Biometry of Upper Cretaceous (Cenomanian – Maastrichtian) coccoliths – a record of long-term stability and interspecies size shifts

Biométrie des coccolites du Crétacé supérieur – un enregistrement de stabilité sur le long-terme et changements de taille interspécifiques

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Abstract

Biometric measurements of Mesozoic coccoliths (coccolith length and width) have been used in short-term biostratigraphic, taxonomic and palaeoecologic studies, but until now, not over longer time scales. Here we present a long time-series study (~30 million years) for the Upper Cretaceous, which aims to identify broad trends in coccolith size and to understand the factors governing coccolith size change over long time scales. We have generated biometric data for the dominant Upper Cretaceous coccolith groups, *Broinsonia*/*Arkhangelskiella*, *Prediscosphaera*, *Retecapsa* and *Watznaueria*, from 36 Cenomanian – Maastrichtian (100.5-66 Ma) samples from Goban Spur in the northeast Atlantic (DSDP Site 549). These data show that the coccolith sizes within *Prediscosphaera*, *Retecapsa* and *Watznaueria* were relatively stable through the Late Cretaceous, with mean size variation less than 0.7µm. Within the *Broinsonia*/*Arkhangelskiella* group there was more pronounced variation, with a mean size increase from ~6µm in the Cenomanian to ~10µm in the Campanian. This significant change in mean size was largely driven by evolutionary turnover (species origination and extinctions), and, in particular, the appearance of larger species/subspecies (*Broinsonia parca parca*, *Broinsonia parca constricta*, *Arkhangelskiella cymbiformis*) in the early Campanian, replacing smaller species, such as *Broinsonia signata* and *Broinsonia enormis*. Shorter-term size fluctuations within *Broinsonia*/*Arkhangelskiella*, observed across the late Cenomanian – Turonian and late Campanian – Maastrichtian intervals, may, however, reflect changing palaeoenvironmental conditions, such as sea surface temperature and nutrient availability.

Résumé

Les dimensions des coccolites du Mésozoïque (longueur et largeur de coccolite) ont été utilisées dans des études biostratigraphique, taxonomique et paléoécologique sur le court-terme mais jusqu'à présent, jamais sur le long-terme. Ici, nous présentons l'étude d'une série chronologique à échelle de temps longue (~30 millions d'années) du Crétacé supérieur visant à identifier les tendances générales de la taille des coccolites et de comprendre les facteurs gouvernant les changements de taille des coccolites sur une échelle de temps longue. Nous avons généré des données biométriques pour les groupes de coccolites dominants au Crétacé supérieur, *Broinsonia*/*Arkhangelskiella*, *Prediscosphaera*, *Retecapsa* et *Watznaueria*, sur 36 échantillons du Cénomanien – Maastrichtien (100.5-66 Ma) provenant du Goban Spur dans l'Atlantique Nord-Est (DSDP Site 549). Ces données montrent que la taille des coccolites appartenant aux groupes *Prediscosphaera*, *Retecapsa* and *Watznaueria* fut relativement stable durant tout le Crétacé supérieur, avec une variation de la taille moyenne inférieure à 0.7 µm. Au sein du groupe *Broinsonia*/*Arkhangelskiella* les variations furent plus prononcées, avec une augmentation de la taille moyenne de ~6µm au Cénomanien jusqu'à ~10µm au Campanien. Ce changement significatif de la taille moyenne fut largement dû aux processus évolutifs (spéciations et extinctions), et en particulier à l'apparition d'espèce/sous-espèces plus larges (*Broinsonia parca parca*, *Broinsonia parca constricta*, *Arkhangelskiella cymbiformis*) au Campanien inférieur, remplaçant des espèces plus petites telles que *Broinsonia signata* et *Broinsonia enormis*. Cependant, les fluctuations à court-terme au sein du groupe *Broinsonia*/*Arkhangelskiella*, observées aux transitions Cénomanien – Turonien et Campanien – Maastrichtien, pourraient refléter un changement des conditions paléoenvironnemental tel que la température superficielle des eaux océanique et la disponibilité en nutriment.

Keywords: Calcareous Nannofossils, Biometry, Late Cretaceous, *Broinsonia*/ *Arkhangelskiella* group, DSDP Site 549

Mots-clés: Nannofossiles calcaires, biométrie, Crétacé supérieur, le groupe *Broinsonia*/*Arkhangelskiella*, DSDP Site 549

1 Introduction

Since Stradner (1963) and Perch-Nielsen (1968) first measured the morphometric features of Mesozoic calcareous nannofossils (coccolith length, coccolith width, ellipticity, etc.), biometry has been applied in a range of different studies, including biostratigraphy (e.g., Girgis, 1987), taxonomy (e.g., Hattner et al., 1980) and palaeoecology (e.g., Bornemann et al., 2003). Some of these studies have used relatively arbitrary biometric limits to aid taxonomic subdivision of otherwise morphologically identical nannofossil taxa (e.g., Wise, 1983; Varol, 1989; Burnett, 1997; Shamrock and Watkins, 2009), while others have applied statistical techniques to discriminate distinct populations of size delineated groups (e.g., Tremolada and Erba, 2002; Mattioli et al., 2004; Fraguas and Erba, 2010). Other studies have investigated the possible environmental forcing of size change, by looking at biometric trends through intervals of significant palaeoceanographic or palaeoclimatic change (e.g., oceanic anoxic event (OAE) 1a: Erba et al., 2010; OAE2: Linnert and Mutterlose, 2013). In some cases it has been claimed that these records reveal size changes across intervals of environmental change (e.g., *Biscutum* - Erba et al., 2010; *Broinsonia* - Linnert and Mutterlose, 2013; *Discorhabdus* - López-Otálvaro et al. 2012; and *Watznaueria britannica* - Giraud et al., 2006), whereas other studies have shown very little or no change (*Watznaueria* - Bornemann and Mutterlose, 2006).

The majority of these biometric studies are focused on short intervals of palaeoenvironmental change (e.g., OAEs and stage boundaries) and there are no long-term records available for the Cretaceous. A small number of long term records have been documented for the Cenozoic interval (e.g. Henderiks and Rickaby, 2007; Hannisdal et al., 2012), and the most comprehensive of these highlights the influence of evolutionary controls on coccolith size changes (Herrmann and Thierstein, 2012). Several medium term (10-30 million years) Cenozoic studies have focused on specific taxonomic groups, such as *Reticulofenestra* (Young, 1990) and *Calcidiscus* (Knappertsbusch, 2000). Here, we document the size record of four dominant Cretaceous taxonomic groups, *Broinsonia*/*Arkhangelskiella*, *Prediscosphaera*, *Retecapsa* and *Watznaueria*, through ~30 million years of the Upper Cretaceous, a time interval of considerable environmental change, including OAEs, extreme warmth and the onset of long term climate cooling (Huber et al., 1995, 2002; Miller et al., 2005; Friedrich et al., 2012). The use of generic groups allows the collection of relatively large amounts of data representing the dominant Cretaceous taxa over long time scales. This enables us to assess the role of intra-generic evolution (species extinctions, originations) and species composition changes, on the size record of nannoplankton. We also present single species data (e.g., *Arkhangelskiella cymbiformis*, *Broinsonia signata*) although these have shorter stratigraphic ranges.

2 Section and material

The study section of Goban Spur (DSDP Site 549) was chosen for its relatively comprehensive coverage of the entire Upper Cretaceous interval (Cenomanian – Maastrichtian) and for the good preservation of calcareous nannofossils. We also have existing quantitative nannofossil assemblage data for this section, providing valuable background information (Linnert et al., 2011). DSDP Site 549 is located 400km west of Ireland (Fig. 1) (49°05.28'N, 13°05.88'W) at a water depth of 2533m (De Graciansky et al., 1985a, b). The study interval includes a 59m thick middle Cenomanian – upper Maastrichtian sequence, but core recovery is poor through the middle Cenomanian – upper Santonian interval (Fig. 2)(De Graciansky et al., 1985a). An unconformity is present between the upper Campanian and the uppermost Maastrichtian cutting out most of the lower, and part of the upper Maastrichtian (~4 – 5Ma). All 36 study samples are nannofossil chalks and the calcareous nannofossils are moderately to well-preserved (De Graciansky et al., 1985a; Müller, 1985, Linnert et al., 2011). The site was located at a palaeolatitude of ~35°N in the Cenomanian and ~40°N in the late Campanian (Voigt et al., 2004, 2008).

3 Methods

3.1 Experimental methods

The samples were processed for calcareous nannofossil study using the settling method of Geisen et al. (1999) adapted from the original description of Beaufort (1991). The biometric work was performed using an Olympus BX51 light microscope with a Colour View II digital camera and the imaging software analySIS®. For each of the 36 samples, 60 specimens of each of the four taxonomic groups (*Arkhangelskiella*/*Broinsonia*, *Prediscosphaera*, *Retecapsa* and *Watznaueria*) were digitally imaged, a total of 240 specimens per sample. Specimens were chosen by scanning random traverses and all specimens were analysed, up to the total count, excluding those that were broken or heavily overgrown. Coccolith lengths and widths were measured using the measuring tool in analySIS®. The morphometric results were processed for mean values, standard deviations and 95% confidence intervals, using the software Statistica9.1. The terms small (3 – 5µm), medium (5 – 8µm), large (8µm – 12µm) and very large (> 12µm) were used, following the terminology of Young et al. (1997).

3.2 Taxonomy

***Broinsonia/Arkhangelskiella* spp.**

All specimens of *Broinsonia* with a cross-shaped central area structure were grouped into *Broinsonia signata* (Fig. 3, A). Medium-sized specimens with a plate-like central structure were included in *Broinsonia enormis* (Fig. 3, B) and larger specimens (> 9µm) were assigned to *Broinsonia parca*. We follow the subspecies descriptions of Wise (1983; Fig. 3, C), including *Broinsonia parca expansa* (width of central area > 2 x rim width), *Broinsonia parca parca* (width of central area > rim width) and *Broinsonia parca constricta* (width of central area < rim width). All specimens of *Arkhangelskiella* were included within *Arkhangelskiella cymbiformis* (Fig. 3, D).

***Prediscosphaera* spp.**

All specimens of *Prediscosphaera* were assigned to two species groups: those with diagonal cross-bars (e.g., *P. cretacea*, *P. columnata*, *P.grandis*, *P. ponticula*) to *Prediscosphaera cretacea* sensu lato (Fig. 3, E) and those with axial cross-bars (e.g., *P. arkhangelskyi*, *P. spinosa*, *P. stoveri*) to *Prediscosphaera spinosa* sensu lato (Fig. 3, F).

***Retecapsa* spp.**

Five species of *Retecapsa* were recognised, including *Retecapsa angustiforata* (Fig. 3, G), *Retecapsa crenulata* (Fig. 3, H), *Retecapsa ficula* (Fig. 3, I), *Retecapsa schizobrachiata* and *Retecapsa surirella* (Fig. 3, J). Indeterminate specimens with damaged or missing diagnostic central area structures were assigned to *Retecapsa* spp.

Watznaueria spp.

Five species of *Watznaueria* were grouped as *Watznaueria* spp., including *Watznaueria barnesiae* (Fig. 3, K), *Watznaueria biporta* (Fig. 3, L), *Watznaueria fossacincta* (Fig. 3, M), *Watznaueria ovata* (Fig. 3, N) and *Watznaueria quadriradiata*. *Watznaueria barnesiae* is by far the most abundant (60-70%).

4 Results

4.1 Size trends

Three of the studied taxonomic groups (*Prediscosphaera*, *Retecapsa*, *Watznaueria*) show no significant size changes throughout the Late Cretaceous interval, as their mean size variations never exceed more than 0.7µm (Figs. 4, 5; Tab. 1). Pronounced size variations are only seen within the *Broinsonia*/*Arkhangelskiella* group, with size increasing from 6 – 7 µm in the Cenomanian-Santonian to 9 – 10µm across the Campanian – Maastrichtian interval (Figs. 4, 5; Tab. 1).

4.2 Species compositions and size range

Within the *Broinsonia*/*Arkhangelskiella* group, *B. signata* dominates throughout the Cenomanian (Fig. 6) but is largely superceded by *B. enormis* in the lower Turonian. The latter dominates through the Turonian – Santonian interval. *A. cymbiformis* and *B. parca* appear in the lower Campanian with the latter dominant in the lower Campanian and the former dominant in the upper Campanian. *A. cymbiformis* is the only species of the group that ranges into the upper Maastrichtian. The size distribution of species within *Broinsonia*/*Arkhangelskiella* differs markedly, with medium sized *B. signata* and *B. enormis*, medium to very large sized *A. cymbiformis* and large to very large *B. parca* (Fig. 7, Tab. 1). Of these species, *A. cymbiformis* is characterised by a very broad range of sizes, ranging from 5.7µm to 14.1µm.

The genus *Prediscosphaera* spp. is dominated by *P. cretacea* s.l., which represents approximately 85% of all *Prediscosphaera* specimens (Fig. 6). With a mean length of 5.8µm (Fig. 7, Tab. 1) this species plexus is slightly larger than the less common *P. spinosa* group (4.6µm).

R. crenulata is the most common species within *Retecapsa* spp., followed by *R. surirella* and *R. angustiforata* (Fig. 6). *R. ficula* and *R. schizobrachiata* are rare. All common species of *Retecapsa* are relatively similar in mean size and size range (Fig. 7, Tab. 1).

W. barnesiae is the most abundant species of *Watznaueria* (60-70%) (Fig. 6). *W. fossacincta*, *W. biporta* and *W. ovata* are rare, and only one specimen of *W. quadriradiata* was observed. With the exception of rare *W. ovata* and *W. quadriata*, all species have a similar size ranges (~3 – 9µm) and mean lengths (5.3 – 5.8µm; Fig. 7, Tab. 1).

4.5 Correlation matrix

A correlation matrix (Pearson Correlation; r-values) displaying various significant (>95%) pairings of the relative abundance (%) and mean length (meanL) of the studied taxa is given in Table 2. Data for absolute calcareous nannofossil abundance, species richness, relative abundances of individual taxa and Nutrient Index are taken from Linnert et al. (2011). The Nutrient Index (= *Biscutum* spp. + *Zeugrhabdotus* spp. + *Tranolithus orionatus* / *Watznaueria* spp.) was originally introduced by Gale et al. (2000) and modified by Linnert et al. (2011). The most pronounced positive pairings are the relative abundance of *Prediscosphaera* spp. with absolute nannofossil abundance (0.76), the relative abundance of *Prediscosphaera* spp. with meanL of *Broinsonia*/*Arkhangelskiella* spp. (0.75), species richness with absolute nannofossil abundance (0.64) and meanL of *Retecapsa* spp. with meanL of *Prediscosphaera* spp. (0.58). The most pronounced negative pairings are meanL of *Watznaueria* spp. with meanL of *Broinsonia*/*Arkhangelskiella* spp. (-0.73), relative abundance of *Watznaueria* spp. with relative abundance of *Broinsonia*/*Arkhangelskiella* spp. (-0.64), Nutrient Index with meanL of *Broinsonia*/*Arkhangelskiella* spp. (-0.62), Nutrient Index with meanL of *Retecapsa* spp. (-0.61) and Nutrient Index with relative abundance of *Prediscosphaera* spp. (-0.60).

4.6 Reworking

The uppermost Campanian interval between samples 393.49 mbsf and 391.19 mbsf includes evidence of nannofossil reworking, shown by the reappearance of *Eiffellithus eximius* and *Reinhardtites anthophorus* (both have last occurrences in Subzone UC15e; Burnett, 1998) above strata assigned to nannofossil Zone UC16 (Linnert et al., 2011). The assumption of reworked material is supported by more frequent occurrences of taxa, which are common in the lower Campanian but rare in the uppermost Campanian (e.g., *B. parca* and *B. signata*; Fig.6). Consequently the size data of these three samples (393.49mbsf, 392.34mbsf, 391.19mbsf) are considered with caution as they may represent a mixed signal of lowermost Maastrichtian and lower Campanian material. In figures 5, 6 and 8 these three samples are marked with grey shading.

5 Discussion

5.1 Size evolution or species turnover of Broinsonia/Arkhangelskiella?

Our data for species within the *Broinsonia*/*Arkhangelskiella* group show some distinct shifts in mean coccolith length, with all species showing some degree of size increase through their evolutionary lifetime (Fig. 8). This is a widely observed feature of Mesozoic and Cenozoic calcareous nannofossil species (e.g. Aubry et al., 2005). The largest size change is seen in *B. parca*, which increases by more than 3 µm through the lowermost Campanian (Fig. 8). This shift is reflected in the taxonomic subspecies classification of relatively small *B. parca expansa* (~9µm) and larger *B. parca parca* and *B. parca constricta* (> 10µm). The taxon *A. cymbiformis* shows another significant size increase from the upper Campanian to upper Maastrictian, confirming a trend seen in earlier studies (Girgis, 1987; Faris, 1995; Linnert and Mutterlose, 2009; Thibault, 2010). The very broad range in coccolith sizes (6-14 µm) within this taxon, however, is a feature not seen in modern species. It most likely indicates that the taxonomic concept of *A. cymbiformis* applied here, represents a species plexus, including discrete taxa with more restricted coccolith size ranges. Varol (1989) and Burnett (1997), for instance, suggest that *A. cymbiformis* could be split into the three species: *A. confusa* (coccolith length < 8µm), *A. cymbiformis* (coccolith length > 8µm, rim width < 1.5µm) and *Arkhangelskiella maastrichtiana* (coccolith length > 10µm, rim width > 1.5µm).

Looking at the broader *Broinsonia*/*Arkhangelskiella* group, mean coccolith length increases markedly from the Santonian into the lower Campanian. This trend reflects a shift in dominance between different species in the group, with the smaller *B. signata* and *B. enormis* superceded by larger *A. cymbiformis* and *B. parca* (Figs 6, 8). Some of this trend, however, appears to include a significant size increase within *B. parca*, following its origination in the early Campanian. Shifts of species composition, in particular decreasing abundances of large *B. parca* (Figs. 6, 8), are perhaps also a reason for decreasing mean sizes of the *Broinsonia*/*Arkhangelskiella* group throughout a part (4 samples from 395.65 – 394.08mbsf) of the upper Campanian interval. This trend of decreasing mean size is, however, also seen within the stand-alone *A. cymbiformis* species data (Fig. 8), suggesting an evolutionary trend. The size trends seen within the *Broinsonia*/*Arkhangelskiella* group therefore reflect both a succession of dominant species with distinct size ranges (*B. enormis*, *B. signata* vs. *B. parca, A. cymbiformis*) and evolutionary trends within putative single species (e.g., *B. parca* and *A. cymbiformis*).

5.2 Size trends of Prediscosphaera, Retecapsa and Watznaueria

In comparison to the size trends seen in the *Broinsonia*/*Arkhangelskiella* group, the other taxa studied - *Prediscosphaera*, *Retecapsa*, *Watznaueria* - show only minor variations in mean coccolith size (<1µm). This is a remarkable record of morphological stability, considering the data represent ~30 million years of evolutionary history. Although, like the *Broinsonia*/*Arkhangelskiella* group, these taxonomic groups incorporate multiple species (see Taxonomy section above), these minor size variations indicate that species within the genera are similar in size and remained so over long timescales. For example, all the dominant species of *Retecapsa* and *Watznaueria* show almost identical ranges in coccolith size (Fig. 7, Tab. 1). *Prediscosphaera* shows a greater range in coccolith size ranges, but following a gradual size increase early in their evolutionary history (Albian – early Turonian; e.g. Perch-Nielsen, 1985; Bown in Kennedy et al., 2000), their mean size record is relatively stable (Fig. 7, Tab. 1). This largely reflects the stable species composition within *Prediscosphaera*, with the dominant species being *P. cretacea* s.l. (>75% of the genus), whereas *P. spinosa* s.l. forms only a minor part (<25% of the genus, Fig. 6). A minor increase in size (~0.7µm) across the Cenomanian – Turonian transition may be related to the changing palaeoenvironments of OAE2 at Goban Spur (Linnert et al., 2011; Linnert and Mutterlose, 2013).

Prediscosphaera, *Retecapsa* and *Watznaueria* represent >50% of the entire calcareous nannofossil assemblage at Goban Spur (Linnert et al., 2011) and demonstrate relatively stable morphometric behaviour through the Upper Cretaceous. Stability in Upper Cretaceous coccolith size was also documented in a literature compilation by Aubry et al. (2005). This stability of the mean coccolith size is also coupled with relatively stable species composition within the three genera. None of the genera show major turnovers in species composition (e.g., replacements, extinctions) and the majority of included species are long ranging and seen throughout the ~30 million year study interval. Such long-term stability of *Prediscosphaera*, *Retecapsa* and *Watznaueria* during the Late Cretaceous contrasts with the early history of these genera. The Jurassic record of *Watznaueria*, for instance, began with a ~15 million year long period (Toarcian – Bathonian), when most of the known species evolved (e.g. Cobianchi et al., 1992; Mattioli and Erba, 1999). These *Jurassic Watznaueria* were morphological more diverse (coexisting forms with cross, bridge or without specific central structure; e.g. Cobianchi et al., 1992; Mattioli and

Erba, 1999) than their Late Cretaceous descendants, which are dominated by specimens without central structures. The mean size of Jurassic *Watznaueria* was more variable as seen on *Watznaueria britannica*, which show fluctuations of (sub-) species composition (morphotypes A – F) significantly affecting their mean size (Giraud et al., 2006). The mid to Late Cretaceous *Watznaueria* are seemingly less affected by changes of subspecies composition as reflected by relatively stable mean sizes recorded here (Bornemann and Mutterlose, 2006; this study). This record of stability seen in Late Cretaceous *Watznaueria* and *Retecapsa,* and to some extent in *Predicosphaera*, is not seen in the Cenozoic evolutionary history of nannofossils, which is characterised by much shorter species longevities and higher turnover rates (Bown, 2005).

5.3 Palaeoenvironmental influence?

Our understanding of the possible effects of environmental change on coccolith size is limited. Data for single strain cultures suggest rather narrow size limits within populations and no obvious change in size under changing environmental conditions (e.g., Young and Westbroeck, 1991, Quinn et al., 2003). Plankton studies, however have suggested that more variability may be present in recent taxa, such as, *Emiliania huxleyi* and *Gephyrocapsa oceanica* (e.g. Bollmann and Klaas, 2008; Bollmann et al., 2009; Triantaphyllou et al., 2010), with coccolith morphology (size, bridge angle, element thickness) showing some link to environmental factors like temperature and salinity. Longer-term geological studies have suggested both increasing size and decreasing coccolith size, in response to changing environmental conditions, such as ocean acidification (Iglesias et al., 2008; Beaufort et al., 2011). Studies in deeper time are problematic because of the difficulty of reconstructing palaeoenvironmental conditions and understanding the possible effects of variable preservation, however, decreasing size is often claimed to represent a response to stressful environmental conditions (e.g., Erba et al., 1995; Giraud et al., 2006; Erba et al., 2010).

During the Late Cretaceous, the proto-North Atlantic was subject to a range of palaeoenvironmental changes, including OAE2 (e.g. Schlanger and Jenkyns, 1976; Arthur et al., 1987), short term warming (Cenomanian – early Turonian; e.g., Gustafsson et al., 2003; Forster et al., 2007), long term cooling (Turonian – Maastrichtian; e.g., Jenkyns et al., 1994; Huber et al., 1995, 2002; Friedrich et al., 2012), changes of ocean circulation (e.g. Barrera and Savin, 1999; Hay 2008) and changes in palaeofertility (Linnert et al., 2011). Calcareous nannofossil data, expressed as a nutrient index (*Biscutum* spp. + *Zeugrhabdotus* spp. + *Tranolithus orionatus* / *Watznaueria* spp.) suggest that palaeofertility decreased from high values in the Cenomanian to lower fertility in the Campanian – Maastrichtian (Linnert et al., 2011). It has been hypothesised that both sea surface temperature and changes in surface water fertility may influence the size of calcareous nannofossils. The muted size variability seen in *Prediscosphaera*, *Retecapsa*, and

Watznaueria, however, suggests little if any link between the Late Cretaceous palaeoenvironmental trends and coccolith size, although some of these taxa do show negative correlations against the Nutrient Index (Tab.2). Previously assumed low nutrient preferences of these taxa (e.g., Erba et al., 1992; Eshet and Almogi-Labin, 1996; Linnert et al., 2011; Watkins et al., 1996), are mainly based on abundance counts and assemblage comparisons. Thus it might be more likely that these taxa migrated from unfavourable conditions (high nutrients) to more favourable ones (low nutrients) rather than demonstrating a response reflected in coccolith size change. Not all previous studies, however, have proposed low nutrient preferences for these taxa, e.g., Pittet and Mattioli (2002) suggested a mesotrophic affinity for *Watznaueria* and the studies of Mutterlose (1991) and Lees et al. (2005) posited a eurytopic character for this genus. Such a eurytopic affinity could explain the relatively stable mean size of *Watznaueria* in a changing environment. A mesotrophic character is also suggested for some species of *Prediscosphaera* (e.g. Eleson and Bralower, 2005; Hardas and Mutterlose, 2007) while other species (especially *P. stoveri*) are considered to be eutrophic (Crux, 1991).

The size variation seen within the *Broinsonia*/*Arkhangelskiella* group, on the other hand, may be seen as a response to palaeoenvironment. Across the Cenomanian – Turonian transition changes in temperature (e.g. Gustafsson et al., 2003) and nutrients (e.g. Linnert et al., 2011) may have triggered the replacement of the medium sized *B. signata* (mean 6.1µm) by the smaller *B. enormis* (mean 5.4µm). The late Campanian – Maastrichtian peak cooling (e.g. Friedrich et al., 2012) may have then caused the disappearance of large specimens of *B. parca* and *A. cymbiformis*. Currently, it is unclear which of these palaeoenvironmental factors (e.g. nutrients, temperature) was the dominant controlling factor on the mean size of *Broinsonia*/*Arkhangelskiella*. A negative correlation is seen between mean coccolith size and the Nutrient Index (-0.62, Tab. 2), suggesting the possibility of size increase in response to decreasing fertility. Previous Cenomanian/Turonian data, however, revealed a positive correlation between *Broinsonia* spp. coccolith length and Nutrient Index (0.59; Linnert and Mutterlose, 2013). The biometric results are also somewhat contradictory with regard to the gradual Late Cretaceous cooling, as the general size trend is one of increase from the Turonian – Campanian, decrease in the uppermost Campanian and increase again in the Maastrichtian (Figs. 5, 6, 8). These results suggest a complex relationship between coccolith size, nutrient levels and temperature, and may well reflect the selection of better-adapted variants with changing environmental conditions (with smaller, larger or similar sized liths) rather than evolutionary size changes of single (sub-) species (e.g., Schmidt et al., 2006).

5.4 Competition of (sub-)species as a control of coccolith size?

Despite all four of the studied generic groups inhabiting the same broad palaeoenvironment, only *Broinsonia*/*Arkhangelskiella* displays significant size variations through this ~30 million year record of the Late Cretaceous. Even the trends in the *Broinsonia*/*Arkhangelskiella* group are arguably driven by species/subspecies replacements rather than by size changes of single (sub-) species per se. Studies of general Cenozoic coccolith size show similar size changes driven by the selection of larger or smaller sized taxa (Schmidt et al., 2006; Hermann and Thierstein, 2012), even if these studies are not directly comparable to our results from *Broinsonia*/*Arkhangelskiella*. The Eocene size maximum, for example, was largely the result of the appearance and abundance increase of large species within *Chiasmolithus*, *Coccolithus*, *Helicosphaera* and *Reticulofenestra*, whereas the Neogene size decrease was due to the demise of some of these large taxa, together with the appearance of small taxa, such as *Emiliania* and *Gephyrocapsa* (Hermann and Thierstein, 2012).

Another approach to understanding the relationship between coccolith morphology and environmental changes is through cultured coccolithophores. Single strain culture experiments using *C. leptoporus*, for example, showed that coccolith size barely responded to changing parameters, such as, light and temperature (Quinn et al., 2003). These experiments led to a reinterpretation of existing Cenozoic *Calcidiscus* size data (~24 million years; Knappertsbusch, 2000) as the observed size variations were therefore explained by abundance fluctuations in different strains, which may represent cryptic species, rather than by adaptation of a single strain to environmental changes (Quinn et al., 2003, Schmidt et al., 2006). *Emiliania huxleyi* is a species plexus with different coccolith morphotypes (Young and Westbroeck, 1991), each apparently genetically distinct, and changes in environmental factors (temperature, nutrients) cannot induce a change from one morphotype to another (Young and Westbroeck, 1991). Plankton studies, however, have suggested some link between environment and coccolith morphology (size, bridge angle, element thickness) but these studies could not distinguish whether this was due to single species plasticity or to the existence of several morphologically-identical sibling species with narrow ecologic niches (*E. huxleyi*: Bollmann et al., 2009; Triantaphyllou et al., 2010; *G. oceanica*: Bollmann and Klaas, 2008). A more recent experiment comparing the plasticity of mono- and polyclonal cultures of *E. huxleyi* at different CO_2 levels, reveals that a single strain may adapt to the changing environmental conditions by evolving new, better adapted genotypes (Lohbeck et al., 2012). This adaption was, however, only seen in growth rate and in the production of particulate inorganic carbon, whereas significant changes in cell size were limited to the multiclonal experiments (Lohbeck et al., 2012).

The morphospecies of *Broinsonia*/*Arkhangelskiella* show far greater morphological disparity than the subspecies of *C. leptoporus* (Quinn et al., 2003), *E. huxleyi* (Young and Westbroeck, 1991) and *G. oceanica* (e.g. Bollmann and Klaas, 2008). It is thus most likely that the large fluctuations in mean coccolith size we have documented represent shifts in abundance between different-sized species (extinctions, origination, species replacements). Furthermore it is likely that even single 'morphospecies' within the *Broinsonia*/*Arkhangelskiella* group (e.g., *A. cymbiformis*) may represent multiple cryptic taxa. Such a pattern of similar morphology but different coccolith size ranges is also seen within the modern taxon *Coccolithus pelagicus*, with two subspecies now recognised, the smaller *C. pelagicus pelagicus* and larger *C. pelagicus braarudii* (Saez et al., 2003; Geisen et al., 2004). These different subspecies also display distinct ecological preferences (*C. pelagicus*: Saez et al., 2003; Geisen et al., 2004; *E. huxleyi*: Poulten et al., 2011). These observations from modern taxa serve as our best models for explaining fossil data from extinct taxa, such as *A. cymbiformis*. Palaeoenvironmental changes may well have caused abundance fluctuations among different *A. cymbiformis* subspecies, causing the observed shifting trends in mean coccolith size. A model for how environmental change may have controlled subspecies composition and mean size is provided by the multiclonal experiment of Lohbeck et al (2012), where increases in ambient CO_2 concentrations led to selection of a single *E. huxleyi* genotype, which was apparently larger then the overall mean of the six starting genotypes.

Does the low size variability of *Prediscosphaera*, *Retecapsa* and *Watznaueria,* on the other hand, indicate lower evolutionary turnover rates during the Late Cretaceous (e.g. originations, extinctions) compared with *Broinsonia*/*Arkhangelskiella*? In the case of *Prediscosphaera*, it appears to have been characterised by a similar rate of species origination throughout the Late Cretaceous. At least nine species of *Prediscosphaera* are recognised within the Upper Cretaceous, a number similar to the ten species/subspecies of *Broinsonia*/*Arkhangelskiella* (e.g., Burnett, 1998). Thus, size changes, and especially mean size, are probably not sensitive enough measures of coccolith morphology to fully describe and reflect evolutionary rates. Even though evolutionary turnovers within *Prediscosphaera* did not affect the mean size, they affected minimum and maximum lengths within the genus. Trends of decreasing minimum and increasing maximum lengths (Fig. 4) are thus linked to the origination of very small (*P. stoveri*) and very large species (*P. grandis*) of *Prediscospheara*.

6 Conclusions

Within the four major Late Cretaceous taxonomic groups studied here, significant coccolith size variations are limited to taxa of the *Broinsonia*/*Arkhangelskiella* group only.

Prediscosphaera, *Retecapsa* and *Watznaueria* show only minor (<0.5µm) size variations through the Late Cretaceous interval. Thus, both palaeoenvironmental factors and intrageneric evolution (species originations, extinctions, replacements), apparently had little influence on the mean size of these three taxa, which represent more than 50% of the Upper Cretaceous calcareous nannofossil assemblage. The large fluctuations of coccolith size observed within *Broinsonia*/*Arkhangelskiella*, on the other hand, were mainly the result of (sub-) species originations, replacements and extinctions. The early Campanian size increase of ~3µm, for instance, was due to the replacement of smaller species (*B. signata*, *B. enormis*) by larger ones (*B. parca*, *A. cymbiformis*). Abundance fluctuations of different-sized subspecies (e.g., large *vs*. small *A .cymbiformis*) may also have influenced the size variations seen within individual morphospecies. Some of these abundance fluctuations were probably induced by palaeoenvironmental changes, as different-sized species or subspecies may have preferred different palaeoecologic conditions. The impact of palaeoenvironmental change on *Broinsonia*/*Arkhangelskiella* is well seen across critical intervals such as the Cenomanian/Turonian and Campanian/Maastrichtian boundaries. During the Cenomanian/Turonian transition, warming combined with changing nutrient availability may thus have favoured smaller sized *B. enormis* rather than larger *B. signata*, resulting in the size reduction seen at that time. The late Campanian cooling, on the other hand, may have caused the replacement of *B. parca* and larger *A. cymbiformis* (>9µm) by the smaller subspecies of *A. cymbiformis* (<8µm).

7 Acknowledgements

Financial support is acknowledged by the Deutsche Forschungsgemeinschaft (Mu 66 7/32-1, -2). Many thanks to François Krencker, who translated our title, key words and abstract into the French language. We thank Fabienne Giraud and Nicolas Thibault for their thoughtful reviews that improved the manuscript.

8 Taxonomic appendix

Calcareous nannofossil taxa mentioned in text and figures; full references of the taxa mentioned herein are given in Bown (1998).

Ahmuellerella Reinhardt 1964
A. octoradiata (Górka 1957) Reinhardt 1966
Arkhangelskiella Vekshina 1959
A. cymbiformis Vekshina 1959
Biscutum Black in Black and Barnes 1959
Broinsonia Bukry 1969
B. enormis (Shumenko 1968) Manivit 1971
B. parca (Stradner 1963) Bukry 1969

B. parca ssp. *constricta* Hattner et al 1980
B. parca ssp. *expansa* Wise and Watkins in Wise 1983
B. parca ssp. *parca* (Stradner 1963) Bukry 1969
B. signata (Noël 1969) Noël 1970
Calcidiscus Kamptner 1950
C. leptoporus (Murray and Blackman 1898) Loeblich and Tappan 1978
Chiasmolithus Hay, Mohler and Wade 1966
Coccolithus Schwarz 1894
C. pelagicus (Wallich 1871) Schiller 1930
C. pelagicus ssp. *braarudii* (Gaarder 1962) Geisen et al. 2002
C. pelagicus ssp. *pelagicus* (Wallich 1871) Schiller 1930
Cyclagelosphaera Noël 1965
C. margerelii Noël 1965
Emiliania Hay and Mohler in Hay et al. 1967
E. huxleyi (Lohmann 1902) Hay and Mohler in Hay et al. 1967
Gartnerago Bukry 1969
G. segmentatum (Stover 1966) Thierstein 1974
Gephyrocapsa Kamptner 1943
G. oceanica Kamptner 1943
Helicosphaera Kampner 1954
Kamptnerius Deflandre 1959
K. magnificus Deflandre 1959
Nephrolithus Górka 1957
N. frequens Górka 1957
Prediscosphaera Vekshina 1959
P. arkhangelskyi (Reinhardt 1965) Perch-Nielsen 1984
P. columnata (Stover 1966) Perch-Nielsen 1984
P. cretacea (Arkhangelsky 1912) Gartner 1968
P. grandis Perch-Nielsen 1979
P. ponticula (Bukry 1969) Perch-Nielsen 1984
P. spinosa (Bramlette and Martini 1964) Gartner 1968
P. stoveri (Perch-Nielsen 1968) Shafik and Stradner 1971
Retecapsa Black 1971
R. angustiforata Black 1971
R. crenulata (Bramlette and Martini 1964) Grün in Grün and Allemann 1975
R. ficula (Stover 1966) Burnett 1998
R. schizobrachiata (Gartner 1968) Grün in Grün and Allemann
R. surirella (Deflandre and Fert 1954) Grün in Grün and Allemann 1975
Reticulofenestra Hay et al. 1966
Tranolithus Stover 1966
T. orionatus (Reinhardt 1966a) Reinhardt 1966b
Watznaueria Reinhardt 1964
W. barnesiae (Black 1959) Perch-Nielsen 1968
W. biporta Bukry 1969
W. britannica (Stradner 1963) Perch-Nielsen 1968
W. fossacincta (Black 1971) Bown in Bown and Cooper 1989
W. manivitiae Bukry 1973
W. ovata Bukry 1969
W. quadriradiata Bukry 1969
Zeugrhabdotus Reinhardt 1965

9 References

Arthur, M.A., Schlanger, S.O., Jenkyns, H.C., 1987. The Cenomanian-Turonian Anoxic Event, II. Palaeoceanographic controls on organic-matter production and preservation. In: Brooks, J., Fleet, A. (Eds.), Marine Petroleum Source Rocks. Geological Society Special Publication 26, Blackwell, Oxford, 401-420.

Aubry, M.-P., Bord, D., Beaufort, L., Kahn, A., Boyd, S., 2005. Trends in size changes in the coccolithophorids, calcareous nannoplankton, during the Mesozoic: A pilot study. Micropaleontology 51, 309-318.

Barrera, E., Savin, S.M., 1999. Evolution of late Campanian-Maastrichtian marine climates and oceans. In: Barrera, E., Johnson, C.C. (Eds.) Evolution of the Cretaceous ocean climate system. Geological Society of America Special Paper 332, 245-282.

Beaufort, L., 1991. Adaption of the random settling method for quantitative studies of calcareous nannofossils. Micropaleontology 37, 415-418

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E.M., Ruiz-Pino, D., Metzl., N., Goyet, C., Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R.E.M., de Vargas, C., 2011. Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. Nature 476, 80-83.

Bollmann, J., Klaas, C., 2008. Morphological Variation of *Gephyrocapsa oceanica* Kamptner 1943 in Plankton Samples: Implications for Ecologic and Taxonomic Interpretations. Protist 159, 369-381.

Bollmann, J., Herrle, J.O., Cortés, M.Y., Fielding, S.R., 2009. The effect of sea water salinity on the morphology of *Emiliania huxleyi* in plankton and sediment samples. Earth and Planetary Science Letters 284, 320-328.

Bornemann, A., Aschwer, U., Mutterlose, J., 2003. The impact of calcareous nannofossils on the pelagic carbonate production across the Jurassic/Cretaceous boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 199, 187-228.

Bornemann, A., Mutterlose, J., 2006. Size analyses of the coccolith species *Biscutum constans* and *Watznaueria barnesiae* from the Late Albian „Niveau Breistroffer“ (SE France): taxonomic and palaeoecological implications. Geobios 39, 599-615.

Bown, P.R., 1998. Calcareous nannofossil biostratigraphy. Chapman and Hall, London, 315p.

Bown, P.R., 2005. Calcareous nannoplankton evolution: a tale of two oceans. Micropaleontology 51, 299-308.

Burnett, J.A., 1997. New species and new combinations of Cretaceous nannofossils, and a note on the origin of *Petrarhabdus* (DEFLANDRE) WIND & WISE. Journal of Nannoplankton Research 19, 133-146.

Burnett, J.A., 1998. Upper Cretaceous. In: Bown, P.R. (Ed.), Calcareous nannofossil biostratigraphy. Chapman and Hall, London, pp. 132-199.

Cobianchi, M.A., Erba, E., Pirini-Radrizzani, C., 1992. Evolutionary trends of calcareous nannofossil genera *Lotharingius* and *Watznaueria* during the Early and Middle Jurassic. Memorie di Scienze Geologiche Padova 43, 19-25.

Crux, J.A., 1991. Albian calcareous nannofossils from the Gault Clay of Munday's Hill (Bedfordshire, England). Journal of Micropalaeontology, 10, 203-221.

De Graciansky, P.C. de, Poag, C.W., Cunningham, R., Loubere, P., Masson, D.G., Mazzullo, J.M., Montadert, L., Müller, C., Otsuka, K., Reynolds, L., Sigal, J., Townsend, H.A., Vaos, S.P., Waples, D., 1985a. Site 549. Initial Reports of the Deep Sea Drilling Project 80, 123-250.

De Graciansky, P. C. de, Poag, C.W., Foss, G., 1985b. Drilling on the Goban Spur: objectives, regional geological setting, and operational summary. Initial Reports of the Deep Sea Drilling Project 80, 5-13.

Eleson J.W., Bralower, T.J., 2005. Evidence of changes in surface water temperature and productivity at the Cenomanian/Turonian Boundary. Micropaleontology 51, 319-332.

Erba, E., Castradori, D., Guasti, G., Ripepe, M., 1992. Calcareous nannofossils and Milankovitch cycles: the example of the Albian Gault Clay Formation (southern England). Palaeogeography, Palaeoclimatology, Palaeoecology 93, 47-69.

Erba, E., Watkins, D., Mutterlose, J., 1995. Campanian dwarf calcareous nannofossils from Wodejebato Guyot in Haggerty. Proceedings of the Ocean Drilling Program, Scientific Results 144, 141-155.

Erba, E., Bottini, C., Weissert, H.J., Keller, C.E., 2010. Calcareous Nannoplankton response to surface-water acidification around Oceanic Anoxic Event 1a. Science 329, 428-432.

Eshet, Y., Almogi-Labin, A., 1996. Calcareous nannofossils as paleoproductivity indicators in Upper Cretaceous organic-rich sequences in Israel. Marine Micropaleontology 29, 37-61.

Faris, M., 1995. Morphometric analysis of *Arkhangelskiella cymbiformis* Vekshina, 1959, in the upper Cretaceous rocks of Egypt and its stratigraphic importance. Annals of the Geological Survey of Egypt 20, 585-601.

Forster, A., Schouten, S., Baas, M., Sinninghe Damsté, J.S., 2007. Mid-Cretaceous (Albian-Santonian) sea surface temperature record of the tropical Atlantic Ocean. Geology 35, 919-922.

Fraguas, A., Erba, E., 2010. Biometric analyses as a tool for the differentiation of two coccolith species of the genus Crepidolithus (Pliensbachian, Lower Jurassic) in the Basque-Cantbrian Basin (Northern Spain). Marine Micropaleontology 77, 125-136.

Friedrich, O., Norris, R.D., Erbacher, J., 2012. Evolution of middle to Late Cretaceous oceans – A 55 m.y. record of Earth's temperature and carbon cycle. Geology 40, 107-110.

Gale, A.S., Smith, A.B., Monks, N.E.A., Young, J.A., Howard, A., Wray, D.S., Hugget, J.M., 2000. Marine biodiversity through the Late Cenomanian – Early Turonian: palaeoceanographic controls and sequence stratigraphic biases. Journal of the Geological Society, London 157, 745-757.

Geisen, M., Bollmann, J., Herrle, J., Mutterlose, J., Young, J., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437-442.

Geisen, M., Young, J., Probert, I., Saez, A., Baumann, K.-H., Sprengel, C., Bollmann, J., Cros, L., de Vargas, C., Medlin, L.K., 2004. Species level variation in coccolithophores. In: Thierstein, H.R., Young, J. (Eds.), Coccolithophores: From Molecular Processes to Global Impact. Springer, Berlin, pp. 327-366.

Giraud, F., Pittet, B., Mattioli, E., Audouin, V., 2006. Paleoenvironmental controls on the morphology and abundance of the coccolith *Watznaueria britannica* (Late Jurassic, southern Germany). Marine Micropaleontology 60, 205-225.

Girgis, M.H., 1987. A morphometric analysis of the *Arkhangelskiella* group and its stratigraphical and palaeoenvironmental importance. In: Crux, J.A., van Heck, S.E. (Eds.), Nannofossils and their applications. Ellis Horwood Limited, Chichester, pp. 327-339

Gustafsson, M., Holbourn, A., Kuhnt, W., 2003. Changes in the northeast Atlantic temperature and carbon flux during the Cenomanian/Turonian paleoceanographic event: the Goban Spur stable isotope record. Palaeogeography, Palaeoclimatology, Palaeoecology 201, 51-66.

Hannisdal, B., Henderiks, J., Hsiang Liow, L., 2012. Long-term evolutionary and ecological responses of calcifying phytoplankton to changes in atmospheric CO_2. Global Change Biology 18, 3504-3516.

Hardas, P., Mutterlose, J., 2007. Calcareous nannofossil assemblages of Oceanic Anoxic Event 2 in the equatoriel Atlantic: Evidence of an eutrophication event. Marine Micropaleontology 66, 52-69.

Hattner, J.G., Wind, F.H., Wise, S.W., 1980. The Santonian-Campanian boundary: comparison of nearshore-offshore calcareous nannofossil assemblages . Cahiers de Micropaléontologie 3, 9-26.

Hay, W.W., 2008. Evolving ideas about the Cretaceous climate and ocean circulation. Cretaceous Research 29, 725-753.

Henderiks, J., Rickaby, R.E.M., 2007. A coccolithophore concept for constraining the Cenozoic carbon cycle. Biogeosciences 4, 323-329.

Herrmann, S., Thierstein, H.R., 2012. Cenozoic coccolith size changes – Evolutionary and/or ecological controls? Palaeogeography, Palaeoclimatology, Palaeoecology 333-334, 92-106.

Huber, B.T., Hodell, D.A., Hamilton, C.P., 1995. Mid- to Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. Geological Society American Bulletin 107, 392-417.

Huber, B.T., Norris, R.D., MacLeod, K.G. 2002. Deep-sea paleotemperature record of extreme warmth during the Cretaceous. Geology 30, 123-126.

Iglesias-Rodriguez, M.D., Halloran, P.R., Rickaby, R.E.M., Hall, I.R., Colmenero-Hidalgo, E., Gittins, J.R., Green, D.R.H., Tyrrell, T., Gibbs, S.J., von Dassow, P., Rehm, E., Armbrust, E.V., Boessenkohl, K.P., 2008. Phytoplankton calcification in a High-CO_2 World. Science 320, 336-340.

Jenkyns, H.C., Gale, A.S., Corfield, R.M., 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. Geological Magazine 131, 1-34.

Kennedy, W.J., Gale, A.S., Bown, P.R., Caron, M., Davey, R.J., Gröcke, D., Wray, D.S., 2000. Integrated stratigraphy across the Aptian-Albian boundary in the Marnes Bleues, at the Col de Pré-Guittard, Arnayon (Drôme), and at Tartonne (Alpes-de-Haute-Provence), France: a candidate Global Boundary Stratotype Section and Boundary Point for the base of the Albian Stage. Cretaceous Research 21, 591-720.

Knappertsbusch, M., 2000. Morphologic evolution of the coccolithophorid *Calcidiscus leptoporus* from the Early Miocene to Recent. Journal of Paleontogy 74, 712-730.

Lees, J.A., 2002. Calcareous nannofossil biogeography illustrates paleoclimate change in the Late Cretaceous Indian Ocean. Cretaceous Research 23, 537-634.

Lees, J.A., Bown, P.R., Mattioli, E., 2005. Problems with proxies? Cautionary tales of calcareous nannofossil paleoenvironmental indicators. Micropaleontology 51, 333-343.

Lohbeck, K.T., Riebesell, U., Reusch, T.B.H., 2012. Adaptive evolution of key phytoplankton species to ocean acidification. Nature Geoscience, DOI: 10.1038/NGEO1441

Linnert, C., Mutterlose, J., 2009. Biometry of the late Cretaceous *Arkhangelskiella* group: ecophenotypes controlled by nutrient flux. Cretaceous Research 30, 1193-1204.

Linnert, C., Mutterlose, J., Herrle, J.O., 2011. Late Cretaceous (Cenomanian– Maastrichtian) calcareous nannofossils from Goban Spur (DSDP Sites 549, 551): Implications for the palaeoceanography of the proto North Atlantic: Palaeogeography, Palaeoclimatology, Palaeoecology 299, 507-528.

Linnert, C., Mutterlose, J., 2013. Biometry of Cenomanian – Turonian placoliths –a proxy for changes of fertility and surface-water temperature? Lethaia 46, 82-97.

López-Otálvaro, G.-E., Suchéras-Marx, B., Giraud, F., Mattioli, E., Lécuyer, C., 2012. *Discorhabdus* as a key coccolith genus for paleoenvironmental reconstructions (Middle Jurassic, Lusitanian Basin): Biometry and taxonomic status. Marine Micropaleontology 94-95, 45-57.

Mattioli, E, Erba, E., 1999. Synthesis of calcareous nannofossil events in Tethyan Lower and Middle Jurassic successions. Rivista Italiana di Paleontologia e Stratigrafia 105, 343-376.

Mattioli, E., Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian-Toarcian (lower Jurassic) coccoliths of the family Biscutaceae: intra- and interspecific variability versus palaeoenvironmental influence. Marine Micropaleontology 52, 5-27

Miller, K.G., Wright, J.D., Browning, J.V., 2005. Visions of ice sheets in a greenhouse world. Marine Geology 217, 215-231.

Müller, C., 1985. Biostratigraphic and paleoenvironmental interpretation of the Goban Spur region based on a study of calcareous nannoplankton. Initial Reports of the Deep Sea Drilling Project Washington 80, 573-599.

Mutterlose, J., 1991. Das Verteilungs- und Migrationsmuster des kalkigen Nannoplanktons in der borealen Unterkreide (Valangin-Apt). Palaeontographica 221, 27-152.

Perch-Nielsen, K., 1968. Der Feinbau und die Klassifikation der Coccolithen aus dem Maastrichtien von Dänemark. Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 16, 1-96.

Perch-Nielsen, K., 1985. Mesozoic calcareous nannofossils. In: Bolli, H.M., Saunders, J.B., Perch-Nielsen, K. (Eds.), Plankton Stratigraphy. Cambridge University Press, Cambridge, pp. 329-426.

Pittet, B., Mattioli, E., 2002. The carbonate signal and calcareous nannofossil distribution in an Upper Jurassic section (Balingen-Tieringen, Late Oxfordian, southern Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 179, 71-96.

Pospichal, J.J., Wise Jr., S.W., 1990. Calcareous nannofossils across the K-T boundary, ODP-Hole 690C, Maud Rise, Weddell Sea. Proceedings of the Oceans Drilling Program, Scientific Results 113, 515-532.

Poulten, A.J., Young J.R., Bates, N.R., William M. Balch. Biometry of detached *Emiliania huxleyi* coccoliths along the Patagonian Shelf. Marine Ecology Progress Series 443, 1-17.

Quinn, P., Thierstein, H.R., Brand, L., Winter , A., 2003. Experimental evidence for the species character of *Calcidiscus leptoporus* morphotypes. Journal of Paleontology 77, 825-830.

Saez, A.G., Probert, I., Geisen, M., Quinn, P., Young, J.R., Medlin, L.K., 2003. Pseudo-cryptic speciation in coccolithophores. Proceedings of the National Academy of Sciences of the United States of America 100, 7163-7168.

Schlanger, S.O., Jenkyns, H.C., 1976. Cretaceous Anoxic Events. Causes and consequences. Geologie en Mijnbouw 55, 179-184.

Schmidt, D.N., Lazarus, D., Young, J.R., Kucera, M., 2006. Biogeography and evolution of body size in marine plankton. Earth-Science Reviews 78, 239-266.

Shamrock, J.L., Watkins, D.K., 2009. Evolution of the Cretaceous calcareous nannofossil genus Eiffellithus and its biostratigraphic significance. Cretaceous Research 30, 1083-1102.

Stradner, H., 1963. New contributions to Mesozoic stratigraphy by the means of nannofossils. Proceedings 6th World Petrol. Congr. Sect. 1, paper 4 (preprint) 1-16.

Thibault, N., 2010. Biometric analysis of the *Arkhangelskiella* group in the upper Campanian-Maastrichtian of the Stevns-1 borehole, Denmark: taxonomic implications and evolutionary trends. Geobios 43, 639-652.

Thierstein, H.R., 1976. Mesozoic calcareous nannoplankton biostratigraphy of marine sediments. Marine Micropaleontology 1, 325-362.

Thierstein, H.R., 1981. Late Cretaceous Nannoplankton and the change at the Cretaceous-Tertiary boundary. SEPM Special Publication 32, 355-394.

Tremolada, F., Erba, E., 2002. Morphometric analyses of Aptian *Assipetra infracreatcea* and *Rucinolithus terebrodentarius* nannoliths: implications for taxonomy, biostratigraphy and paleoceanography. Marine Micropaleontology 44, 77-92

Triantaphphyllou, M., Dimiza, M., Krasakopoulou, E., Malinverno, E., Lianou, V., Souvermezoglou, E., 2010. Seasonal variation in *Emiliania huxleyi* coccolith morphology and calcification in the Aegean Sea (Eastern Mediterranean). Geobios 43, 99-110.

Varol, O., 1989. Quantitative analysis of the Arkhangelskiella cymbiformis Group and Biostratigraphic usefulness in the North Sea Area. J. micropalaeontol 8, 131-134.

Voigt, S., Gale A.S., Flögel, S., 2004. Midlatitude shelf seas in the Cenomanian-Turonian greenhouse world: Temperature evolution and North Atlantic circulation. Paleoceanography 19, PA4020, doi:10.1029/2004PA001015

Voigt, S., Erbacher, J., Mutterlose, J., Weiss, W., Westerhold, T., Wiese, F.,Wilmsen, M., Wonik, T., 2008. The Cenomanian – Turonian of the Wunstorf section – (North Germany): global stratigraphic reference section and new orbital time scale for Oceanic Anoxic Event 2. Newsletters on Stratigraphy 43, 65-89.

Watkins, D.K., Wise, S.W., Pospichal, J.J., Crux, J., 1996. Upper Cretaceous calcareous nannofossil biostratigraphy and paleoceanography of the Southern Ocean. In: Moguilevsky, A., Whatley, R. (Eds.), Microfossils and Oceanic Environments. University of Wales, Aberystwyth Press, pp. 355-381.

Wind, F.H., 1979. Maastrichtian-Campanian nannofloral provinces of the southern Atlantic and Indian Oceans. – In: Talwani, M., Hay, W., Ryan, W.B.F. (Eds.) Deep Drilling Results in the Atlantic Ocean: Continental Margins and Paleoenvironment. American Geophysical Union, Washington, pp. 123-137.

Wise, S.W., 1983. Mesozoic and Cenozoic calcareous nannofossils recovered by Deep Sea Drilling project Leg 71 in the Falkland Plateau Region, Southwest Atlantic Ocean. Initial Reports of the Deep Sea Drilling Project 71, 481-550.

Young, J.R., 1990. Size variation of Neogene *Reticulofenestra* coccoliths from Indian Ocean DSDP Cores. Journal of Micropalaeontology 9, 71-85.

Young, J.R., Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. Marine Micropaleontology 18, 5-23.

Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., Niel, B.E. van, Romein, A.J.T., von Salis, K., 1997. Guidelines for coccolith and Calcareous nannofossil terminology. *Palaeontology* 40, 875-912.

Figure captions:

Fig.1: Map of the northeast Atlantic showing DSDP Leg 80 sites (modified after De Graciansky et al., 1985b).

Fig.2: Schematic lithology, stratigraphy, recovery and samples here of the Cenomanian – Maastrichtian interval from DSDP Site 549 (after De Graciansky et al., 1985a; Linnert et al., 2011; Upper Cretaceous nannofossil zonation after Burnett, 1998).

Fig.3: LM images of specimens of the studied genera (scale bar = 10µm).

Fig.4: Scatter plots of coccolith length (Lmax) vs. coccolith width (Wmax) of the studied genera.

Fig.5: Fluctuation of mean length and mean width of the studied genera through the Cenomanian – Maastrichtian interval of DSDP Site 549. Calcareous nannofossil biostratigraphy after Linnert et al. (2011).

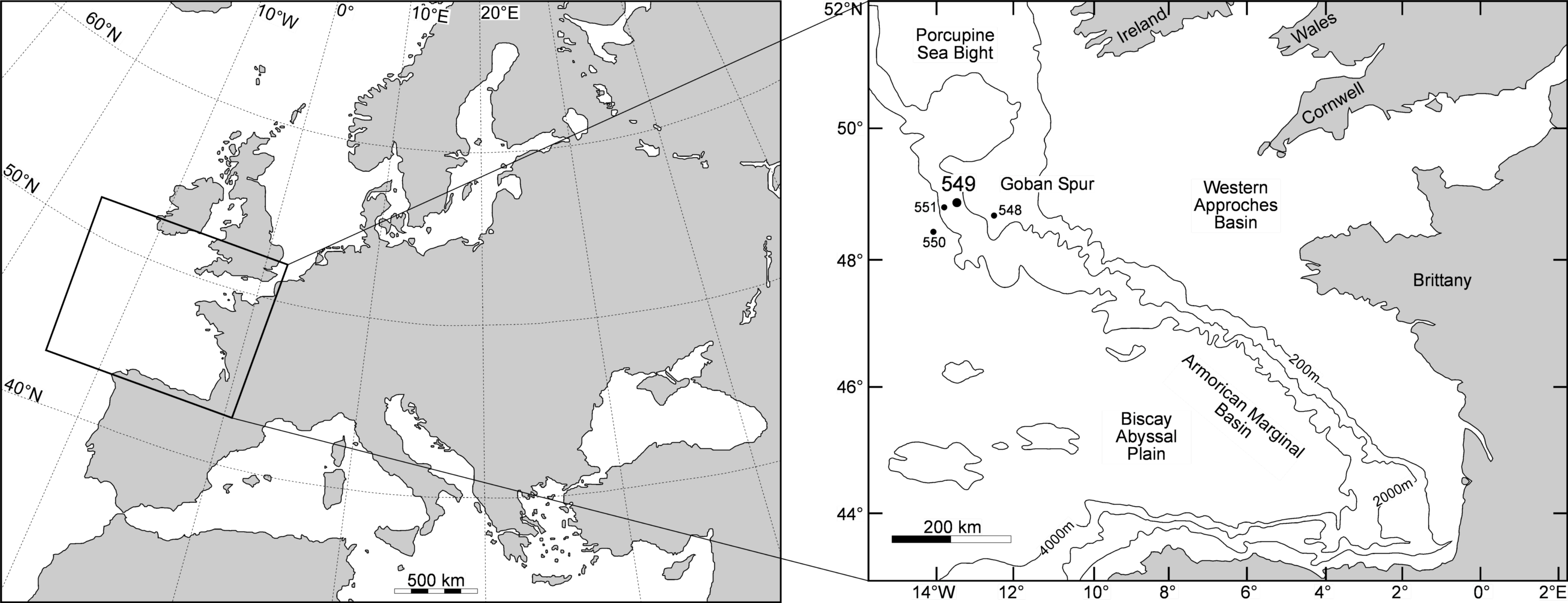
Fig.6: Comparison of mean lengths of the studied genera with their relative abundances, their species compositions, the Nutrient Index and the relative abundance of cool water taxa (*A. octoradiata*, *G. segmentatum*, *K. magnificus*, *N. frequens*; e.g. Thierstein, 1976, 1981; Wind, 1979; Pospichal and Wise, 1990; Lees, 2002).

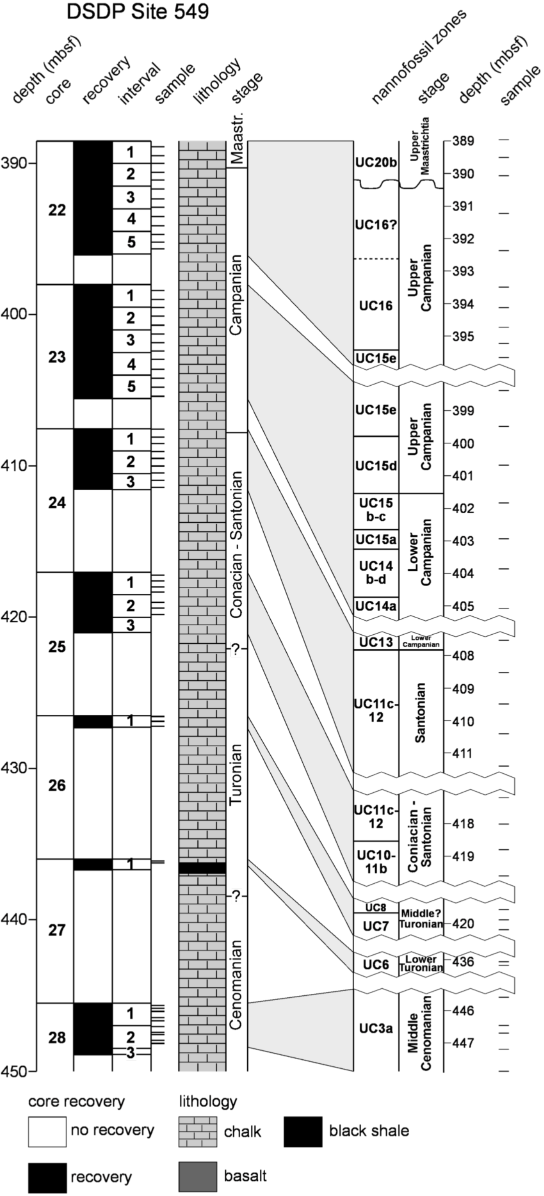
Fig.7: Size histograms showing the length distribution of the species within the studied genera.

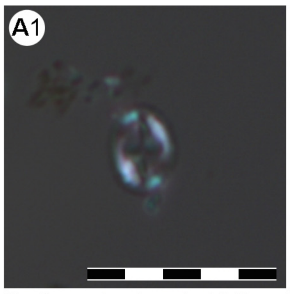
Fig.8: Mean size fluctuations of the single species of *Broinsonia*/*Arkhangelskiella* spp. (black curves with dots) against the size evolution of the entire group (grey shaded area in the background). The table below is giving the numbers of specimens of each species observed in each sample.

Tab.1: Summary of biometric data through time intervals and for single species. minL = minimum length; meanL = mean length; maxL = maximum length; meanW = mean width

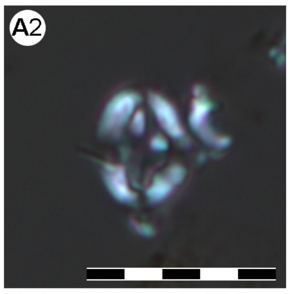
Tab.2: Correlation matrix (r-values) of absolute abundance, species richness, mean lengths and relative abundances of the studied genera, Nutrient Index and frequency of cool water taxa (*A. octoradiata*, *G. segmentatum*, *K. magnificus*, *N. frequens*; e.g. Thierstein, 1976, 1981; Wind, 1979; Pospichal and Wise, 1990; Lees, 2002). All data except the size data are from Linnert et al. (2011).


60°N
10°W
0°
10°E
20°E
50°N
40°N
500 km
52°N
50°
48°
46°
44°
Porcupine Sea Bight
Ireland
Wales
Cornwell
Goban Spur
549
551
548
550
Western Approches Basin
Brittany
Armorican Marginal Basin
Biscay Abyssal Plain
200m
2000m
4000m
200 km
14°W
12°
10°
8°
6°
4°
2°
0°
2°E

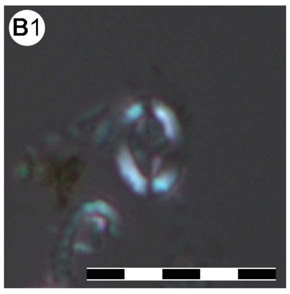

DSDP Site 549
depth (mbsf)
core
recovery
interval
sample
lithology
stage
nannofossil zones
stage
depth (mbsf)
sample
390
400
410
420
430
440
450
22
23
24
25
26
27
28
1
2
3
4
5
Maastr.
Campanian
Conacian - Santonian
?
Turonian
?
Cenomanian
UC20b
UC16?
UC16
UC15e
UC15e
UC15d
UC15 b-c
UC15a
UC14 b-d
UC14a
UC13
UC11c-12
UC11c-12
UC10-11b
UC8
UC7
UC6
UC3a
Upper Maastrichtia
Upper Campanian
Upper Campanian
Lower Campanian
Lower Campanian
Santonian
Coniacian - Santonian
Middle? Turonian
Lower Turonian
Middle Cenomanian
389
390
391
392
393
394
395
399
400
401
402
403
404
405
408
409
410
411
418
419
420
436
446
447
core recovery
no recovery
recovery
lithology
chalk
basalt
black shale



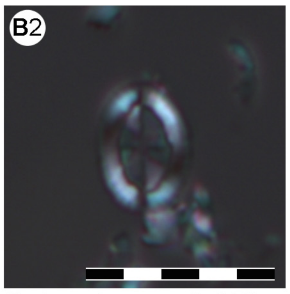
Broinsonia signata (4,8µm)
sample 549 - 446.75mbsf



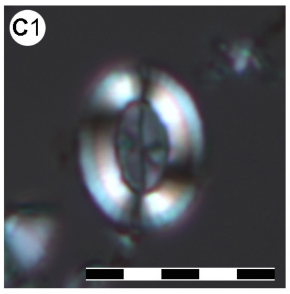
Broinsonia signata (6,9µm)
sample 549 - 446.75mbsf



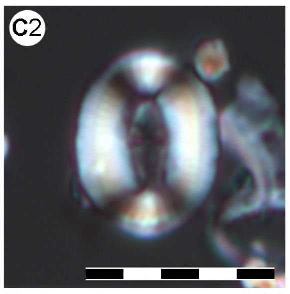
Broinsonia enormis (5.5µm)
sample 549 - 426.87mbsf



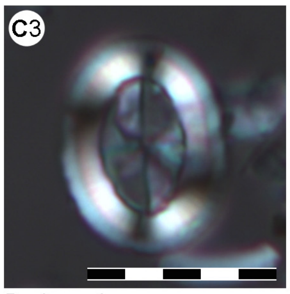
Broinsonia enormis (7.0µm)
sample 549 - 419.21mbsf



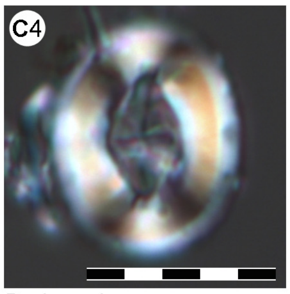
Broinsonia parca parca
(9.1µm)
sample 549 - 405.08mbsf



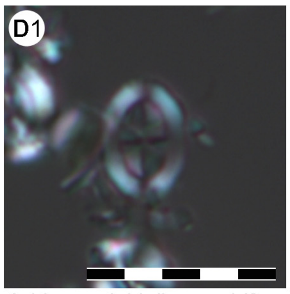
Broinsonia parca constricta
(10.0µm)
sample 549 - 403.88mbsf



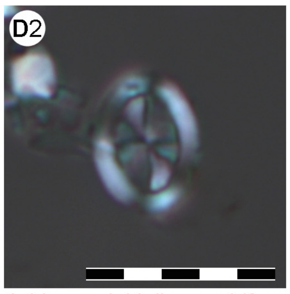
Broinsonia parca expansa
(11.6µm)
sample 549 - 405.08mbsf



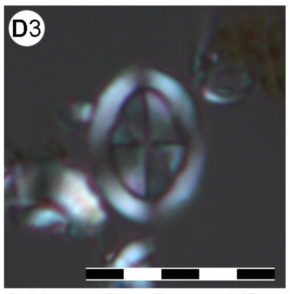
Broinsonia parca parca
(13.0µm)
sample 549 - 394.69mbsf



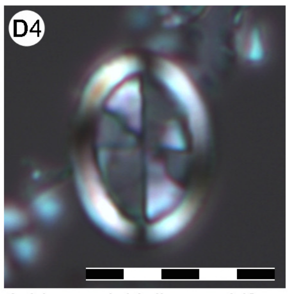
Arkhangelskiella cymbiformis
(6.4µm)
sample 549 - 394.69mbsf



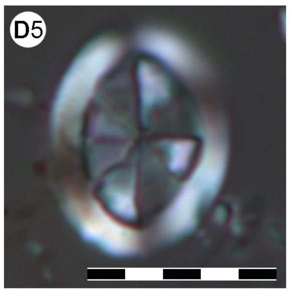
Arkhangelskiella cymbiformis
(7.5µm)
sample 549 - 394.69mbsf



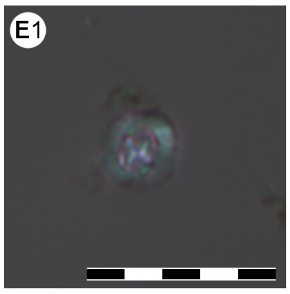
Arkhangelskiella cymbiformis
(8.3µm)
sample 549 - 394.69mbsf



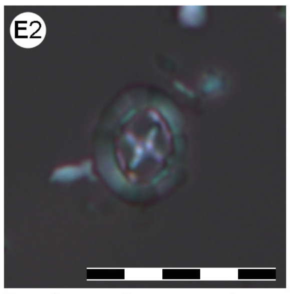
Arkhangelskiella cymbiformis
(10.6µm)
sample 549 - 405.08mbsf



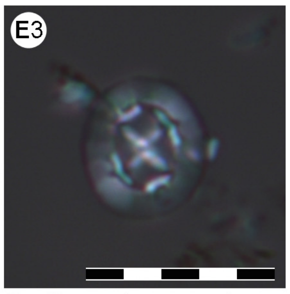
Arkhangelskiella cymbiformis
(12.5µm)
sample 549 - 388.89mbsf



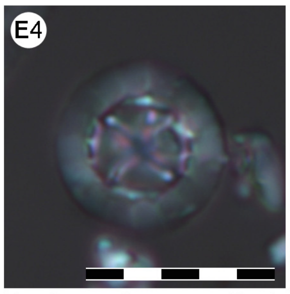
Prediscosphaera cretacea
(4.4µm)
sample 549 - 446.75mbsf



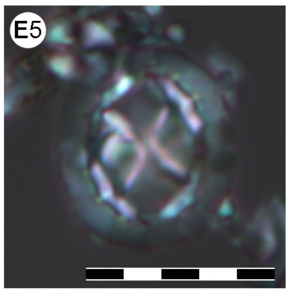
Prediscosphaera cretacea
(6.3µm)
sample 549 - 405.08mbsf



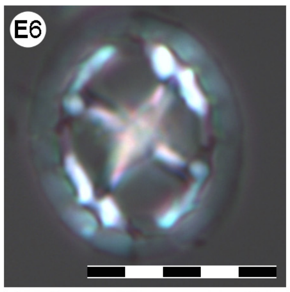
Prediscosphaera cretacea
(7.5µm)
sample 549 - 403.88mbsf



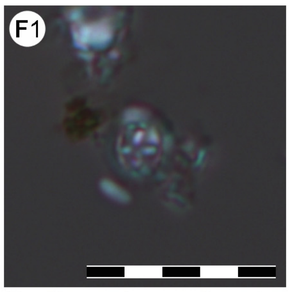
Prediscosphaera ponticula
(9.1µm)
sample 549 - 403.88mbsf



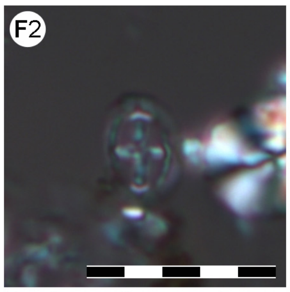
Prediscosphaera grandis
(10.7µm)
sample 549 - 400.69mbsf



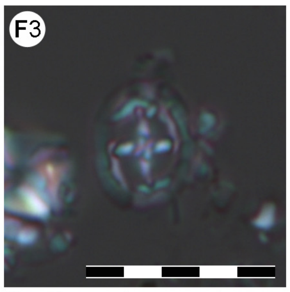
Prediscosphaera grandis
(13.1µm)
sample 549 - 388.89mbsf



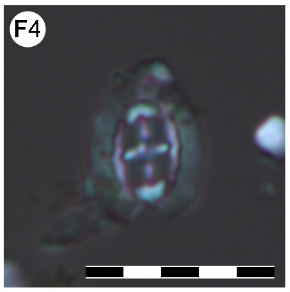
Prediscosphaera stoveri
(4.6µm)
sample 549 - 405.08mbsf



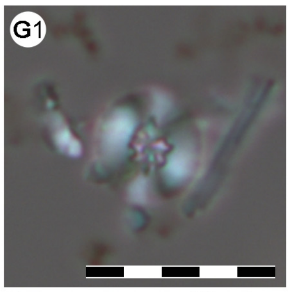
Prediscosphaera spinosa
(6.0µm)
sample 549 - 405.08mbsf



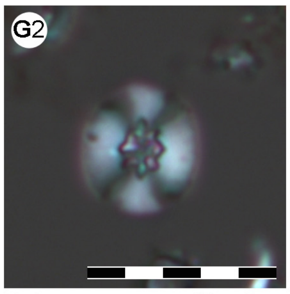
Prediscosphaera spinosa
(7.0µm)
sample 549 - 404.48mbsf



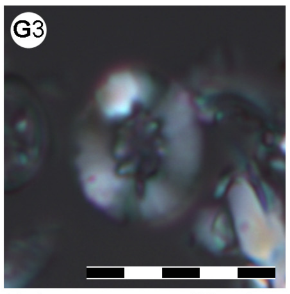
Prediscosphaera
arkhangelskyi (8.0µm)
sample 549 - 405.08mbsf



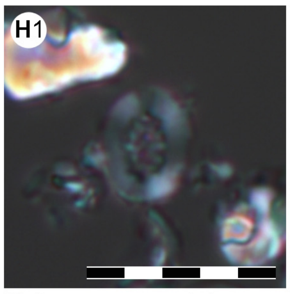
Retecapsa angustiforata
(5.9µm)
sample 549 - 447.26mbsf



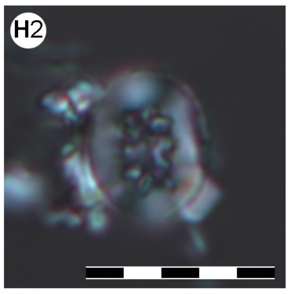
Retecapsa angustiforata
(7.2µm)
sample 549 - 447.26mbsf



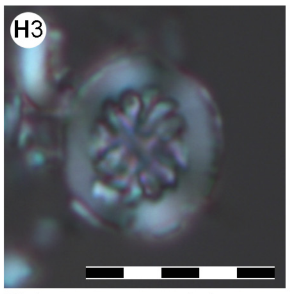
Retecapsa angustiforata
(8.2µm)
sample 549 - 403.88mbsf



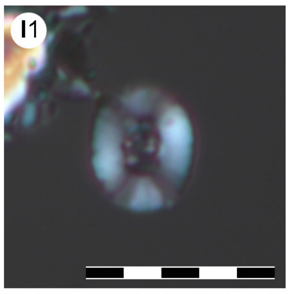
Retecapsa crenulata
(6.2µm)
sample 549 - 404.48mbsf



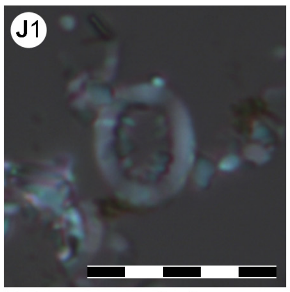
Retecapsa crenulata
(7.8µm)
sample 549 - 400.69mbsf



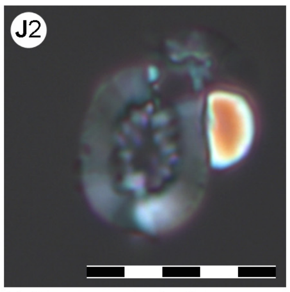
Retecapsa crenulata
(9.9µm)
sample 549 - 400.69mbsf



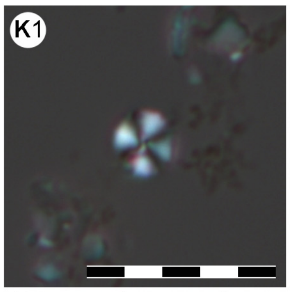
Retecapsa ficula (6.7µm)
sample 549 - 402.39mbsf



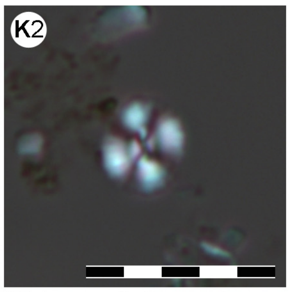
Retecapsa surirella
(6.6µm)
sample 549 - 400.69mbsf



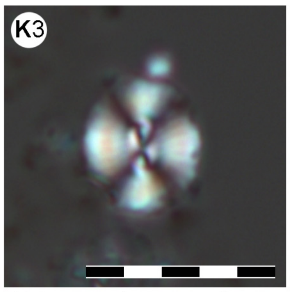
Retecapsa surirella
(9.3µm)
sample 549 - 400.69mbsf



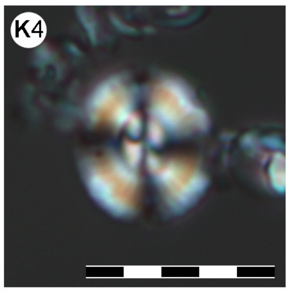
Watznaueria barnesiae
(3.7µm)
sample 549 - 447.26mbsf



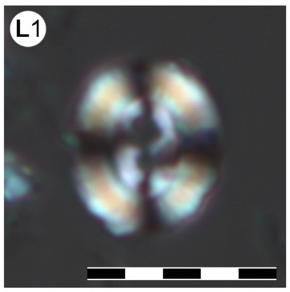
Watznaueria barnesiae
(5.2µm)
sample 549 - 447.26mbsf



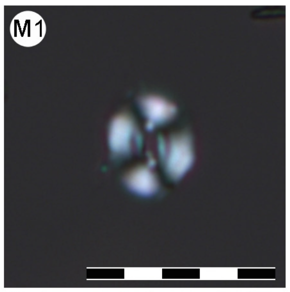
Watznaueria barnesiae
(7.2µm)
sample 549 - 447.26mbsf



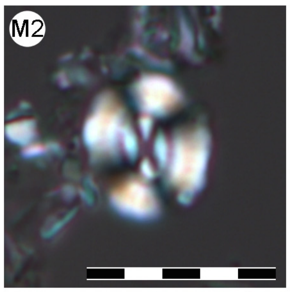
Watznaueria barnesiae
(8.7µm)
sample 549 - 404.48mbsf



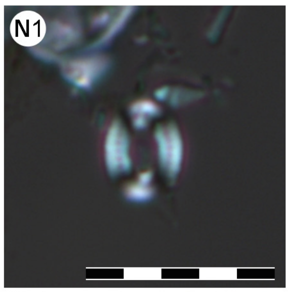
Watznaueria biporta
(9.7µm)
sample 549 - 447.26mbsf



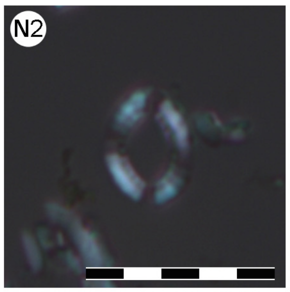
Watznaueria fossacincta
(5.5µm)
sample 549 - 419.21mbsf



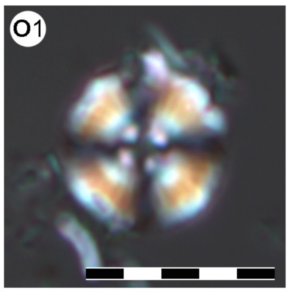
Watznaueria fassacincta
(7.8µm)
sample 549 - 419.21mbsf



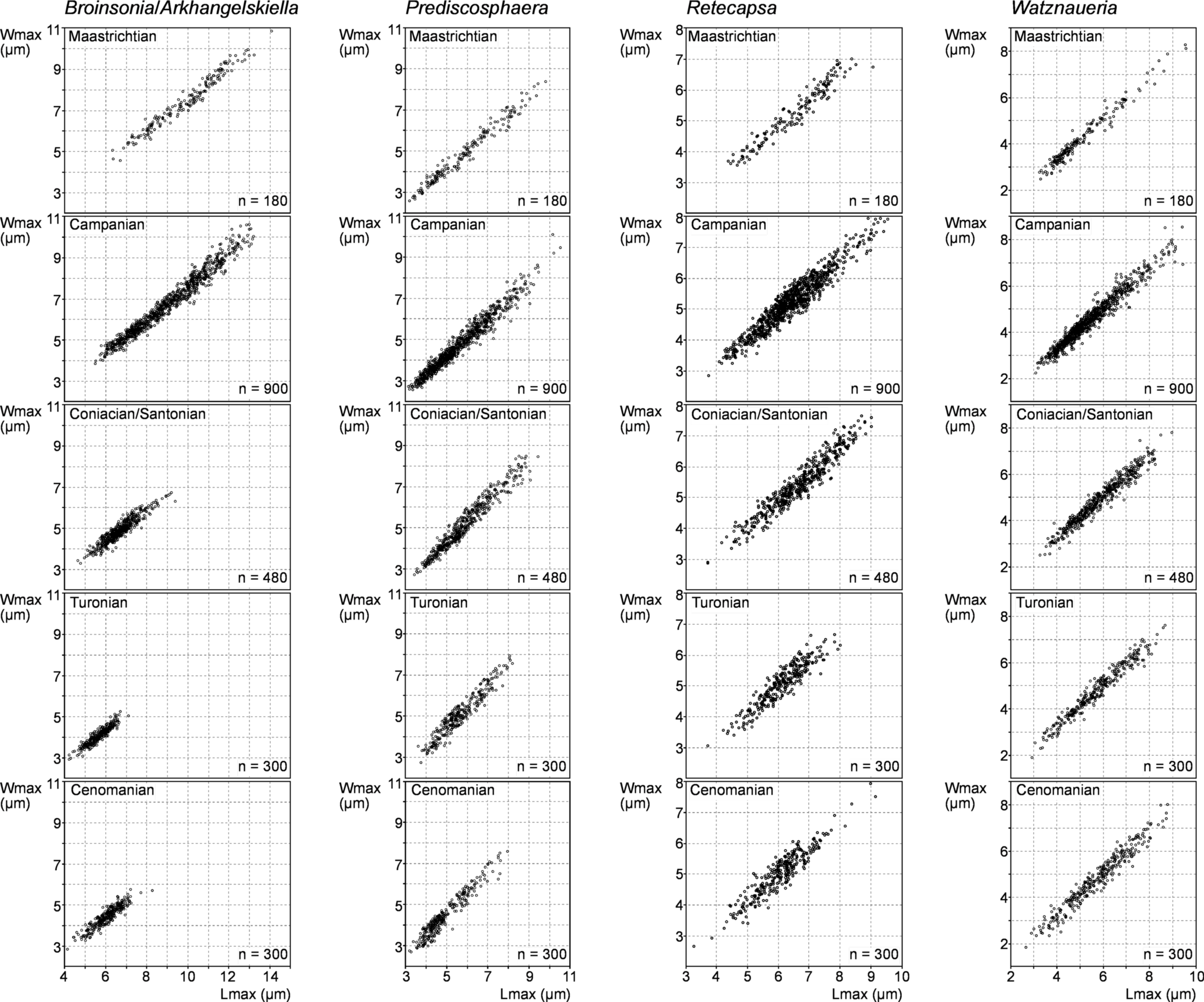
Watznaueria ovata (5.5µm)
sample 549 - 447.26mbsf



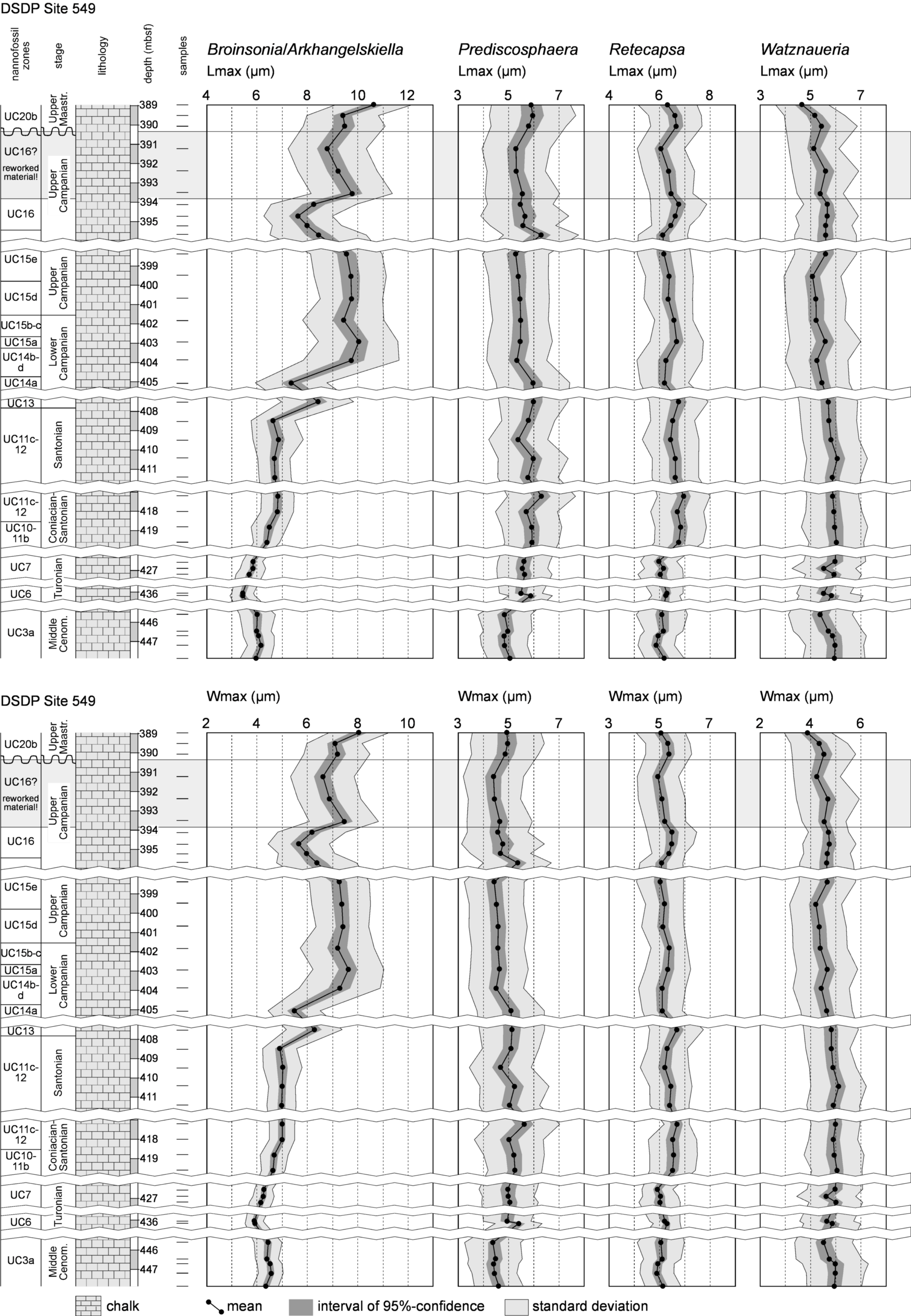
Watznaueria ovata (6.3µm)
sample 549 - 403.88mbsf

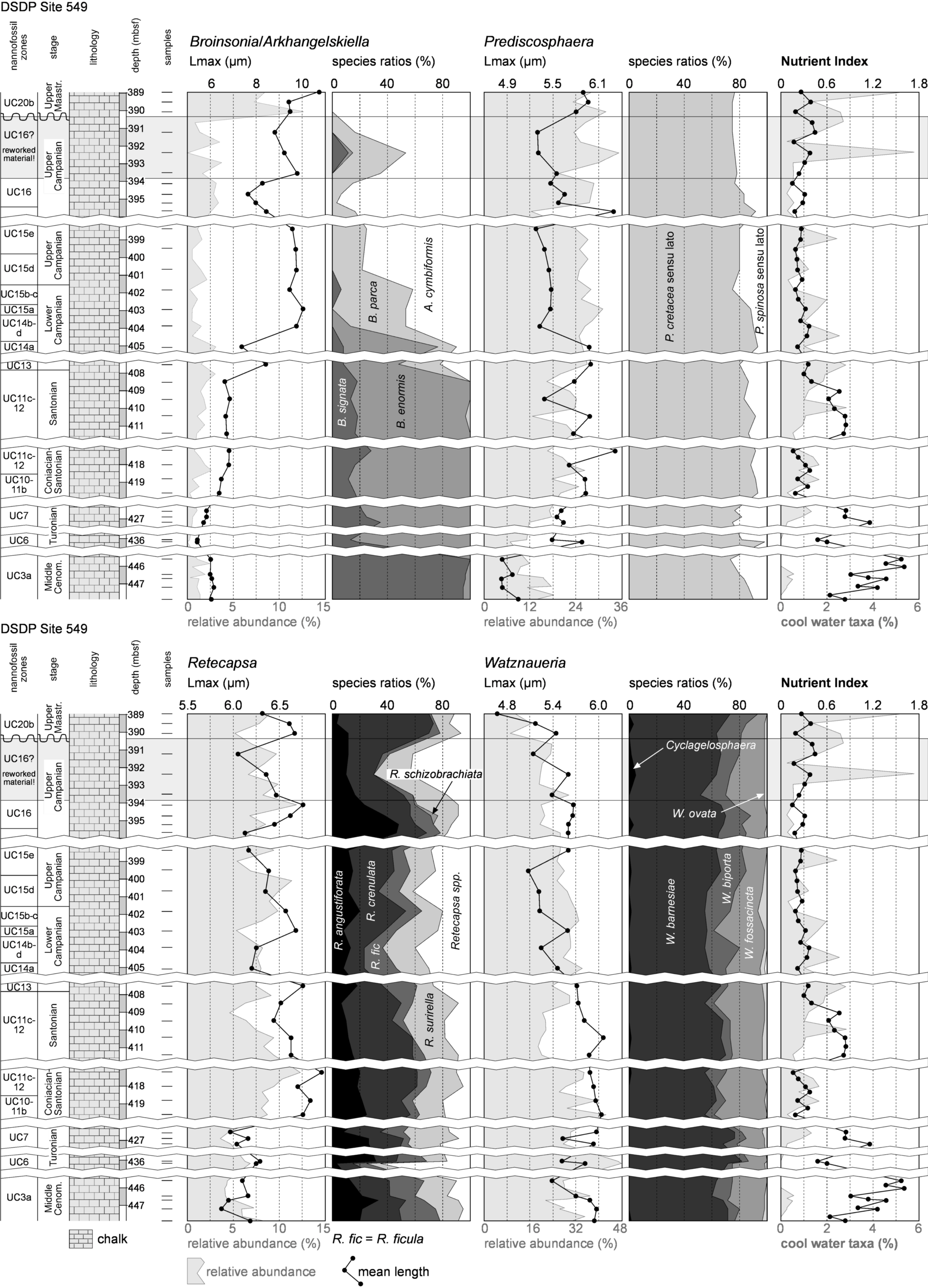


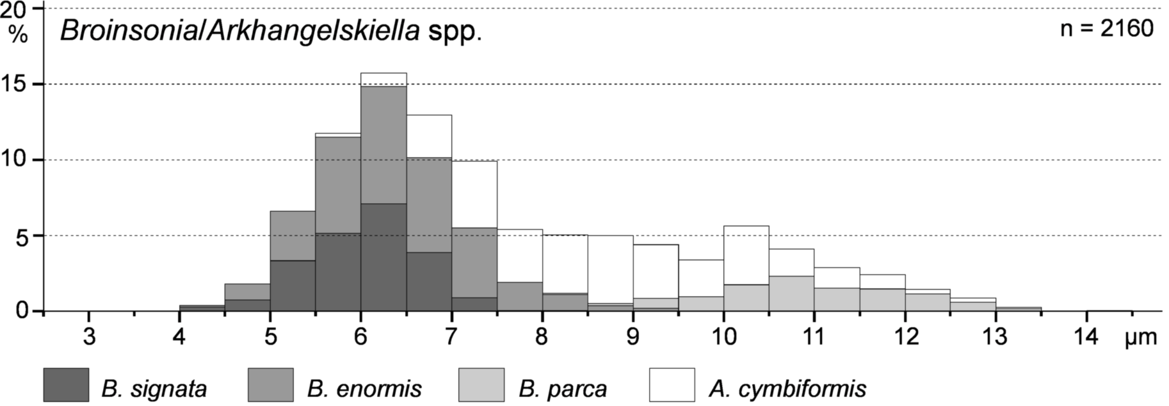
Cyclagelosphaera margerelii
(9.0µm)
sample 549 - 400.69mbsf

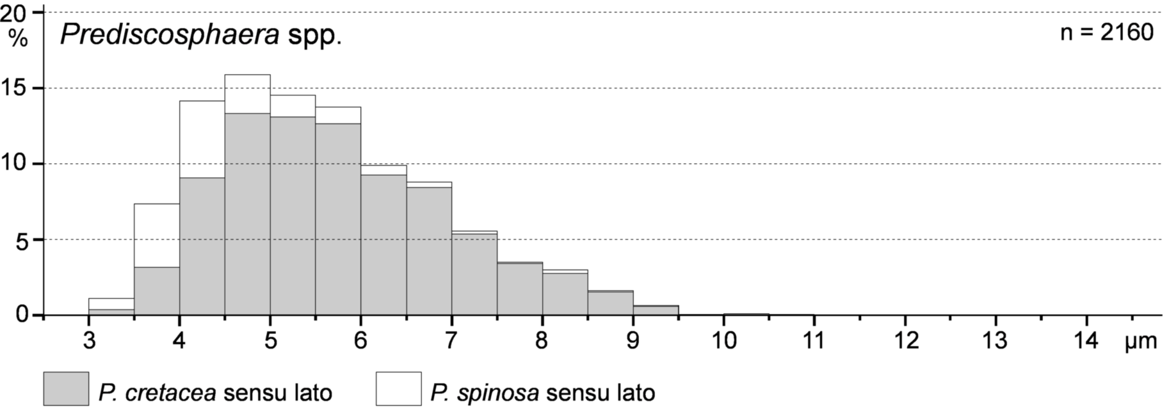

Broinsonia/Arkhangelskiella
Prediscosphaera
Retecapsa
Watznaueria
Wmax (µm)
Maastrichtian
Campanian
Coniacian/Santonian
Turonian
Cenomanian
n = 180
n = 900
n = 480
n = 300
n = 300
3
5
7
9
11
2
4
6
8
4
6
8
10
12
14
3
5
7
9
11
3
4
5
6
7
8
9
10
2
4
6
8
10
Lmax (µm)

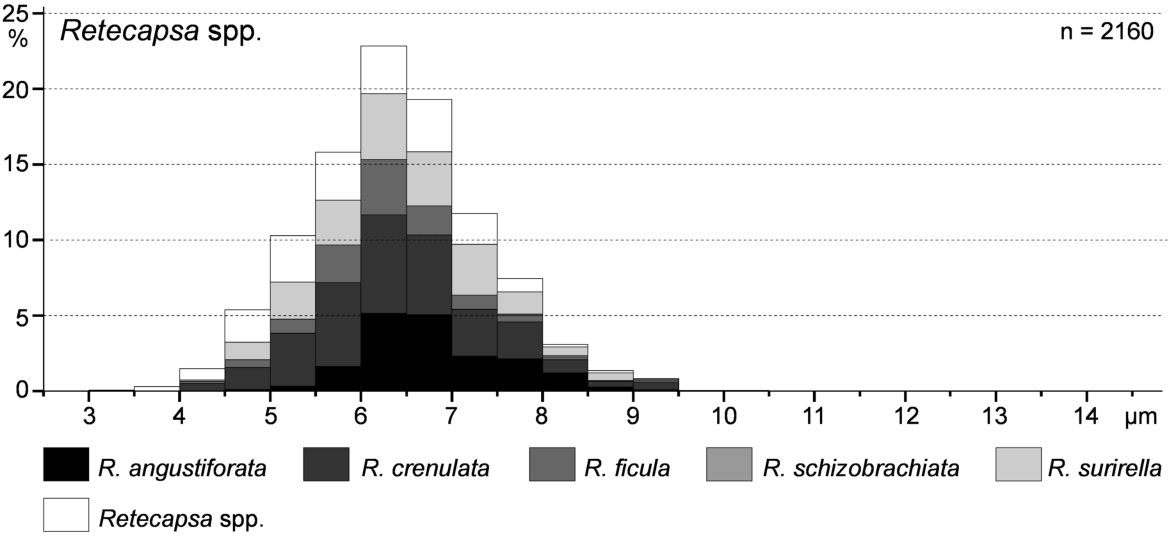
Mean and standard deviation

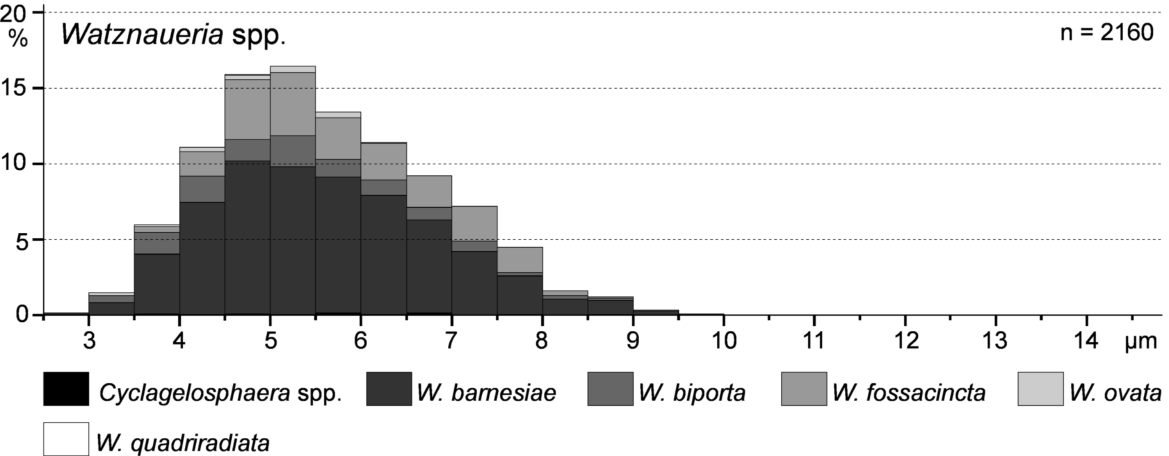



DSDP Site 549
nannofossil zones
stage
lithology
depth (mbsf)
samples
Broinsonia/Arkhangelskiella
Lmax (µm)
6
8
10
species ratios (%)
0
40
80
Prediscosphaera
Lmax (µm)
4.9
5.5
6.1
species ratios (%)
0
40
80
Nutrient Index
0
0.6
1.2
1.8
UC20b
Upper Maastr.
UC16?
reworked material!
Upper Campanian
UC16
UC15e
UC15d
Upper Campanian
UC15b-c
UC15a
UC14b-d
UC14a
Lower Campanian
UC13
UC11c-12
Santonian
UC11c-12
UC10-11b
Coniacian-Santonian
UC7
UC6
Turonian
UC3a
Middle Cenom.
389
390
391
392
393
394
395
399
400
401
402
403
404
405
408
409
410
411
418
419
427
436
446
447
A. cymbiformis
B. parca
B. signata
B. enormis
P. cretacea sensu lato
P. spinosa sensu lato
0
5
10
15
relative abundance (%)
0
12
24
36
relative abundance (%)
0
2
4
6
cool water taxa (%)
DSDP Site 549
nannofossil zones
stage
lithology
depth (mbsf)
samples
Retecapsa
Lmax (µm)
5.5
6.0
6.5
species ratios (%)
0
40
80
Watznaueria
Lmax (µm)
4.8
5.4
6.0
species ratios (%)
0
40
80
Nutrient Index
0
0.6
1.2
1.8
R. schizobrachiata
R. angustiforata
R. crenulata
R. fic
Retecapsa spp.
R. surirella
Cyclagelosphaera
W. ovata
W. barnesiae
W. biporta
W. fossacincta
0
5
10
15
relative abundance (%)
R. fic = R. ficula
0
16
32
48
relative abundance (%)
0
2
4
6
cool water taxa (%)
chalk
relative abundance
mean length

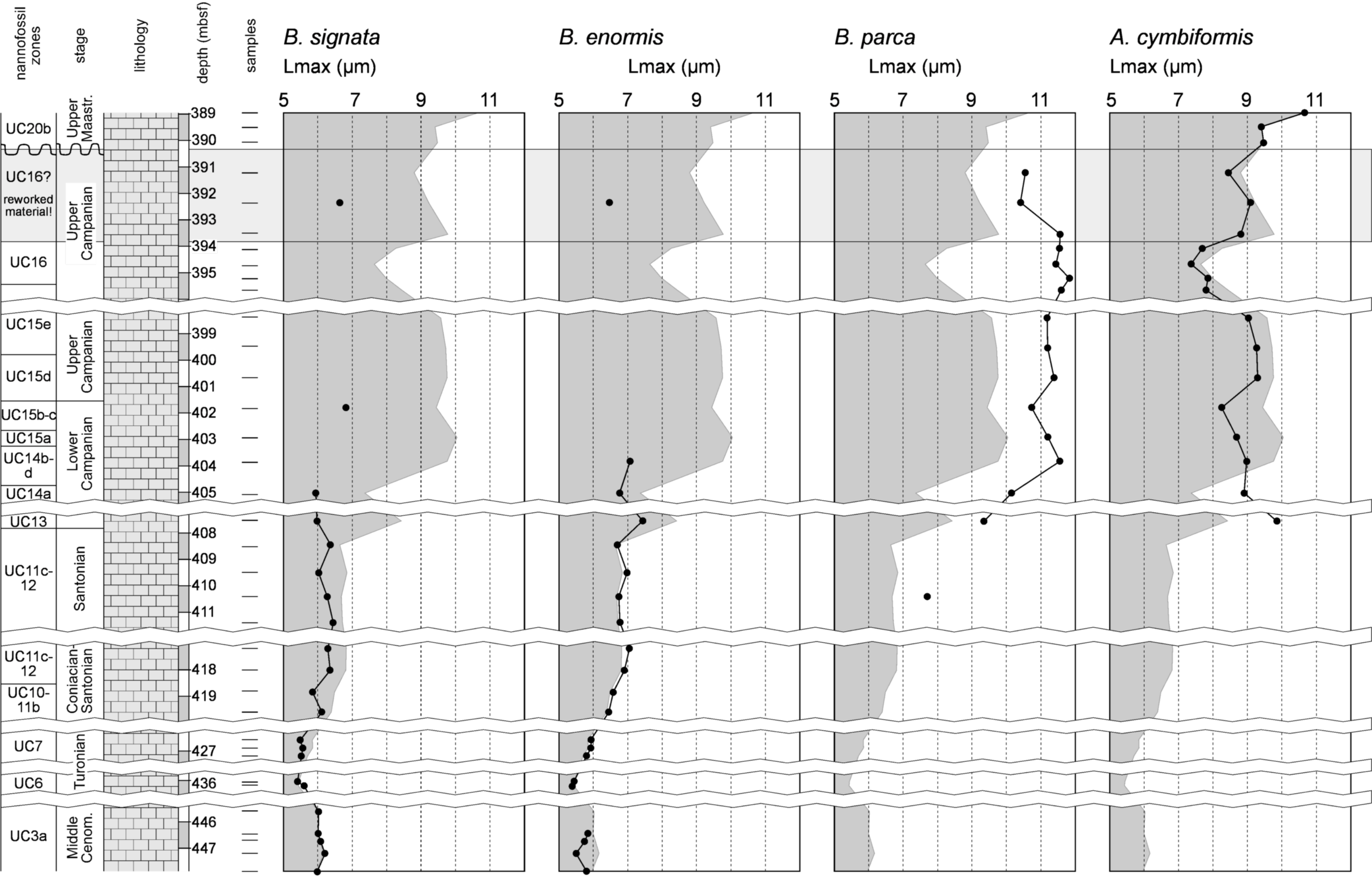

Broinsonia/*Arkhangelskiella* spp.
n = 2160
20 %
15
10
5
0
3
4
5
6
7
8
9
10
11
12
13
14
µm
B. signata
B. enormis
B. parca
A. cymbiformis


Prediscosphaera spp.
n = 2160
20 %
15
10
5
0
3
4
5
6
7
8
9
10
11
12
13
14
µm
P. cretacea sensu lato
P. spinosa sensu lato


Retecapsa spp.
n = 2160
25 %
20
15
10
5
0
3
4
5
6
7
8
9
10
11
12
13
14
µm
R. angustiforata
R. crenulata
R. ficula
R. schizobrachiata
R. surirella
Retecapsa spp.


Watznaueria spp.
n = 2160
20 %
15
10
5
0
3
4
5
6
7
8
9
10
11
12
13
14
µm
Cyclagelosphaera spp.
W. barnesiae
W. biporta
W. fossacincta
W. ovata
W. quadriradiata

DSDP Site 549



numbers of specimens encountered

sample	447.87 mbsf	447.26 mbsf	446.75 mbsf	446.46 mbsf	445.64 mbsf	436.22 mbsf	436.12 mbsf	427.19 mbsf	426.87 mbsf	426.55 mbsf	419.61 mbsf	418.81 mbsf	417.99 mbsf	417.21 mbsf	411.41 mbsf	410.44 mbsf	409.49 mbsf	408.49 mbsf	407.53 mbsf	405.08 mbsf	403.88 mbsf	402.95 mbsf	401.84 mbsf	400.69 mbsf	399.54 mbsf	398.39 mbsf	395.65 mbsf	395.18 mbsf	394.69 mbsf	394.08 mbsf	393.49 mbsf	392.34 mbsf	391.19 mbsf	390.04 mbsf	389.47 mbsf	388.89 mbsf
B. signata	57	57	58	58	60	11	8	21	15	13	10	7	10	17	10	11	8	11	5	5			4									7				
B. enormis	3	3	2	2		49	52	39	45	47	50	53	50	43	50	47	52	49	24	41	8											2				
B. parca																2			18	8	24	32	31	13	14	15	10	2	4	9	21	23	10			
A. cymbif.																			13	6	28	28	25	47	46	45	50	58	56	51	39	28	50	60	60	60

Broinsonia/Arkhangelskiella

	minL	meanL	maxL	meanW
all specimens (n=2160)	4.1	7.7	14.1	5.7
Cenomanian specimens (n=300)	4.1	6.1	8.3	4.5
Turonian specimens (n=300)	4.2	5.7	7.1	4.1
Coniacian - Santonian spec. (n=480)	4.6	6.7	9.4	4.9
Campanian specimens (n=900)	5.5	9.0	13.2	6.7
Maastrichtian specimens (n=180)	6.3	9.9	14.1	7.5
Broinsonia signata (n=463)	4.1	6.0	8.3	4.4
Broinsonia enormis (n=711)	4.2	6.4	9.4	4.7
Broinsonia parca ssp. (n=236)	7.3	11.0	13.2	8.5
Arkhangelskiella cymbiformis (n=750)	5.7	8.8	14.1	6.6

Prediscosphaera spp.

	minL	meanL	maxL	meanW
all specimens (n=2160)	3.1	5.6	10.5	4.8
Cenomanian specimens (n=300)	3.2	4.9	8.0	4.5
Turonian specimens (n=300)	3.6	5.6	8.2	5.1
Coniacian - Santonian spec. (n=480)	3.4	5.9	9.4	5.2
Campanian specimens (n=900)	3.1	5.6	10.5	4.7
Maastrichtian specimens (n=180)	3.2	5.9	9.8	4.9
Prediscosphaera cretacea s.l. (n=1799)	3.1	5.8	10.5	5.1
Prediscosphaera spinosa s.l. (n=361)	3.2	4.6	9.0	3.7

Retecapsa spp.

	minL	meanL	maxL	meanW
all specimens (n=2160)	3.3	6.4	10.3	5.2
Cenomanian specimens (n=300)	3.3	6.1	9.2	5.0
Turonian specimens (n=300)	3.7	6.1	8.0	5.1
Coniacian - Santonian spec. (n=480)	3.7	6.7	9.0	5.5
Campanian specimens (n=900)	3.8	6.4	9.6	5.3
Maastrichtian specimens (n=180)	4.4	6.5	10.3	5.3
Retecapsa angustiforata (n=394)	4.8	6.8	9.0	5.8
Retecapsa crenulata (n=652)	4.2	6.4	9.4	5.2
Retecapsa ficula (n=245)	4.4	6.3	9.3	5.2
Retecapsa schizobrachiata (n=4)	7.7	8.0	8.5	6.7
Retecapsa surirella (n=446)	4.2	6.5	9.6	5.2
Retecapsa spp. (n=419)	3.3	6.0	10.3	4.9

Watznaueria spp.

	minL	meanL	maxL	meanW
all specimens (n=2160)	2.7	5.6	9.6	4.7
Cenomanian specimens (n=300)	2.7	5.8	8.8	4.8
Turonian specimens (n=300)	2.9	5.8	8.7	4.8
Coniacian - Santonian spec. (n=480)	3.3	5.9	9.0	5.0
Campanian specimens (n=900)	3.1	5.5	9.5	4.6
Maastrichtian specimens (n=180)	3.3	5.1	9.6	4.3
Watznaueria barnesiae (n=1388)	2.7	5.6	9.6	4.7
Watznaueria biporta (n=247)	2.9	5.3	8.8	4.4
Watznaueria fossacincta (n=471)	3.7	5.8	9.1	4.9
Watznaueria ovata (n=38)	3.1	4.8	6.0	3.9
Watznaueria quadriradiata (n=1)	4.9	4.9	4.9	4.3
Cyclogelasphaera spp. (n=15)	3.8	5.8	8.7	5.6

	abs. abundance	simple diversity	meanL Broinsonia/Arkhangelskiella	meanL Prediscosphaera	meanL Retecapsa	meanL Watznaueria	%Broinsonia/Arkhangelskiella	%Prediscosphaera spp.	%Retecapsa spp.	%Watznaueria spp.	Nutrient Index
abs. abundance	1.00										
simple diversity	**0.64**	1.00									
meanL Broinsonia/Arkhangelskiella	**0.53**	0.37	1.00								
meanL Prediscosphaera	0.17	-0.21	0.11	1.00							
meanL Retecapsa	0.38	0.01	0.23	**0.58**	1.00						
meanL Watznaueria	-0.30	-0.17	**-0.73**	0.04	0.10	1.00					
%Broinsonia/Arkhangelskiella	0.16	-0.07	0.40	0.24	0.16	-0.42	1.00				
%Prediscosphaera spp.	**0.76**	**0.50**	**0.75**	0.11	0.42	**-0.44**	0.36	1.00			
%Retecapsa spp.	0.31	0.13	0.34	0.36	**0.54**	-0.09	-0.01	0.31	1.00		
%Watznaueria spp.	**-0.45**	**-0.47**	**-0.49**	0.03	-0.06	0.30	**-0.64**	**-0.54**	-0.05	1.00	
NutrientIndex1	**-0.49**	-0.10	**-0.62**	**-0.59**	**-0.61**	0.35	-0.25	**-0.60**	**-0.57**	-0.01	1.00
cool water taxa	0.37	0.19	**0.49**	0.17	0.16	-0.35	0.37	**0.57**	0.05	**-0.47**	-0.29
significant at the level of 95%	0.36										
significant at the level of 99%	**-0.45**										