

# The fossil record of coastal coccolithophores

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Manuscript received 30th June, 2016; revised manuscript accepted 16th February, 2019

**Abstract** Modern coastal environments support low-diversity communities of eurytopic coccolithophore species, but also non-oceanic coastal taxa, which are often small and weakly calcified. Our understanding of palaeocoastal coccolithophores is limited by the infrequent study of shallow-water sediments, first, because they provide only stratigraphically incomplete records, and second, because they typically contain poorly-preserved fossils, sometimes reworked fossils, or none at all. The geological past, however, was characterised by higher sea-levels than present, and so sediments from vast, non-analogue epicontinental seaways form the basis for a significant proportion of Mesozoic and Paleogene coccolithophore studies. These reveal clear distinctions between neritic and oceanic coccolithophorid assemblages, which is particularly evident in the distribution of large and highly distinctive braarudosphaerids and nannoconids, but also non-coccolith fossils, such as *Lithostromation*, calcareous dinoflagellates (calcispheres) and ascidian spicules. Like modern coastal coccolithophorid assemblages, the ancient examples tend to be dominated by opportunistic or stenotypic species – the watznauerids in the Mesozoic and noelaerhabdids in the Cenozoic. Despite the relatively poor record of fossil coastal taxa, it has become apparent that they played a disproportionately significant role in the evolutionary history of the group, with several extant species among the handful that survived the Cretaceous–Paleogene mass extinction event forming the basis for recolonisation and diversification in the oceanic realm.

**Keywords** Coastal, neritic, coccolithophores, calcareous nannofossils

## 1. Introduction

Extant coccolithophores are widespread in all marine photic-zone environments, with biogeographic variability controlled principally by the temperature and nutrient characteristics of water-masses and oceanographic features such as divergence, upwelling, ocean gyres and seasonal mixing. Modern coastal and estuarine environments usually support lower-diversity communities, comprising eurytopic species (e.g. *Emiliania* and *Gephyrocapsa*), but also non-oceanic, neritic or coastal taxa, with many of the latter group being small and weakly calcified, and therefore with little or no fossil record – for example, *Hymenomonas* and *Pleurochrysis* (Konno & Jordan, 2006). Our understanding of palaeocoastal and nearshore coccolithophores is limited by the lack of studies on these environments, first, because they provide incomplete stratigraphic records, and second, because coarser-grained, shallow-water sediments typically contain poorly-preserved fossils, sometimes reworked fossils, or none at all.

The poor preservation or absence of fossils is often the result of high porosity, which facilitates dissolution. Despite the lack of study of coastal palaeoenvironments, much of the geological past was characterised by higher sea-levels than present, and so sediments deposited in vast, non-analogue epicontinental shelf seas form the basis of a significant proportion of studies of Mesozoic and, to a lesser extent, Paleocene and Eocene coccolithophores.

The clear distinction between neritic (i.e. shelf, including coastal habitats) and oceanic coccolithophorid assemblages was recognised early on in Mesozoic and Paleogene studies, particularly because of the strongly neritic affinities of the large and highly distinctive braarudosphaerids and, additionally, in the Cretaceous, the nannoconids (Bybell & Gartner, 1972; Thierstein, 1976; Roth & Krumbach, 1986; Applegate et al., 1989). Here, we review the fossil record of coastal coccolithophores, including observations on neritic vs oceanic distributions that are relatively well established for most geological time intervals.

## 2. Neritic and coastal fossil coccolithophores

Until the advent of ocean drilling, through the Deep Sea Drilling Project and subsequent Ocean Drilling Program, fossil coccolithophore study was focused predominantly on shelf sediments, ranging from the inner to outer shelf and water-depths of several metres to around 1500m. The switch in emphasis to open-ocean deep-sea sediments was accompanied by the recognition of clear differences between the two oceanographic settings, most obviously apparent in the distribution of large and distinctive shelf nannoplankton, such as *Micrantholithus*, *Braarudosphaera* and *Nannoconus*, which appear to represent primary, biogeographic features (e.g. Bybell & Gartner, 1972; Thierstein, 1976; Roth & Bowdler, 1981; Plate 1). Other

coccolithophore taxa have also been identified as having predominantly shelf distributions, most obviously holococcoliths and Paleogene rhabdoliths (*Blackites*; Perch-Nielsen, 1985; Plate 1), but in these cases, the records are strongly affected by the taphonomic differences between shelf and oceanic environments and their sediments, as both these groups have low preservation potentials (Roth & Thierstein, 1972; Roth & Berger, 1975; Bown et al., 2008). This taphonomic bias operates because, in older, deeply-buried sediments, it is the clay-rich hemipelagic sediments of shelf environments that provide more favourable preservation scenarios, with higher diversities and greater numbers of small and fragile taxa (especially holococcoliths) being conserved (Bown et al., 2008). In deep-sea oozes, but also shallow-water carbonates, the destructive effects of carbonate diagenesis are pervasive, and these tend to destroy small and fragile coccoliths, while causing overgrowth on larger liths. This effect increases with burial depth, and therefore sediment age. In addition, as depositional settings approach the calcite compensation depth and beyond, the destructive effects of dissolution also come into effect.

The most obvious difference between neritic and oceanic assemblages is shown by braarudosphaerids in the Lower Cretaceous (Berriasian–Aptian – *Micrantholithus*) and Paleogene (Paleocene–Eocene – *Braarudosphaera*, *Micrantholithus* and *Pemma*), where these taxa can be dominant assemblage components. In addition, in Lower Cretaceous sediments, the braarudosphaerids are often accompanied by abundant nannoconids, especially in the mid to low latitudes. The distribution of other important groups has also been linked to neritic environments; for example, holococcoliths (Mesozoic to Cenozoic) and, in the Paleogene, *Blackites*, *Helicosphaera*, *Pontosphaera* and *Scyphosphaera* (e.g. Perch-Nielsen, 1985), but in all of these cases, the influence of preservation is probably the predominant factor (e.g. Bown, 2005a; Bown et al., 2008). By contrast, the occurrence of exclusively oceanic taxa is not particularly evident from the fossil record.

The explicit study of ancient nearshore and coastal settings is uncommon because coccolithophores are often absent or poorly preserved in the coarser-grained silty and sandy sediments or lithified carbonates that typify such environments. When nearshore or lagoonal sediments do contain nannofossils, they tend to be represented by low-diversity assemblages, dominated by taxa that are

considered to be eurytopic or opportunistic – namely, the Watznaueriaceae (e.g. *Watznaueria*) in the Mesozoic (e.g. Keupp, 1977; Tribovillard et al., 1992) and the Noelaerhabdaceae (e.g. *Reticulofenestra*) in the Cenozoic (Bukry, 1974; Wade & Bown, 2006). In many cases, these taxa also tend to be the most robust and most likely to survive unfavourable taphonomic processes.

### 3. The neritic distribution of *Nannoconus* and braarudosphaerids

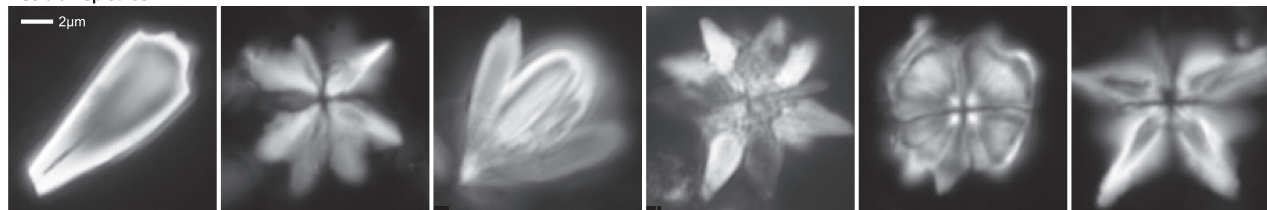
*Nannoconus* is a nannolith genus that appeared in the Late Jurassic (Tithonian, ~148Ma) and was a significant component of Tethyan Early Cretaceous assemblages, until a numerical decline in the Late Barremian–Early Aptian (Erba, 1994). They are especially abundant in the marginal basins of the western Tethys, proto-Atlantic and Caribbean, where they can be rock forming (Thierstein, 1976; Mutterlose, 1989, 1992; Street & Bown, 2000). By contrast, they are much less common in oceanic sediments, and are virtually absent from the Pacific and Indian Oceans, which represented around 80% of the Cretaceous marine ecosystem (Bown, 2005b). They are more frequently found in Atlantic Ocean sites, but this ocean was a narrow basin at the time, and sediment transport from surrounding shelves was common, with nannoconids (and braarudosphaerids) being associated with shelf-sourced turbidites (Applegate et al., 1989). Sporadic occurrences in the Pacific Ocean are also associated with transported material, sourced from shallow-water platforms and guyots (Thierstein, 1976; Bown, 2005b).

This distinct distribution pattern has led to a wide range of explanations concerning nannoconid biology and palaeoecology, with a focus on the link with low-latitude (tropical), sediment-starved epicontinental basins and the close association with braarudosphaerids (Roth & Krumbach, 1986; Mutterlose, 1989; Street & Bown, 2000; Bown, 2005b). Busson & Noël (1991) suggested that nannoconids may have been meroplanktonic (i.e. having a benthic life-cycle stage) and excluded from deep and anoxic marine environments by water-depth constraints on cyst viability. They further suggested that they might be dinoflagellates. There is little doubt that the palaeoecology of nannoconids was in some way related to water-depth and, to some extent, latitude (they are most common in the subtropics and tropics, 30°N–30°S), and their distribution may have been limited by large ocean basins, such

## Plate 1

### Selected examples of coastal and neritic nannoplankton from the fossil record

#### Ascidian spicules



ascidian spicule U. Pal., Tanz.

ascidian U. Eo., Aust.

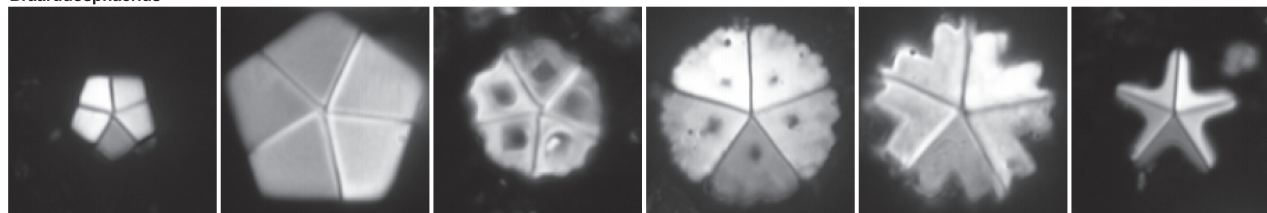
ascidian spicule L. Eo., Tanz.

ascidian spicule Oligo., Tanz.

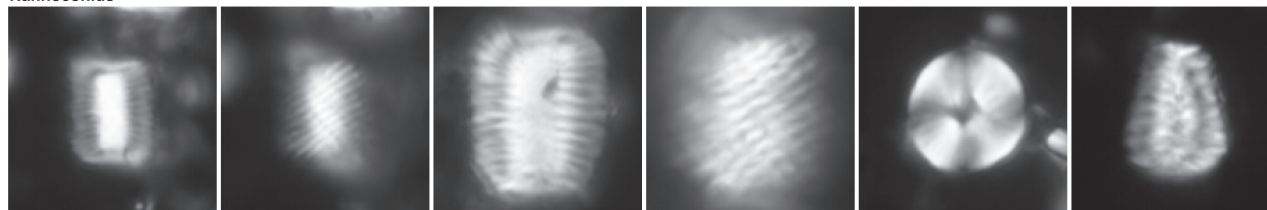
ascidian U. Eo., Aust.

ascidian U. Eo., Aust.

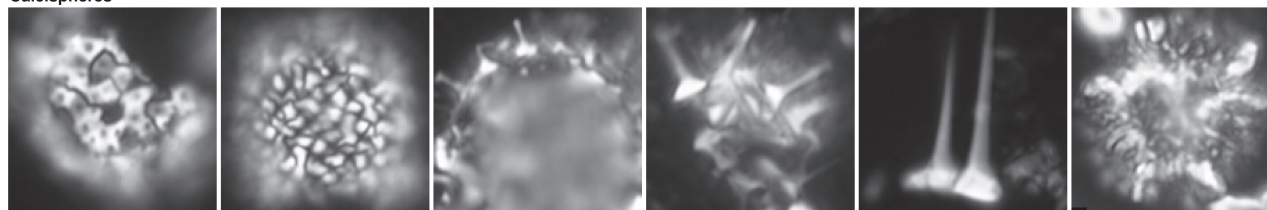
#### Braarudosphaerids

*Braarudo. bigelowii* U. Pal., Tanz.*Braarudo. perampla* U. Eo., Aust.*Pemma basquensis* U. Eo., Aust.*Pemma basquensis* M. Eo., Tanz.*Micranth. crenulatus* M. Eo., Tanz.*Micranth. astrum* Oligo., Aust.

#### Nannoconids

*Nannoconus truttii* Alb., ODP 1052, Atl. Oc.*Nannoconus truttii* Alb., ODP 1052, Atl. Oc.*Nanno. truttii* Alb., ODP 1052*Nann. steinmannii* Berr., Pacific

#### Calcispheres

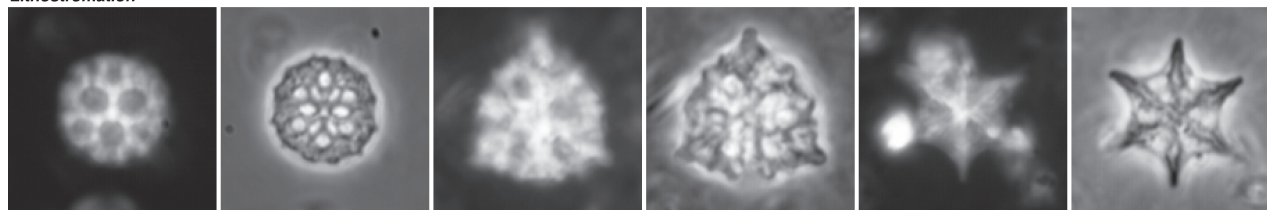
*Thoracosph. heimii* L. Eo., Tanz.

calcisphere U. Pal., Tanz.

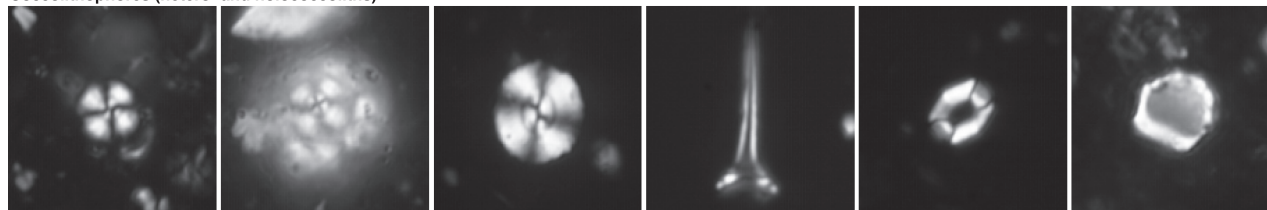
*Scrippsiella* ODP1052-41-2*Scrippsiella* fragment U. Eo., Tanz.*Scrippsiella* fragment U. Eo., Aust.

calcisphere M. Eo., Tanz.

#### Lithostromation

*Lithostromation operosum* U. Eo., Aust.*Lithostromation perdurum* U. Eo., Gulf Coast, USA*Lithostromation stellaris* U. Eo., Gulf Coast, USA

#### Coccolithophores (hetero- and holococcoliths)

*Cyclagelo. margerelii* Oxf., UK*Cyclagelo. margerelii* Oxf., UK*Watznaueria barnesiae* Oxf., UK*Bl. cf. Bl. spinosus* U. Eo., Aust.*Lanternithus minutus* Oligo., Aust.*Dakylethra unitatis* M. Eo., Tanz.

**Abbreviations:** L. – lower, M. – middle, U. – upper, Oxf. – Oxfordian (U. Jurassic), Berr. – Berriasian (L. Cretaceous), Alb. – Albian (L. Cretaceous), Pal. – Paleocene, Eo. – Eocene, Oligo. – Oligocene, Atl. Oc. – Atlantic Ocean, Aust. – Australia, Tanz. – Tanzania

as the eastern Tethys, Indian and Pacific. Extra-Tethyan nannoconid occurrences most likely occurred along shallow-water migration routes via epicontinental basins or via island-hopping, with nannoconids living above and around certain Pacific atolls and guyots (Bown, 2005b). It is interesting to note that modern coastal species, such as *Crucioplacolithus neohelis* and *Braarudosphaera bigelowii*, also have global distributions, and so this coastal ecology is not a barrier to widespread dispersal (Fresnel, 1986; Takano et al., 2006; Hagino et al., 2015).

The distribution of nannoconids is closely associated with that of braarudosphaerids in the Early Cretaceous, which suggests a shared ecological strategy and, alongside morphological and evolutionary considerations, may be evidence for a phylogenetic link between the two groups (Lees & Bown, 2016). Despite the braarudosphaerids being an extant group, their ecology remains something of a puzzle, but information gained from living braarudosphaerids may well also be directly applicable to the extinct nannoconids.

Extant *Braarudosphaera* has a modern distribution that is unusual for coccolithophores, being limited to neritic or coastal environments. It has been especially studied in the seas around Japan, where it is restricted to water-depths of <70m and, in places, is found very close to shore (Tanaka, 1991; Hagino et al., 2013, 2015). Hagino et al. (2013) showed that *Braarudosphaera*-bearing cells are part of a life-cycle that includes an organic-scale-bearing phase, formerly known as *Chrysochromulina parkeae*, which may be lightly calcified (Saez et al., 2004). The *Braarudosphaera* phase is only represented in the water-column for very short periods of time (several weeks) during the year (Hagino et al., 2015). Some *Chrysochromulina*, and many other non-coccolithophorid prymnesiophytes, are coastal haptophytes with benthic resting stages. Such a life-cycle suggests that the distribution of *Braarudosphaera* is probably constrained by the shallow-water requirements in one stage of its life-cycle. *Nannoconus* may well have had a similar constraint, as originally suggested by Busson & Noël (1991).

#### 4. Lagoonal nannofossils

The best examples of ancient nearshore nannofossils come from lagoonal sediments, predominantly of Jurassic age. These include the well known Solnhofen Lithographic Limestone (also famous for the iconic bird-like dinosaur

fossil *Archaeopteryx*), which was deposited in a shallow, lagoonal environment with marine influence (e.g. ammonites and radiolarians are also present). The nannofossil assemblages are of low diversity and dominated by watznaueriaceans, particularly *Watznaueria* and *Cyclagelosphaera* (e.g. Keupp, 1977; Plate 1). *Watznaueria* is a ubiquitous Mesozoic coccolithophore with eurytopic and opportunistic ecology (Lees et al., 2006). *Cyclagelosphaera* appears to have been more specifically adapted to shelf environments, and may have become more restricted in its distribution through time, being rarely observed in the open ocean after the mid Cretaceous. The abundance of *Cyclagelosphaera* in ancient coastal sediments is intriguing, given this taxon has recently been rediscovered as a 'living fossil' (*Tergestiella adriatica*) in the nearshore waters of Japan, usually alongside *Braarudosphaera* (Hagino et al., 2015). There are other claims of relatively widespread Mesozoic lagoonal nannofossils, but the images of these 'diagenetically-altered coccoliths', interpreted as being relict tube cycles, are questionable (Busson et al., 1993). Erba et al. (1995) also suggested that dwarfing of otherwise relatively normal-diversity Cretaceous nannofossils may have been related to the lagoonal setting on a central Pacific guyot.

A number of Neogene examples of shallow-water nannoplankton assemblages also exist, notably in the Paratethys, and in association with the drying of the Mediterranean during the Late Miocene Messinian Event. Sediments both underlying and overlying thick Messinian evaporitic deposits contain assemblages that are low in diversity and dominated by reticulofenestrids (e.g. *Reticulofenestra antarctica*, *R. minuta*), *Umbilicosphaera jafarii*, *Helicosphaera carteri* and *Pontosphaera japonica*, but also, more unusually, with common to dominant sphenoliths (*Sphenolithus abies*; Wade & Bown, 2006; Lozar et al., 2010). These taxa are widely distributed marine species, but evidently were also able to flourish in the pre- and post-Messinian rapidly-fluctuating environments, which included eutrophic, hypersaline and brackish conditions that excluded most other open-ocean taxa. This is consistent with our knowledge of modern lagoonal environments, which also feature noelaerhabdaceans (*Emiliania* and *Gephyrocapsa*), *Helicosphaera* and *Umbilicosphaera* (Konno & Jordan, 2006). The Paratethyan basins of modern day Eastern Europe became increasingly isolated from the open ocean through the Miocene, and assemblages in



them are typically of low diversity and may contain abundant braarudosphaerids (e.g. Bartol et al., 2008), and even some distinctive endemic species, such as *Bekelithella echinata* and *Noelaerhabdus bozinovicae* (Young et al., Nannotax3; Galovic & Young, 2012).

## 5. Ascidians and calcareous dinoflagellates

Nannofossil assemblages from shallow-water environments may also include calcareous fossils that originate from other biological groups and, in particular, ascidians and calcareous dinoflagellates can be conspicuous. In general, both groups produce structures that are larger than coccoliths and smaller than foraminifera, so they are often overlooked by micropalaeontologists; however, small representatives or abundant broken fragments of larger specimens can be conspicuous to dominant components in assemblages from shallow to coastal environments (Plate 1; see also Young et al., Nannotax3, [http://www.mikrotax.org/Nannotax3/index.php?dir=non\\_cocco](http://www.mikrotax.org/Nannotax3/index.php?dir=non_cocco)).

Ascidians are a class of extant benthic invertebrates belonging to the Phylum Chordata, and certain taxa, especially the Family Didemnidea (didemnids), produce numerous aragonitic spicules, typically <0.1mm in diameter (Brookfield, 1988; Varol & Houghton, 1996). They mostly live in warm, shallow-water environments, ranging from 0 to 50m deep, especially carbonate-rich environments associated with reefs and carbonate banks. Certain species do live at greater depths, and it is likely that spicules are also transported into deeper-water sediments. The spicules are often fibrous, and form globular, stellate clusters, but also include a wide variety of other forms (Plate 1). They can be common in nannofossil samples – and may dominate smear-slides – especially from tropical, shallow-water environments that lack other nannofossils (Varol, 2006). They are not particularly well documented, but reviews have been provided by Varol & Houghton (1996) and Varol (2006).

Some dinoflagellates form hollow, spherical to oblate calcitic tests. They have a long fossil record, stretching from the Triassic to Recent (Streng et al., 2004; Kohring et al., 2005; Zonneveld et al., 2005). They are relatively widely distributed, but are more abundant in shelf to coastal settings, and may be particularly associated with intervals of environmental perturbation – for example, Cretaceous Oceanic Anoxic Event 2, the Cretaceous–Paleogene

(K–Pg) boundary mass extinction and the Paleocene–Eocene Thermal Maximum (Hildebrand-Habel et al., 1999). Shelf taxa, such as *Scrippsiella*, have tests constructed from relatively large crystal units that are distinctive when disaggregated (Plate 1), and these have, on occasion, been identified as nannofossil species – for example, *Anacanthoica mitra* (Varol, 1989; and see Bown, 2005a, pl. 26; [http://www.mikrotax.org/Nannotax3/index.php?taxon=Scrippsiella&module=non\\_cocco](http://www.mikrotax.org/Nannotax3/index.php?taxon=Scrippsiella&module=non_cocco)).

Lastly, a Cenozoic (Eocene–Pliocene) group of enigmatic, globular and stellate nannofossils, mainly classified in the genus *Lithostromation* (<http://www.mikrotax.org/Nannotax3/index.php?id=820>), is also virtually restricted to nearshore and coastal environments, but they are usually rare (e.g. Perch-Nielsen, 1985; Plate 1).

## 6. The evolutionary significance of coastal and neritic coccolithophores

Although the geological study of coastal coccolithophores has not been widespread or systematic, the evolutionary significance of these taxa is beyond doubt, and especially their role in survivorship and recovery following the K–Pg mass extinction event. Only a handful of nannoplankton species escaped extinction during this event, and several of the most conspicuous survivors, which display striking acmes in the immediate aftermath, are now known to be extant, obligate coastal coccolithophores, namely *B. bigelowii*, *Cyclagelosphaera/Tergestiella reinhardtii* and *C. neohelis* (Bown, 2005c; Hagino et al., 2015). This suggests that the K–Pg extinctions were highly selective, eliminating the diverse oceanic coccolithophores, and that subsequent recolonisation of the oceanic realm occurred from the surviving coastal nannoflora. Survivorship was likely the result of these coastal nannoplankton being necessarily adapted to more variable environmental conditions, and therefore less vulnerable to the environmental shocks (cooling, darkness, thermal shock, acidification) that accompanied the bolide impact at the K–Pg boundary.

As well as their significance during the atypical post-K–Pg mass extinction interval, the geological record of coastal and neritic nannoplankton has revealed a contrast between intervals when they were common and periods when they were rare. Most obviously, the Early Cretaceous and Early Paleogene were intervals of common occurrences, whereas during the Late Cretaceous and Oligocene to Recent they were less common. One possible expla-

nation for this broad-scale trend might be the influence of sea-level, with periods of high sea-levels in the Early Cretaceous and Early Paleogene creating shallow-shelf seaways where taxa with neritic adaptations could flourish (e.g. *Braarudosphaerids*). Even higher sea-levels in the Late Cretaceous appear to have created unusual oceanic-like conditions across the shelf areas, as evidenced by the widespread deposition of shelfal pelagic ooze sediments (chalk), which resulted in lower abundances of neritic taxa. Falling sea-levels following the build-up of Antarctic ice-sheets at the Eocene–Oligocene boundary resulted in less extensive shelf seas and relatively low abundances of distinctly neritic nannoplankton taxa from the Oligocene to Recent.

## 7. Summary

Although the infrequent study of ancient coastal sediments has resulted in little fossil evidence of obligate coastal coccolithophores, what information we *do* have is consistent with modern observations that these environments tend to be dominated by widely distributed opportunistic or stenotypic species – watznauerids in the Mesozoic and noelaerhabdids in the Cenozoic. In one case, *Cyclagelosphaera* (*Tergerstrella*) is demonstrably coastal and neritic in the Mesozoic, and remains similarly adapted in the present day, although it has rarely been identified in the fossil record for much of the post-Paleocene Cenozoic. The extant *Braarudosphaerids* and extinct nannoconids also display long-term coastal–neritic adaptation, and were especially abundant in the Early Cretaceous (both groups) and Eocene (*Braarudosphaerids*). The main controlling factor on the distribution of modern *Braarudosphaera* (and, by association, their extinct ancestors) is still uncertain, but a life-cycle stage requiring shallow water remains a strong possibility. Finally, other calcareous components are also characteristic of shallow-water sediments, and an abundance of ascidian spicules and calcispheres is particularly diagnostic.

## Acknowledgements

Dr Kyoko Hagino-Tomioka and Prof David Watkins are thanked for their reviews.

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