.60	<i>S. predistentus</i>
9	29.51	2.45	0.95	2.59	<i>S. predistentus</i>	9	29.51	3.29	1.44	2.28	<i>S. predistentus</i>
9	29.51	3.06	0.92	3.34	<i>S. predistentus</i>	9	29.51	3.94	1.24	3.17	<i>S. predistentus</i>
9	29.51	3.22	0.97	3.34	<i>S. predistentus</i>	9	29.51	3.16	1.01	3.11	<i>S. predistentus</i>
9	29.51	3.24	1.24	2.61	<i>S. predistentus</i>	9	29.51	3.08	0.98	3.13	<i>S. predistentus</i>
9	29.51	3.13	1.03	3.03	<i>S. predistentus</i>	9	29.51	3.57	1.37	2.60	<i>S. predistentus</i>
9	29.51	2.49	0.80	3.10	<i>S. predistentus</i>	9	29.51	2.91	1.06	2.74	<i>S. predistentus</i>
9	29.51	3.11	1.28	2.44	<i>S. predistentus</i>	9	29.51	3.14	1.24	2.53	<i>S. predistentus</i>
9	29.51	2.95	1.05	2.81	<i>S. predistentus</i>	9	29.51	2.86	1.05	2.73	<i>S. predistentus</i>
9	29.51	3.84	1.21	3.18	<i>S. predistentus</i>	9	29.51	3.45	1.46	2.37	<i>S. predistentus</i>
9	29.51	3.62	1.37	2.63	<i>S. predistentus</i>	9	29.51	3.17	1.36	2.34	<i>S. predistentus</i>
9	29.51	2.41	0.74	3.27	<i>S. predistentus</i>	9	29.51	3.16	1.52	2.08	<i>S. distentus</i>
9	29.51	2.68	1.11	2.41	<i>S. predistentus</i>	9	29.51	2.81	1.44	1.95	<i>S. distentus</i>
9	29.51	2.59	0.85	3.04	<i>S. predistentus</i>	9	29.51	3.14	1.39	2.26	<i>S. distentus</i>
9	29.51	3.53	1.24	2.84	<i>S. predistentus</i>	9	29.51	3.32	1.57	2.11	<i>S. distentus</i>
9	29.51	3.99	1.62	2.46	<i>S. predistentus</i>	9	29.51	3.14	0.97	3.25	<i>S. distentus</i>
9	29.51	3.89	1.47	2.64	<i>S. predistentus</i>	9	29.51	3.01	1.26	2.39	<i>S. distentus</i>
9	29.51	3.17	0.90	3.53	<i>S. predistentus</i>	9	29.51	2.47	1.41	1.76	<i>S. distentus</i>
9	29.51	3.09	1.21	2.55	<i>S. predistentus</i>	9	29.51	2.95	1.37	2.14	<i>S. distentus</i>
9	29.51	3.57	1.46	2.45	<i>S. predistentus</i>	9	29.51	3.37	1.64	2.06	<i>S. distentus</i>
9	29.51	3.13	1.13	2.77	<i>S. predistentus</i>	9	29.51	3.34	1.90	1.76	<i>S. distentus</i>
9	29.51	2.90	1.36	2.13	<i>S. predistentus</i>	9	29.51	3.53	1.90	1.86	<i>S. distentus</i>
9	29.51	3.24	1.42	2.28	<i>S. predistentus</i>	9	29.51	3.29	1.29	2.54	<i>S. distentus</i>
9	29.51	2.81	1.10	2.57	<i>S. predistentus</i>	9	29.51	3.01	1.26	2.39	<i>S. distentus</i>
9	29.51	2.73	1.29	2.11	<i>S. predistentus</i>	9	29.51	3.62	1.39	2.60	<i>S. distentus</i>
9	29.51	3.19	1.29	2.47	<i>S. predistentus</i>	9	29.51	3.40	1.60	2.12	<i>S. distentus</i>
9	29.51	2.85	1.26	2.26	<i>S. predistentus</i>	9	29.51	3.88	1.64	2.37	<i>S. distentus</i>
9	29.51	3.84	1.52	2.53	<i>S. predistentus</i>	9	29.51	2.52	0.85	2.96	<i>S. distentus</i>
9	29.51	3.86	1.36	2.84	<i>S. predistentus</i>	9	29.51	3.06	1.28	2.40	<i>S. distentus</i>
9	29.51	3.35	1.31	2.56	<i>S. predistentus</i>	9	29.51	3.44	1.52	2.26	<i>S. distentus</i>
9	29.51	2.68	1.36	1.98	<i>S. predistentus</i>	9	29.51	3.58	1.31	2.74	<i>S. distentus</i>
9	29.51	3.42	1.23	2.79	<i>S. predistentus</i>	9	29.51	2.54	1.18	2.15	<i>S. distentus</i>
9	29.51	3.80	1.28	2.97	<i>S. predistentus</i>	9	29.51	2.95	1.16	2.54	<i>S. distentus</i>
9	29.51	3.27	1.15	2.86	<i>S. predistentus</i>	9	29.51	3.24	1.41	2.30	<i>S. distentus</i>
9	29.51	2.75	0.70	3.91	<i>S. predistentus</i>	9	29.51	3.27	1.54	2.13	<i>S. distentus</i>
9	29.51	3.32	1.05	3.17	<i>S. predistentus</i>	9	29.51	3.21	1.34	2.39	<i>S. distentus</i>
9	29.51	2.83	0.74	3.84	<i>S. predistentus</i>	9	29.51	3.37	1.34	2.51	<i>S. distentus</i>
9	29.51	3.27	1.06	3.08	<i>S. predistentus</i>	10	29.86	2.91	0.97	3.02	<i>S. predistentus</i>
9	29.51	2.77	0.74	3.76	<i>S. predistentus</i>	10	29.86	3.05	1.13	2.70	<i>S. predistentus</i>
9	29.51	3.40	1.24	2.74	<i>S. predistentus</i>	10	29.86	2.98	1.05	2.84	<i>S. predistentus</i>
9	29.51	3.31	1.08	3.06	<i>S. predistentus</i>	10	29.86	3.09	1.13	2.74	<i>S. predistentus</i>
9	29.51	2.49	0.93	2.67	<i>S. predistentus</i>	10	29.86	3.41	1.11	3.06	<i>S. predistentus</i>
9	29.51	3.53	1.33	2.67	<i>S. predistentus</i>	10	29.86	3.78	1.13	3.35	<i>S. predistentus</i>
9	29.51	2.70	1.15	2.36	<i>S. predistentus</i>	10	29.86	3.21	0.77	4.17	<i>S. predistentus</i>
9	29.51	3.01	1.16	2.59	<i>S. predistentus</i>	10	29.86	2.96	1.06	2.78	<i>S. predistentus</i>
9	29.51	3.96	1.54	2.57	<i>S. predistentus</i>	10	29.86	2.62	0.85	3.08	<i>S. predistentus</i>
9	29.51	3.04	1.03	2.95	<i>S. predistentus</i>	10	29.86	3.16	1.13	2.80	<i>S. predistentus</i>
9	29.51	3.50	1.37	2.55	<i>S. predistentus</i>	10	29.86	3.34	1.33	2.52	<i>S. predistentus</i>
9	29.51	3.08	1.42	2.16	<i>S. predistentus</i>	10	29.86	3.06	0.87	3.53	<i>S. predistentus</i>
9	29.51	3.27	1.16	2.82	<i>S. predistentus</i>	10	29.86	2.41	0.88	2.72	<i>S. predistentus</i>
9	29.51	2.62	1.10	2.39	<i>S. predistentus</i>	10	29.86	3.47	1.28	2.72	<i>S. predistentus</i>
9	29.51	3.09	1.11	2.78	<i>S. predistentus</i>	10	29.86	2.72	0.95	2.86	<i>S. predistentus</i>
9	29.51	3.09	1.19	2.59	<i>S. predistentus</i>	10	29.86	3.09	0.98	3.15	<i>S. predistentus</i>
9	29.51	2.65	1.03	2.57	<i>S. predistentus</i>	10	29.86	2.77	0.97	2.86	<i>S. predistentus</i>
9	29.51	3.24	1.60	2.02	<i>S. predistentus</i>	10	29.86	3.37	0.98	3.43	<i>S. predistentus</i>
9	29.51	3.66	1.21	3.03	<i>S. predistentus</i>	10	29.86	3.67	1.11	3.29	<i>S. predistentus</i>
9	29.51	2.80	0.97	2.90	<i>S. predistentus</i>	10	29.86	2.41	0.69	3.50	<i>S. predistentus</i>
9	29.51	3.94	1.26	3.13	<i>S. predistentus</i>	10	29.86	3.31	0.87	3.81	<i>S. predistentus</i>
9	29.51	2.73	1.08	2.53	<i>S. predistentus</i>	10	29.86	3.00	0.82	3.66	<i>S. predistentus</i>
9	29.51	3.13	1.16	2.69	<i>S. predistentus</i>	10	29.86	3.24	1.05	3.09	<i>S. predistentus</i>

Table A1. Continued.

Table A1. Continued.

Oligocene *Sphenolithus* evolutionary lineage

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
10	29.86	2.96	0.90	3.29	<i>S. predistentus</i>
10	29.86	2.91	0.88	3.30	<i>S. predistentus</i>
10	29.86	2.78	0.77	3.62	<i>S. predistentus</i>
10	29.86	2.73	0.67	4.07	<i>S. predistentus</i>
10	29.86	2.72	0.82	3.32	<i>S. predistentus</i>
10	29.86	3.62	1.39	2.60	<i>S. predistentus</i>
10	29.86	2.65	0.93	2.84	<i>S. predistentus</i>
10	29.86	3.32	1.00	3.33	<i>S. predistentus</i>
10	29.86	4.00	1.44	2.77	<i>S. predistentus</i>
10	29.86	2.78	0.75	3.70	<i>S. predistentus</i>
10	29.86	3.00	1.11	2.69	<i>S. predistentus</i>
10	29.86	3.08	1.26	2.44	<i>S. predistentus</i>
10	29.86	3.13	1.16	2.69	<i>S. predistentus</i>
10	29.86	3.42	0.84	4.10	<i>S. predistentus</i>
10	29.86	3.50	1.15	3.06	<i>S. predistentus</i>
10	29.86	2.98	0.84	3.57	<i>S. predistentus</i>
10	29.86	2.60	0.88	2.94	<i>S. predistentus</i>
10	29.86	3.34	1.21	2.76	<i>S. predistentus</i>
10	29.86	2.85	0.90	3.16	<i>S. predistentus</i>
10	29.86	3.46	1.16	2.97	<i>S. predistentus</i>
10	29.86	3.52	0.85	4.13	<i>S. predistentus</i>
10	29.86	3.34	0.98	3.40	<i>S. predistentus</i>
10	29.86	3.68	1.02	3.63	<i>S. predistentus</i>
10	29.86	3.18	1.20	2.66	<i>S. predistentus</i>
10	29.86	3.62	1.24	2.91	<i>S. predistentus</i>
10	29.86	2.88	1.05	2.75	<i>S. predistentus</i>
10	29.86	2.77	0.70	3.93	<i>S. predistentus</i>
10	29.86	3.34	1.20	2.79	<i>S. predistentus</i>
10	29.86	2.98	0.93	3.19	<i>S. predistentus</i>
10	29.86	2.72	0.84	3.25	<i>S. predistentus</i>
10	29.86	2.64	0.87	3.04	<i>S. predistentus</i>
10	29.86	2.49	0.87	2.87	<i>S. predistentus</i>
10	29.86	2.96	0.93	3.18	<i>S. predistentus</i>
10	29.86	2.23	0.75	2.96	<i>S. predistentus</i>
10	29.86	2.65	1.00	2.66	<i>S. predistentus</i>
10	29.86	3.09	1.00	3.10	<i>S. predistentus</i>
10	29.86	3.06	0.97	3.17	<i>S. predistentus</i>
10	29.86	3.09	0.85	3.63	<i>S. predistentus</i>
10	29.86	3.08	0.80	3.84	<i>S. predistentus</i>
10	29.86	2.57	0.92	2.80	<i>S. predistentus</i>
10	29.86	3.72	1.03	3.60	<i>S. predistentus</i>
10	29.86	2.91	0.87	3.36	<i>S. predistentus</i>
10	29.86	3.50	1.29	2.71	<i>S. predistentus</i>
10	29.86	2.95	1.00	2.95	<i>S. predistentus</i>
10	29.86	2.88	1.23	2.35	<i>S. predistentus</i>
10	29.86	2.28	0.97	2.36	<i>S. predistentus</i>
10	29.86	3.23	1.20	2.70	<i>S. predistentus</i>
10	29.86	3.57	1.21	2.95	<i>S. predistentus</i>
10	29.86	3.60	1.39	2.59	<i>S. predistentus</i>
10	29.86	3.49	1.33	2.63	<i>S. predistentus</i>
10	29.86	2.51	0.82	3.06	<i>S. predistentus</i>
10	29.86	3.23	1.34	2.40	<i>S. predistentus</i>
10	29.86	2.91	1.41	2.07	<i>S. predistentus</i>
10	29.86	2.75	0.92	3.00	<i>S. predistentus</i>
10	29.86	3.03	1.24	2.43	<i>S. predistentus</i>
10	29.86	3.60	1.15	3.14	<i>S. predistentus</i>
10	29.86	2.88	1.05	2.75	<i>S. predistentus</i>
10	29.86	2.54	1.08	2.35	<i>S. distentus</i>
10	29.86	2.55	1.08	2.36	<i>S. distentus</i>
10	29.86	2.78	1.21	2.30	<i>S. distentus</i>
10	29.86	2.72	1.23	2.21	<i>S. distentus</i>
10	29.86	3.14	1.47	2.13	<i>S. distentus</i>
10	29.86	2.98	1.16	2.56	<i>S. distentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
10	29.86	3.09	1.78	1.73	<i>S. distentus</i>
10	29.86	3.47	1.33	2.62	<i>S. distentus</i>
10	29.86	3.50	1.28	2.74	<i>S. distentus</i>
10	29.86	3.21	1.51	2.13	<i>S. distentus</i>
10	29.86	3.18	1.24	2.55	<i>S. distentus</i>
10	29.86	3.16	1.18	2.68	<i>S. distentus</i>
10	29.86	3.03	1.28	2.37	<i>S. distentus</i>
10	29.86	3.65	1.29	2.82	<i>S. distentus</i>
10	29.86	3.29	1.18	2.79	<i>S. distentus</i>
10	29.86	3.31	1.03	3.21	<i>S. distentus</i>
10	29.86	3.23	1.39	2.32	<i>S. distentus</i>
10	29.86	2.51	1.11	2.25	<i>S. distentus</i>
10	29.86	3.54	1.06	3.32	<i>S. distentus</i>
10	29.86	2.98	1.36	2.19	<i>S. distentus</i>
11	31.6	2.15	0.97	2.22	transitional
11	31.6	2.36	0.86	2.73	transitional
11	31.6	1.63	0.65	2.49	transitional
11	31.6	1.76	0.66	2.66	transitional
11	31.6	1.85	0.69	2.67	transitional
11	31.6	1.91	0.90	2.13	transitional
11	31.6	1.89	0.80	2.35	transitional
11	31.6	2.22	0.71	3.12	transitional
11	31.6	2.74	1.27	2.17	transitional
11	31.6	1.78	0.67	2.67	transitional
11	31.6	1.70	0.70	2.41	transitional
11	31.6	2.08	0.96	2.18	transitional
11	31.6	1.99	0.90	2.20	transitional
11	31.6	2.01	0.84	2.38	transitional
11	31.6	2.23	1.16	1.93	transitional
11	31.6	2.64	1.06	2.50	transitional
11	31.6	2.43	1.08	2.24	transitional
11	31.6	2.00	0.66	3.01	transitional
11	31.6	2.30	0.97	2.37	transitional
11	31.6	1.85	0.44	4.24	transitional
11	31.6	2.12	0.82	2.59	transitional
11	31.6	2.17	0.84	2.59	transitional
11	31.6	2.42	0.98	2.48	transitional
11	31.6	1.72	0.62	2.78	transitional
11	31.6	1.94	0.67	2.88	transitional
11	31.6	2.10	0.96	2.19	transitional
11	31.6	2.20	0.67	3.30	transitional
11	31.6	2.03	0.99	2.06	transitional
11	31.6	1.81	0.59	3.08	<i>S. predistentus</i>
11	31.6	1.86	0.60	3.12	<i>S. predistentus</i>
11	31.6	1.86	0.59	3.12	<i>S. predistentus</i>
11	31.6	2.14	0.90	2.39	<i>S. predistentus</i>
11	31.6	2.28	0.64	3.56	<i>S. predistentus</i>
11	31.6	2.43	0.92	2.65	<i>S. predistentus</i>
11	31.6	2.20	0.48	4.53	<i>S. predistentus</i>
11	31.6	1.76	0.29	6.03	<i>S. predistentus</i>
11	31.6	2.15	0.55	3.88	<i>S. predistentus</i>
11	31.6	1.37	0.51	2.68	<i>S. predistentus</i>
11	31.6	2.02	0.52	3.88	<i>S. predistentus</i>
11	31.6	2.34	0.39	6.00	<i>S. predistentus</i>
11	31.6	1.96	0.58	3.40	<i>S. predistentus</i>
11	31.6	2.61	1.14	2.30	<i>S. predistentus</i>
11	31.6	2.50	0.68	3.70	<i>S. predistentus</i>
11	31.6	2.03	0.68	2.98	<i>S. predistentus</i>
11	31.6	2.13	0.51	4.16	<i>S. predistentus</i>
11	31.6	2.34	0.46	5.13	<i>S. predistentus</i>
11	31.6	1.73	0.44	3.92	<i>S. predistentus</i>
11	31.6	2.17	0.71	3.07	<i>S. predistentus</i>
11	31.6	2.36	0.80	2.95	<i>S. predistentus</i>

Table A1. Continued.

Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID	Sample #	Age (Ma)	Width (μm)	Height (μm)	Ratio W/H	Species ID
11	31.6	2.05	0.58	3.55	<i>S. predistentus</i>	12	33.02	2.27	0.81	2.79	transitional
11	31.6	2.40	0.47	5.13	<i>S. predistentus</i>	12	33.02	2.00	0.64	3.14	transitional
11	31.6	2.46	0.47	5.25	<i>S. predistentus</i>	12	33.02	2.43	0.98	2.48	transitional
11	31.6	1.94	0.43	4.50	<i>S. predistentus</i>	12	33.02	2.69	0.98	2.74	transitional
11	31.6	2.06	0.34	6.02	<i>S. predistentus</i>	12	33.02	2.55	0.93	2.73	transitional
11	31.6	2.13	0.73	2.93	<i>S. predistentus</i>	12	33.02	2.23	0.62	3.61	transitional
11	31.6	2.06	0.50	4.13	<i>S. predistentus</i>	12	33.02	2.65	0.75	3.55	transitional
11	31.6	1.89	0.35	5.34	<i>S. predistentus</i>	12	33.02	3.36	1.02	3.29	transitional
11	31.6	1.86	0.63	2.96	<i>S. predistentus</i>	12	33.02	2.26	0.75	3.01	transitional
11	31.6	1.96	0.64	3.08	<i>S. predistentus</i>	12	33.02	2.79	0.75	3.72	transitional
11	31.6	1.56	0.59	2.64	<i>S. predistentus</i>	12	33.02	3.07	1.32	2.33	transitional
11	31.6	2.14	0.45	4.79	<i>S. predistentus</i>	12	33.02	2.32	0.70	3.29	transitional
11	31.6	2.31	0.98	2.35	<i>S. predistentus</i>	12	33.02	2.31	0.70	3.30	transitional
11	31.6	3.20	0.77	4.17	<i>S. predistentus</i>	12	33.02	1.93	0.62	3.09	transitional
11	31.6	2.50	0.87	2.87	<i>S. predistentus</i>	12	33.02	2.56	0.52	4.90	<i>S. predistentus</i>
11	31.6	2.43	0.86	2.82	<i>S. predistentus</i>	12	33.02	2.27	0.55	4.10	<i>S. predistentus</i>
11	31.6	1.72	0.58	2.95	<i>S. predistentus</i>	12	33.02	2.47	0.54	4.58	<i>S. predistentus</i>
11	31.6	1.81	0.79	2.30	<i>S. predistentus</i>	12	33.02	2.72	0.73	3.75	<i>S. predistentus</i>
11	31.6	1.99	0.74	2.70	<i>S. predistentus</i>	12	33.02	2.94	0.98	3.00	<i>S. predistentus</i>
11	31.6	1.80	0.78	2.31	<i>S. predistentus</i>	12	33.02	2.77	0.75	3.71	<i>S. predistentus</i>
11	31.6	1.71	0.63	2.73	<i>S. predistentus</i>	12	33.02	2.62	0.78	3.36	<i>S. predistentus</i>
11	31.6	2.37	1.03	2.31	<i>S. predistentus</i>	12	33.02	1.92	0.55	3.48	<i>S. predistentus</i>
11	31.6	1.70	0.60	2.85	<i>S. predistentus</i>	12	33.02	2.53	0.58	4.34	<i>S. predistentus</i>
11	31.6	1.74	0.40	4.38	<i>S. predistentus</i>	12	33.02	2.33	0.74	3.16	<i>S. predistentus</i>
11	31.6	2.76	0.65	4.26	<i>S. predistentus</i>	12	33.02	2.21	0.56	3.94	<i>S. predistentus</i>
11	31.6	1.86	0.57	3.24	<i>S. predistentus</i>	12	33.02	3.63	0.91	4.00	<i>S. predistentus</i>
11	31.6	2.27	0.64	3.54	<i>S. predistentus</i>	12	33.02	2.16	0.60	3.59	<i>S. predistentus</i>
11	31.6	1.97	0.51	3.83	<i>S. predistentus</i>	12	33.02	2.56	0.77	3.31	<i>S. predistentus</i>
11	31.6	2.58	0.95	2.72	<i>S. predistentus</i>	12	33.02	3.06	0.79	3.90	<i>S. predistentus</i>
11	31.6	1.86	0.62	3.01	<i>S. predistentus</i>	12	33.02	2.29	0.57	4.05	<i>S. predistentus</i>
11	31.6	2.64	0.91	2.91	<i>S. predistentus</i>	12	33.02	1.95	0.63	3.09	<i>S. predistentus</i>
11	31.6	2.45	0.51	4.78	<i>S. predistentus</i>	12	33.02	2.20	0.69	3.19	<i>S. predistentus</i>
11	31.6	2.41	0.36	6.77	<i>S. predistentus</i>	12	33.02	2.69	0.81	3.34	<i>S. predistentus</i>
11	31.6	1.81	0.58	3.12	<i>S. predistentus</i>	12	33.02	3.30	0.98	3.35	<i>S. predistentus</i>
11	31.6	2.25	0.51	4.44	<i>S. predistentus</i>	12	33.02	3.09	0.55	5.58	<i>S. predistentus</i>
11	31.6	2.23	0.66	3.39	<i>S. predistentus</i>	12	33.02	2.36	0.73	3.26	<i>S. predistentus</i>
11	31.6	1.98	0.46	4.30	<i>S. predistentus</i>	12	33.02	2.33	0.70	3.32	<i>S. predistentus</i>
11	31.6	2.35	0.43	5.40	<i>S. predistentus</i>	12	33.02	3.12	0.61	5.08	<i>S. predistentus</i>
11	31.6	2.12	0.92	2.31	<i>S. predistentus</i>	12	33.02	2.46	0.72	3.40	<i>S. predistentus</i>
11	31.6	2.17	0.49	4.45	<i>S. predistentus</i>	12	33.02	2.68	0.64	4.15	<i>S. predistentus</i>
11	31.6	2.04	0.67	3.06	<i>S. predistentus</i>	12	33.02	2.39	0.55	4.38	<i>S. predistentus</i>
11	31.6	2.00	0.61	3.29	<i>S. predistentus</i>	12	33.02	2.69	0.66	4.07	<i>S. predistentus</i>
11	31.6	2.55	0.42	6.11	<i>S. predistentus</i>	12	33.02	2.48	0.55	4.51	<i>S. predistentus</i>
11	31.6	2.56	0.94	2.72	<i>S. predistentus</i>	12	33.02	2.35	0.97	2.41	<i>S. predistentus</i>
11	31.6	1.90	0.70	2.73	<i>S. predistentus</i>	12	33.02	2.59	0.44	5.84	<i>S. predistentus</i>
11	31.6	1.89	0.75	2.54	<i>S. predistentus</i>	12	33.02	3.13	0.83	3.78	<i>S. predistentus</i>
11	31.6	1.84	0.48	3.82	<i>S. predistentus</i>	12	33.02	2.28	0.55	4.15	<i>S. predistentus</i>
11	31.6	3.09	1.07	2.90	<i>S. predistentus</i>	12	33.02	2.76	0.64	4.33	<i>S. predistentus</i>
11	31.6	2.04	0.74	2.77	<i>S. predistentus</i>	12	33.02	2.80	0.72	3.86	<i>S. predistentus</i>
11	31.6	1.84	0.48	3.86	<i>S. predistentus</i>	12	33.02	2.70	0.44	6.12	<i>S. predistentus</i>
11	31.6	2.06	0.74	2.78	<i>S. predistentus</i>	12	33.02	1.99	0.48	4.12	<i>S. predistentus</i>
11	31.6	1.68	0.76	2.19	<i>S. predistentus</i>	12	33.02	2.63	0.60	4.39	<i>S. predistentus</i>
11	31.6	1.91	0.52	3.65	<i>S. predistentus</i>	12	33.02	2.62	0.54	4.87	<i>S. predistentus</i>
11	31.6	1.87	0.47	3.99	<i>S. predistentus</i>	12	33.02	2.06	0.39	5.27	<i>S. predistentus</i>
11	31.6	1.82	0.55	3.32	<i>S. predistentus</i>	12	33.02	2.06	0.39	5.27	<i>S. predistentus</i>
11	31.6	2.23	0.62	3.60	<i>S. predistentus</i>	12	33.02	3.07	0.83	3.70	<i>S. predistentus</i>
11	31.6	1.94	0.55	3.52	<i>S. predistentus</i>	12	33.02	1.99	0.50	3.97	<i>S. predistentus</i>
11	31.6	1.79	0.40	4.47	<i>S. predistentus</i>	12	33.02	2.59	0.58	4.48	<i>S. predistentus</i>
11	31.6	2.22	0.63	3.55	<i>S. predistentus</i>	12	33.02	2.30	0.50	4.57	<i>S. predistentus</i>
12	33.02	2.12	0.72	2.94	transitional	12	33.02	2.50	0.76	3.27	<i>S. predistentus</i>
12	33.02	3.03	0.96	3.16	transitional	12	33.02	2.96	0.96	3.10	<i>S. predistentus</i>
12	33.02	2.65	0.95	2.78	transitional	12	33.02	3.80	0.99	3.83	<i>S. predistentus</i>
12	33.02	2.77	0.95	2.93	transitional	12	33.02	2.36	0.57	4.13	<i>S. predistentus</i>

Table A1. Continued.

Table A1. Continued.

Sample #	Age (Ma)	Width (µm)	Height (µm)	Ratio W/H	Species ID
12	33.02	3.89	1.15	3.39	<i>S. predistentus</i>
12	33.02	2.27	0.49	4.67	<i>S. predistentus</i>
12	33.02	2.48	0.68	3.64	<i>S. predistentus</i>
12	33.02	2.33	0.45	5.22	<i>S. predistentus</i>
12	33.02	3.01	0.53	5.68	<i>S. predistentus</i>
12	33.02	3.09	0.70	4.39	<i>S. predistentus</i>
12	33.02	2.12	0.61	3.50	<i>S. predistentus</i>
12	33.02	2.72	0.50	5.40	<i>S. predistentus</i>
12	33.02	2.15	0.65	3.32	<i>S. predistentus</i>
12	33.02	2.66	0.45	5.94	<i>S. predistentus</i>
12	33.02	2.36	0.64	3.65	<i>S. predistentus</i>
12	33.02	2.33	0.50	4.66	<i>S. predistentus</i>
12	33.02	2.15	0.41	5.26	<i>S. predistentus</i>
12	33.02	2.87	0.46	6.29	<i>S. predistentus</i>
12	33.02	2.21	0.60	3.67	<i>S. predistentus</i>
12	33.02	2.70	0.66	4.11	<i>S. predistentus</i>
12	33.02	2.73	0.88	3.12	<i>S. predistentus</i>
12	33.02	2.24	0.61	3.67	<i>S. predistentus</i>
12	33.02	2.20	0.47	4.73	<i>S. predistentus</i>
12	33.02	3.41	0.99	3.43	<i>S. predistentus</i>
12	33.02	2.57	0.65	3.95	<i>S. predistentus</i>
12	33.02	2.12	0.42	5.02	<i>S. predistentus</i>
12	33.02	2.33	0.52	4.48	<i>S. predistentus</i>
12	33.02	2.80	0.75	3.75	<i>S. predistentus</i>
12	33.02	3.39	0.82	4.12	<i>S. predistentus</i>
12	33.02	2.76	0.65	4.26	<i>S. predistentus</i>
12	33.02	3.12	0.91	3.41	<i>S. predistentus</i>
12	33.02	3.09	0.96	3.22	<i>S. predistentus</i>
12	33.02	2.60	0.63	4.14	<i>S. predistentus</i>
12	33.02	2.67	0.59	4.54	<i>S. predistentus</i>
12	33.02	2.64	0.63	4.20	<i>S. predistentus</i>
12	33.02	2.47	0.66	3.77	<i>S. predistentus</i>
12	33.02	2.84	0.90	3.15	<i>S. predistentus</i>
12	33.02	2.53	0.70	3.64	<i>S. predistentus</i>
12	33.02	3.14	0.82	3.83	<i>S. predistentus</i>
12	33.02	2.22	0.59	3.76	<i>S. predistentus</i>
12	33.02	1.93	0.61	3.16	<i>S. predistentus</i>
12	33.02	3.42	0.77	4.45	<i>S. predistentus</i>
12	33.02	3.19	0.61	5.27	<i>S. predistentus</i>
12	33.02	2.31	0.48	4.82	<i>S. predistentus</i>

Table A1. Continued.

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