Paleoceanographic changes across the Jurassic/Cretaceous boundary: The calcareous phytoplankton response

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Abstract

Calcareous nannoplankton experienced rapid diversification at the Jurassic/Cretaceous boundary, including the appearance of several highly successful and long-ranging Cretaceous genera. This study examines, at high-resolution, calcareous nannofossil assemblages and bulk-rock oxygen and carbon isotopes of lower Tithonian to lower Berriasian (~151 to 142 Ma) sediments recovered in Deep Sea Drilling Project Hole 534A, central Atlantic Ocean. The results show major changes in assemblage composition and abundance of three genera (Conusphaera, Nannoconus, and Polycostella). Conusphaera dominates the nannolith assemblage in the late middle Tithonian (“Conusphaera world”), while the nannoconid dominance (“Nannoconus world”) began in the Berriasian. The acme peak of the genus Polycostella in the late Tithonian partially superimposes that of Conusphaera. Although these genera are indicators of warm, oligotrophic surface waters, stable isotope data suggest that the individual taxa may flourishes in slightly different ecological regimes. Nannoconus flourished under warmer and possibly more nutrient-depleted surface waters than Polycostella, a genus that thrived in relatively cooler waters. These findings imply paleoceanographic changes across the J/K boundary interval with a cooling in the late Tithonian, followed by a temperature increase in the Berriasian. Because the transfer of these heavily calcified nannolith taxa to the seafloor is more efficient than that of average coccolithophorids, the J/K evolutionary event changed carbonate cycling and burial in the oceans.

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1. Introduction

The Jurassic/Cretaceous boundary [J/K; 144.2 Ma, 1] is considered to be one of eight major mass extinc-
Calcareous nannoplankton evolved in the Triassic and experienced major diversifications in the Early Jurassic, across the Jurassic/Cretaceous (J/K) and at the Cretaceous/Tertiary (K/T) boundary ([6] and references therein). Calcareous nannofossil is a broad term used to describe calcitic fossil remains smaller than ~30 μm. In general, they are categorized into two groups: coccoliths (disc-shaped calcite plates of coccolithophores) and nannoliths (calcitic bodies with highly variable shape and/or simple crystal structure). Whereas coccoliths are produced by haptophyte algae, the origin of nannoliths is uncertain. They are presumably produced by haptophyte algae or calcareous dinoflagellates (e.g., [8]). Since photoautotrophic algae mineralize nannoliths, paleoceanographic factors such as temperature and nutrients control their spatial and temporal distribution. Most contemporary coccolithophores thrive in the upper photic zone, but a few species such as *Florisphaera profunda* and some calcareous dinoflagellates inhabit the deep-chlorophyll maximum, the lower portion of the photic zone (e.g., [9,10]). Variations in nutricline depth hence regulate certain calcareous nanoplankton, and possibly controlled the fluctuations in abundance of fossil haptophytes. The habitats and mode of life of most Mesozoic species are still unclear or not fully understood, but it is plausible that several taxa followed trophic and temperature gradients in a similar fashion to modern species.

Our study uses a multidisciplinary approach to constrain the origin of calcareous nannofossil diversification in the J/K boundary interval. Previously, quantitative studies of calcareous nannofossils from this time interval have only been performed at low resolution [11,12]. We have carried out a high-resolution, quantitative analysis of calcareous nannofossil assemblages to determine major variations in their abundance and composition. Stable isotope analyses were conducted to constrain environmental changes during this interval of significant evolution. The burst of diversification of calcareous nanoplankton in the Jurassic/Cretaceous boundary interval was a watershed event in the evolution of the group with the appearance of several highly successful Cretaceous taxa. Moreover, the evolution of three large and heavily calcified genera greatly increased the transfer and burial efficiency of

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**Fig. 1.** Paleoceanographic reconstruction of the Central Atlantic during the Late Jurassic and location of DSDP Sites 534 and 105 after Bornemann et al. [12].
carbonate and therefore profoundly altered marine geochemical cycles.

2. Material and methods

Analyses were performed on samples collected from the Deep Sea Drilling Project (DSDP) Hole 534A, drilled in the Blake Bahama Basin, Central Atlantic Ocean (Fig. 1) [13]. The investigated sedimentary interval spans from cores 88R to 101R, dated as Tithonian to early Berriasian [5] and consists mostly of claystones and limestones. The same interval was recently studied at low resolution by Bornemann et al. [12]. Here the resolution was increased (1 sample/20 ky) to more accurately constrain the fluctuations in abundance and composition of nannofloral assemblages.

Calcareous nannofossils were analyzed in 378 smear slides prepared from all lithologies under a light microscope at 1250 × magnification. In order to obtain relative abundances at least 300 specimens were counted in each slide. All specimens were identified at the species level and grouped at the generic level with the exception of Cyclagelosphaera and Watznaueria. The species Cyclagelosphaera margerelii represents 99% of Cyclagelosphaera specimens observed in Hole 534A, whereas C. deflandrei and C. tubulata constitute only 1% and display insignificant fluctuations. The abundances of the placolith-bearing Watznaueria were subdivided in three subgroups: W. britannica, W. manivitae and Watznaueria spp., that mostly consists of W. barnesae (>80% of this subgroup) and minor quantities of W. ovata, W. biporta, W. communis and W. fossacineta.

Carbon and oxygen isotope analyses were carried out on the bulk carbonate fraction in 158 samples using a VG Optima mass spectrometer with a multipreparation peripheral attachment for calcium carbonate measurements. Values are reported in terms of Vienna-PDB (‰) by analyzing NBS-19 and an internal standard. The 1-sigma standard deviations of δ18O and δ13C values from the standards analyzed during the sample runs are 0.08‰ and 0.04‰, respectively.

Fig. 2. Fluctuations of the most abundant calcareous nannofossil taxa (expressed as %) in DSDP Hole 534A. Magnetostratigraphy after Ogg [70], biostratigraphy after Bralower et al. [5] with modifications by Bornemann et al. [12]. The gray bands indicate microturbidite layers.
3. Results

3.1. Calcareous nannofossils

Quantitative analyses reveal that only seven taxa (*Nannoconus* spp., *Conusphaera* spp., *Polycostella* spp., *C. margerelii*, *Watznaueria* spp., *W. manivitae*, and *W. britannica*) display significant abundances and are discussed in this work (Fig. 2). Nannofossils indicative of eutrophic environments such as *Zeugrabdothus erectus*, *Biscutum constans*, *Diazomatolithus lehmanii*, *Discorhabdus rotatorius* (attributed to *D. ignotus* by several authors) show very low abundances. The highest percentages of these taxa are recorded in the interval between cores 101R and 99R (~7–8% of the total assemblage; Fig. 3).

The preservation of calcareous nannofossils is generally moderate and the dissolution-resistant genus *Watznaueria* (e.g., [14–17]) is the most abundant taxon (mean = ~50% of the total assemblage; Fig. 2). In particular, the highest percentages of this genus occur from cores 101R to 99R in a sedimentary interval characterized by the presence of microturbidites [13]. A few peaks in abundance (>70%) have been observed in samples from cores 97R to 88R and may be the result of increased diagenetic alteration. The percentages of *W. manivitae* range from 4% to 17% of the total assemblage and the highest abundances are recorded from cores 95R to 90R. The taxon *W. britannica* shows the highest percentages (~12%) in the lower part of the section and minor abundances from core 99R to the top of the interval investigated (<5% of the total assemblage). This taxon is mostly represented by small specimens (<6 µm). The coccolith *C. margerelii* is present in all investigated samples, its abundances range from 4% to 16% (mean = 11%) and the lowest percentages are recorded in cores 95R and 96R.

The most significant fluctuations in nannofloral communities are those of three nannoliths (*Incertae sedis*): *Nannoconus* spp., *Conusphaera* spp. and *Polycostella* spp. (Fig. 2). The first occurrence (FO) of *Conusphaera* spp. lies in core 100R, but its abundance is <1%. A peak of up to 37% has been detected in cores 97R and 96R. Above that level the quantities of *Conusphaera* spp. decrease progressively towards the top of the section where this taxon occurs sporadically. The nannolith *Polycostella* spp.

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Fig. 3. C- and O-isotope values (expressed as %) and CaCO₃ contents (expressed as %) measured in DSDP Hole 534A plotted against the abundances (expressed as %) of *Polycostella* spp., *Conusphaera* spp., *Nannoconus* spp, and eutrophic taxa. The thick line represents the O- and C-isotope trend generated by using the software SigmaPlot-Systat Corp. (running average). Magnetostratigraphy after Ogg [70], biostratigraphy after Bralower et al. [5] with modifications by Bornemann et al. [12].
gets a similar distribution pattern to that of \textit{Conusphaera} spp. (Fig. 2), but its abundance peak occurs from the top of core 96R through core 95R. The sharp drop in \textit{Conusphaera} spp. and \textit{Polycostella} spp. percentages in core 93R corresponds to the increase in abundance of \textit{Nannoconus} spp. The conical-shaped nannolith \textit{Nannoconus} spp. increases from core 93 (~12%) to the top of the section (mean = ~34%) with a peak in abundance (42%) in core 89R. Other taxa such as \textit{Stephanolithion} spp., \textit{Microstaurus chiaius}, \textit{Zeugrhadlotus} spp., \textit{Vagialapilla} spp., \textit{Cruciellipsis cuvillieri}, \textit{Zeugrhadlotus embergeri}, \textit{Lithraphidites} spp., \textit{Rhadodiscus} spp., \textit{Faviconus} spp., \textit{C. deflandrei}, \textit{C. tubulata}, \textit{Umbria granulosa} and \textit{Hexalithus noeliae} combined account for less than 2% of the total assemblage.

3.2. Geochemistry

Bulk carbonate carbon isotope ($\delta^{13}$C$_{\text{carb}}$) measurements show three distinct trends. Samples collected from cores 101R through 99R display the most marked oscillations in $\delta^{13}$C$_{\text{carb}}$ values ranging from 0.34‰ to 2.82‰ (Fig. 3). These variations could be the result of diagenetic alteration and/or a significant contribution from reworking (microturbidites). The interval between cores 97R and 95R shows moderate oscillations in $\delta^{13}$C$_{\text{carb}}$ values (<1‰). On the contrary, the interval from core 94R to the top of the investigated section is characterized by quite stable values (mean 1.52‰).

The $\delta^{18}$O$_{\text{carb}}$ record shows a general trend of decreasing values from the bottom to the top of the section with small fluctuations. Cores 101R to 99R show fluctuations that correlate with those in $\delta^{13}$C$_{\text{carb}}$. $\delta^{18}$O$_{\text{carb}}$ measurements range from $-0.48‰$ to $-4.68‰$ from core 97R to the top of the section with heavier (mean = $-1.95‰$) values from the top of core 96R through core 95R. Moreover, a low $\delta^{18}$O$_{\text{carb}}$ value of $-5.68‰$ was obtained in sample 97-1, 40–41 cm (Fig. 3). Replicate analyses of this sample yielded similar values but it is likely that this unusually low value results from diagenetic alteration. In general, the lowest $\delta^{18}$O values correlate with the highest abundance of the nannofossil taxa \textit{Nannoconus} spp and \textit{Conusphaera} spp., whereas high percentages of \textit{Polycostella} spp. are associated with the highest $\delta^{18}$O$_{\text{carb}}$ values.

Calcium carbonate contents show an increase from the bottom (mean = ~29%) to the top of the section (mean = ~85%) with peaks as high as 92% in cores 89R and 88R.

4. Discussion

4.1. Calcareous nannofossil paleoecology

Quantitative calcareous nannofossil assemblage data from DSDP Site 534 correlate well with other sites in the Atlantic Ocean [12] and with land sections from Italy [11]. Moreover, the trends and magnitude of relative abundances obtained in this study are in excellent agreement with the former study of Bornemann et al. [12]. The most abundant taxa are considered to be quite dissolution-resistant and thus their fluctuations can be interpreted in terms of changes in paleoceanographic and paleoclimatic conditions.

The placolith \textit{W. barnesae} is generally regarded as a cosmopolitan taxon particularly abundant in oligotrophic surface water settings [12,17–23], although this interpretation has been challenged, at least for some intervals. Lees et al. [24], however, interpreted blooms of this taxon in the Upper Jurassic Kimmeridge Clay Formation as indicative of eutrophic environments. Thomsen [25] documented a dominance of \textit{W. barnesae} in well-preserved nannofossil assemblages from Barremian laminated sediments in the North Sea Basin following the winter clay-rich laminae. This author interpreted this dominance as a spring bloom suggesting an opportunist life strategy for \textit{W. barnesae}. Perhaps this taxon is adapted to thrive under extreme conditions more efficiently than other taxa [26]. The taxon \textit{W. manivitae} is particularly abundant in low-latitude nannofloral assemblages of Late Jurassic–Early Cretaceous age [27], and its distribution is possibly controlled by temperature. Alternatively, Pittet and Mattioli [28] and Oliver et al. [29] proposed that this species proliferates under oligotrophic conditions. \textit{Watznaueria Britannica} has been suggested as a mesotrophic (e.g., [24]) or eutrophic taxon [30,31]. The smallest specimens of \textit{W. Britannica} could be indicative of more eutrophic conditions [28,29]. The ecological affinities of \textit{C. margerelii} are still unclear. Pittet and Mattioli [28] and Oliver et al. [29] suggested that \textit{C. margerelii} occupied an intermediate position in the trophic preference continuum between \textit{W. manivitae} (more oligotrophic) and small-sized \textit{W. Britannica} (more eutrophic). Several authors [30–32] described extremely high abundance of \textit{C. margerelii} in lagoonal environments characterized by low-diversity nannofloral assemblages and marked salinity variations. This taxon survived the Cretaceous/Tertiary boundary extinction and has been interpreted as a neritic species [6,33]. However, it is unclear if the small fluctuations in abundance of this taxon are driven by increases and decreases of other taxa or salinity variations.
The paleoecology of nannoconids is controversial, but several hypotheses about their environmental preferences have been postulated. *Nannoconus* spp. are generally interpreted to have preferred warm waters based on their high abundances in low-latitude locations [34–37,33]. Street and Bown [26,33] and Scarparo Cunha and Koutsoukos [38] argued that *Nannoconus* spp. was a eutrophic or mesotrophic taxon, respectively. However, most studies suggest that this taxon thrived in oligotrophic environments [22,39–41] and fluctuations in nannoconid abundance are generally out of phase with those of universally accepted eutrophic taxa in the Cretaceous [23]. Moreover, Erba [42] proposed that the genus *Nannoconus* was a deep-dwelling (lower photic zone) taxon that flourished with a deep nutrient line and marked oligotrophic conditions in surface waters. This interpretation was supported by recently published studies of Herrle [21], Bornemann et al. [43], and Watkins et al. [44]. The paleoecological affinities of *Conusphaera* spp. and *Polycostella* spp. are still unclear owing to the scarcity of studies regarding these taxa. Furthermore, the J–K transition is the only stratigraphic interval that records significant quantities of *Conusphaera* spp. (especially *C. mexicana*) and *Polycostella* spp. Based on similarities in their shape and size to the nannoconids it seems plausible that they inhabited a similar environmental niche [12].

### 4.2. Stable isotopes

The $\delta^{13}C$ and $\delta^{18}O$ records obtained from bulk carbonates in Hole 534A are a function of changes in regional and/or global paleoceanographic changes (primary productivity, seawater pH, temperature, salinity and shifts in the fractions of organic and inorganic carbon burial), changes in carbonate mineralogy (i.e., calcite and aragonite), assemblage composition (i.e., changes in nannofossil abundance), and diagenetic overprint. The extent of diagenetic alteration of $\delta^{13}C$ and $\delta^{18}O$ ratios depends primarily on the burial history. In particular, the $\delta^{18}O$ ratio is shifted towards lighter values during recrystallization at increased burial temperatures or by the precipitation of isotopically light cements during deep burial [45,46].

Carbon and oxygen isotopes are also influenced by vital effects, with individual calcareous nannofossil taxa exerting different degrees of isotopic fractionation [47–49]. Because the bulk carbonate at Site 534 is mostly composed of nannofossils, or micrite derived largely from the mechanical break-up of nannofossils, fluctuations in carbon isotopes likely reflect compositional changes in nannofossil assemblages.

Both $\delta^{13}C$ and $\delta^{18}O$ show major fluctuations in cores 101R through 99R that could represent diagenetic alteration. In Hole 534A the most pronounced isotopic excursions, observed from cores 101R to 99R, were detected in presumed microturbidite layers (Fig. 3) characterized by high abundances of carbonate and detrital particles of unknown origin and moderate preservation of calcareous nannofossils [13].

Isotopic variations observed from core 97R to the top of the section correlate with $\delta^{13}C$ and $\delta^{18}O$ oscillations recorded at DSDP Site 105 (Fig. 4) and in several sections in the western Tethys [50–52] characterized by different burial histories. This may point to a supraregional, environmental control of the isotope signal rather than local diagenetic alteration. C- and O-isotope records and nannofossil distribution patterns at Site 105 parallel those at Site 534, although abundances of strongly calcified nannofossils are considerably different (e.g., nannoconids <20% at Site 105, >30% at Site 534). This may suggest that the vital effect of nannoliths had a minor impact on the isotopic signal.

The $\delta^{13}C$ record shows only very small-scale fluctuations (Fig. 3) implying that the C-cycle and, in particular, the partitioning of the global carbon pool between reduced (organic carbon) and oxidized (carbonate, carbon dioxide and bicarbonate) reservoirs experienced only slight variations [50]. Low C-isotope values are interpreted as resulting from low rates of transfer of light carbon to the sedimentary reservoir due to limited fluxes of organic matter from the photic zone [53] and reduced organic carbon burial rates [54].

The $\delta^{18}O$ record is controlled by temperature and the oxygen isotopic composition of seawater (resulting from the combination of changes in salinity and ice volume). If we assume that the Tithonian–Berriasian transition was an ice-free world or characterized by small or ephemeral ice caps [55], a $\Delta T$ decrease of approximately 4–6 °C (1 °C per 0.25‰ [56]) is recorded in cores 96R through 95R in the late Tithonian. Consequently, a temperature increase of about 4 °C is calculated across the Jurassic/Cretaceous boundary and into the Berriasian. Because such large temperature changes are difficult to explain, a decrease in salinity likely explains part of the apparent warming signal. Changes in paleocirculation of Atlantic water masses may account to some extent for these temperature and salinity variations. In particular, the final opening of the Atlantic-Pacific gateway during magnetic chron CM 19 [57] played a crucial role as suggested by Bornemann et al. [12]. The early Atlantic Ocean is generally viewed to be highly saline and is interpreted to be an important source of intermediate or deep-waters to the Pacific after the Atlantic-Pacific gate-
way was open [58,59]. Enhanced mixing of Atlantic saline waters with lower salinity Pacific waters may thereby have contributed to the shift observed in the $\delta^{18}O$ values, which coincides with the rise of nannocnids. Moreover, the opening of this gateway may have established a circum equatorial current system [60], which possibly had a major impact on the circulation pattern of the early Atlantic. Our interpretation of bulk oxygen isotope patterns obtained in Hole 534A is in agreement with temperature changes derived from palynological investigations [61].

### 4.3. Paleoceanographic response of calcareous phytoplankton

The combination of nannofossil and stable isotope records provide new insights into the calcareous nannofloral assemblage changes that occurred during the J–K transition. Although lower in resolution, investigation of calcareous nannofossil assemblages in other locations at low latitudes across the J/K boundary [11,12,62–64] show very similar temporal distribution and fluctuations in abundance of the genera *Conusphaera*, *Polycostella* and *Nannoconus*. This implies that nannofloral changes observed at DSDP Site 534 represent a supraregional to global event.

In Hole 534A the lower Tithonian interval shows the highest abundances of eutrophic taxa and small-sized specimens of *W. britannica*. These sediments are characterized by conspicuous terrigenous material and negligible quantities of oligotrophic nannoliths such as *Nannoconus*, *Conusphaera* and *Polycostella*. These data can be interpreted in terms of higher nutrient fluxes resulting from increased runoff and continental weathering under humid conditions [61, 65,66]. The stepwise increase in heavily calcified nannoliths after the mid-Tithonian could be the result of drier atmospheric conditions [50,61] that led to a diminished nutrient supply from the continents, and more oligotrophic conditions. The appearance of abundant nannoliths in the middle Tithonian corresponds to a general increase in CaCO$_3$ and carbonate accumulation rates in the deep Atlantic and western Tethys [12,66] as well as to a prolific production of biogenic carbonate on platforms and reefs [67]. Bornemann et al. [12] named this interval “Nannofossil Calcification Event” due to the occurrence of highly calcified nannoliths and *Watznaueria* specimens (especially *W. manivitae*). These authors addressed numerous possible causes for this shift. These include changes in the oceanic circulation due to a plate-tectonic reconfiguration of the Caribbean [60], which allowed more vigorous water-mass exchange between the Atlantic and the Pacific Oceans. Other causes may be surface water alkalinity changes due to a presumed drop in $p$CO$_2$ [68,69] and/or oligotrophic surface-water conditions, which might have favored increased calcification by nannoplankton [12,66]. Nevertheless, the acme peaks (>20% of the total nannofloral assemblage) of *Nannoconus* spp., *Conusphaera* spp. and *Polycostella* spp. occur at different stratigraphic levels that may indicate slightly distinct ecological affinities. Also, the duration of *Conu-
sphaera and Polycostella acme peaks, derived from sedimentation rates and magnetostratigraphy at DSDP Site 534 [70], is 1.21 my and 0.42 my, respectively, whereas the nannoconid dominance extended through the Early Cretaceous ([12], Fig. 5). The offset among the abundances of Nannoconus spp., Conusphaera spp. and Polycostella spp. could be the result of biological competition for the same ecological niche [12] through significant changes in temperature and nutrient availability during the J–K transition. Nannoconids were the most successful group presumably because they adapted better to warmer and stratified water masses. However, it is actually possible that cooling recorded from the top of core 96R through core 95R triggered, or at least accelerated, the switch from the Conusphaera-dominated (“Conusphaera world”) nannolith assemblage temporarily through the dominance of Polycostella spp. to the new Nannoconus-dominated (“Nannoconus world”) nannolith assemblage. The age of the presumed cooling and the Polycostella acme correlates with that of the 80-km diameter Morokweng impact structure in South Africa (144.7 ± 1.9 Ma, [71]). However, the duration of the cooling, as interpreted from oxygen isotope data, is too long (>400 ky) to have been triggered by an impact event. The quantities of dust particles released from the impact were probably inadequate to result in global effects because target rocks were granites [71]. In addition, no well-defined distal impact ejecta layer has been identified across the J–K transition [72].

The J–K transition is also characterized by a rapid diversification in calcareous nannofossil communities [5,6,12]. Major changes in composition of nannolith assemblages described here occurred in a geologically short time (Fig. 5), whereas the coccolith diversification was continuous, but at slower rates [5,12]. Faster coccolith speciation rates associated with increasing nutrient availability [73] are recorded across the Pliensbachian–Toarcian, Barremian–Aptian and Cenomanian–Turonian transitions in the Mesozoic [6]. We infer that stratified and nutrient-depleted waters, and environmental stability favor slow diversification and increasing abundances of nannoliths, whereas rapid diversification of Mesozoic coccoliths seem to be mainly stimulated by environmental instability associated with more eutrophic and/or turbulent surface waters.

5. Conclusions

This study documents major changes in abundance and composition of calcareous nannofossil assemblages across the J–K boundary transition. Nannoliths such as Nannoconus spp., Conusphaera spp. and Polycostella spp. show the most marked fluctuations in abundance. The appearance and increase in abundance of these taxa was probably caused by drier atmospheric conditions from the middle Tithonian onwards that led to the decrease in continental weathering and runoff and diminished the nutrient fluxes from the continents, lowering the fertility of surface waters. High abundances of presumably warm water and oligotrophic taxa such as Nannoconus spp. and Conusphaera spp. correlate with low δ18O and δ13C values suggesting fairly similar ecological affinities. The shift in abundance between Conusphaera spp. and Nannoconus spp. might have been triggered by a competition to occupy the same niche. The minor cooling at the middle Tithonian/late Tithonian

![Fig. 5. Temporal distribution of Nannoconus, Conusphaera (1.21 my), and Polycostella (0.42 my) acme peaks (abundances >20% of the total nannofloral assemblage). Timescale after Hardenbol et al. [1].](image)

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boundary associated with a conspicuous increase in abundances of *Polycostella* spp. recorded in cores 95R and 96R could have been the cause that led to the demise of the “Conusphaera world” and the onset of the “Nannoconus world”. The increase in abundance of robust nannoliths such as *Conusphaera* spp., *Polycostella* spp. and *Nannoconus* spp. corresponds to higher CaCO$_3$ contents. The evolution of these robust taxa had a major effect on the burial and cycling of carbonate in the oceans.

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