Calcareous nannoplankton evolution and diversity through time

Paul R. BOWN[1], Jackie A. LEES[1] and Jeremy R. YOUNG[2]

[1] Department of Earth Sciences, University College London, Gower Street, London, WC1E 6BT, England. p.bown@ucl.ac.uk, j.lees@ucl.ac.uk

[2] Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, England. j.young@nhm.ac.uk

Summary

Planktic microfossils arguably provide the most complete (stratigraphic and taxonomic) record of biodiversity of any group of organisms. The phytoplankton record is of particular significance as it most likely tracks global changes in the climate-ocean system and, in turn, influenced biodiversity and productivity of higher trophic levels of the biosphere. Coccolithophores and associated calcareous nannoplankton first appear in the fossil record in Upper Triassic sediments (~225 Ma) and, despite significant extinctions at the Triassic/Jurassic boundary, the Mesozoic diversity record is one of relatively uniform increase punctuated by short periods of turnover and decline. Rates of speciation that are significantly above background were restricted to the Late Triassic, Early Jurassic and Tithonian-Berriasian intervals. Enhanced rates of extinction occurred at the Triassic/Jurassic, Jurassic/Cretaceous and Cretaceous/Tertiary boundaries.

There is no clear correlation between coccolithophore diversity and Mesozoic climate, as it is currently understood, but the dominant trajectory of diversity increase suggests long-term stability and widespread oligotrophy in photic zone environments. The Neocomian and Campanian–Early Maastrichtian intervals of diversity increase are clearly associated with increased numbers of endemic taxa at both low and high latitudes. These intervals have been interpreted as periods of cooling or cooler climates, and greater differentiation of the photic zone environment may have led to the biogeographic partitioning. Notably, none of the mid-Cretaceous Oceanic Anoxic Events are associated with above-background evolutionary rates or significant taxonomic loss or innovation.

Cenozoic nannoplankton diversity patterns are markedly more variable than those of the Mesozoic, and rates of speciation, extinction and turnover are consistently higher. There is also good correlation between diversity and climate trends, with higher diversities associated with warm climates. This is best illustrated by

the Paleogene record, where the Cenozoic diversity maximum, at the Paleocene/Eocene boundary, coincided with climates of extreme warmth, and significant diversity decline tracked climate cooling through the Late Eocene and into the Oligocene. This relationship between climate and coccolithophore diversity is contrary to that observed in the Mesozoic, and suggests different controls on evolution during the two eras. The Cretaceous record suggests that cooling within a greenhouse-mode climate system may have stimulated diversification at all viable latitudes via biogeographic partitioning. In contrast, the Cenozoic data indicates that cooling tended to drive diversity decrease. This may be explained by the greater magnitude and longevity of Cenozoic cooling, in an icehouse-mode climate system, which prevented coccolithophore diversification at higher latitudes where, instead, diatoms became established as the dominant group of phytoplankton.

Introduction

Coccolithophores and associated calcareous phytoplankton are the most abundant calcifying organisms inhabiting our planet. Their fossil record is equally impressive, perhaps being the most abundant and stratigraphically complete of any fossil group. As such, they provide a valuable proxy for Mesozoic–Cenozoic phytoplankton health and robust data concerning rates and patterns of evolutionary change. Their present biogeography and diversity is closely correlated with climatic and oceanographic zones, and their fossils provide a record of this relationship through time.

This paper will review our current understanding of calcareous nannoplankton evolution through their 225 million year history (Triassic–present) using stratophenetic phylogenetic models and a new synthesis of diversity data and rates of evolutionary change. We will discuss the adequacy of the nannoplankton fossil record, specifically potential preservational bias introduced by size, delicacy and life-cycle coccolith dimorphism. Finally, we will examine the temporal relationship between evolutionary events and the ocean-climate system and discuss the possible controlling mechanisms on nannoplankton speciation, extinction and diversity.

Methodology

Phylogenetic trees

The phylogenetic trees we present here (Fig. 1), one for coccolithophores and one for nannoliths, are based on large stratigraphic databases which have resulted from the extensive use of nannofossils in academic and industrial biostratigraphic studies over the last 50 years. Taxonomic concepts are based largely on morphological

observations of coccoliths and nannoliths using light and scanning electron microscopy: a recent review of generic and higher taxonomy was presented in Bown and Young (1997) and Young and Bown (1997). Nannofossil biostratigraphy has provided a data-set that is stratigraphically continuous and geographically widespread cross the spectrum of marine environments, thus minimizing well-documented stratigraphic biases, such as preservation and sample failure, and the modified stratigraphic range phenomena that often result from these (range extension, ghost lineages, Lazarus taxa).

Although basic phylogenetic logic has been used to predict relationships of taxa, a formal cladistic analysis of coccolithophore relationships has not been undertaken. This might seem a strange omission, given both that individual coccoliths show great complexity, offering a wide range of potential characters, and that assemblages with exquisite preservation are known from many stratigraphic levels. However, there is a fundamental problem of lack of homology between different groups. This is obviously the case when comparing any nannoliths and coccoliths but also holds between coccolith groups. The V/R model (see Young et al. 1992; Young et al. this volume) provides a basic framework for interpreting homology but also highlights the degree to which different coccolith families have adopted these fundamental building blocks into intrinsically different structures. Furthermore, it is clear that coccolith structure simplification, with concomitant character loss, is a common pattern in coccolithophore evolution. One good example is the evolution of the Noelaerhabdaceae from the Prinsiaceae, which involved reduction of the V-units to vestigial nuclei, and consequent loss of characters associated with the previous, complex V-unit form. Analogously, evolution of the Calcidiscaceae from the Coccolithaceae (which is well supported by both molecular and paleontological data) involved structural simplification, with loss of the complex inner tube-cycles. Since a basic assumption of parsimony analysis is that character loss is unlikely (e.g. Smith 1994), this type of pattern further compromises cladistic analysis of the group.

Essentially, coccolith morphology is too plastic to provide sufficient robust characters for a cladistic analysis of the complete group. This does mean that, whilst we have very high confidence that the conventional families represent phylogenetic units (because the included taxa share morphological characters and/or have continuous stratigraphic ranges with plausible stratophenetic linkages), predictions of relationships between them are tenuous. Molecular genetic data (Saez et al. this volume) have broadly confirmed this pattern: conventional family- and genus-level groupings have been well-supported, but some surprising relationships between them have been revealed.

Diversity

Nannoplankton diversity has been compiled from published stratigraphic data, and notably a number of comprehensive works of synthesis (Aubry 1984, Perch- Nielsen 1985a, b; Aubry 1988, 1989, 1990, 1998, Bown 1998a; Aubry 1999). This

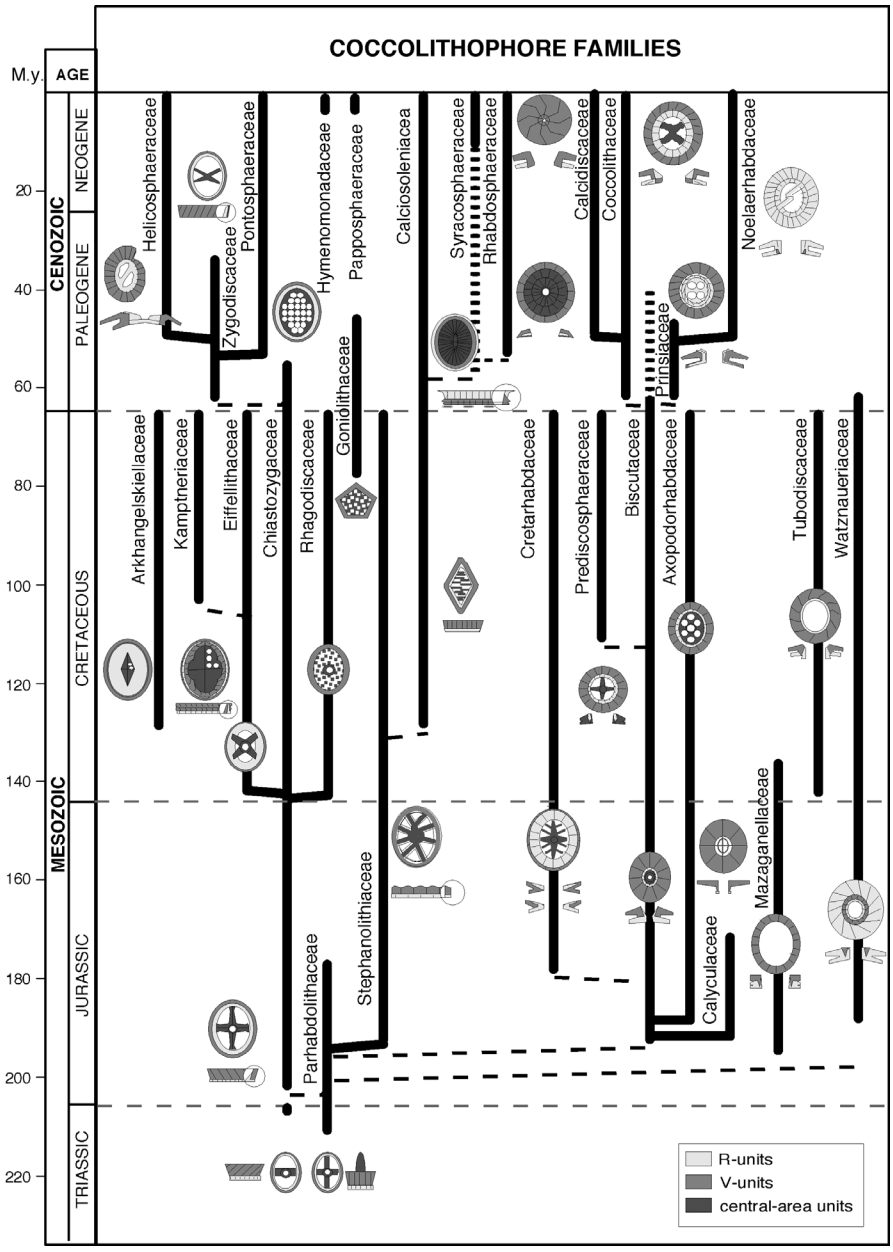
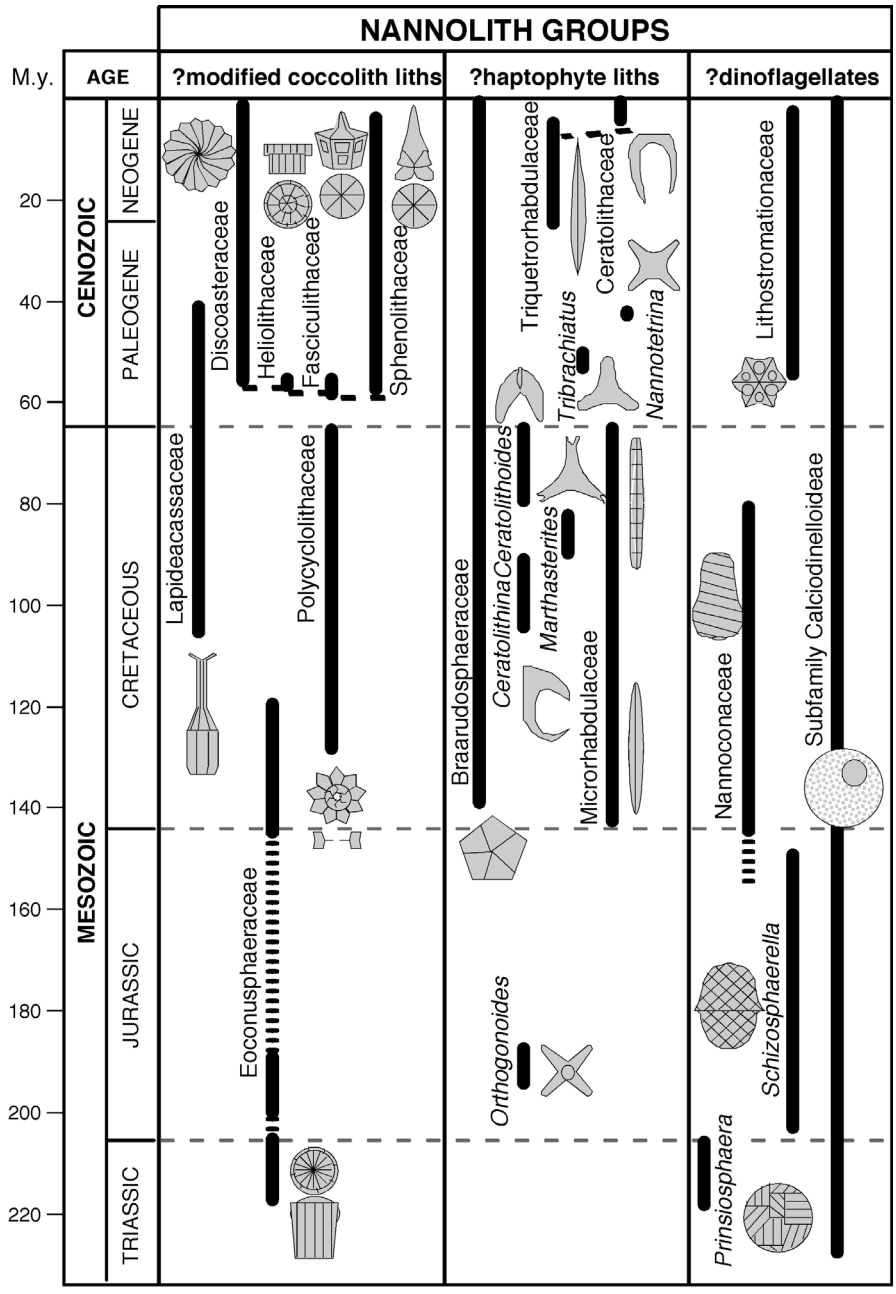


Fig. 1. Coccolithophore and nannolith family-level phylogeny.


NANNOLITH GROUPS
M.y.
AGE
?modified coccolith liths
?haptophyte liths
?dinoflagellates
CENOZOIC
MESOZOIC
NEOGENE
PALEOGENE
CRETACEOUS
JURASSIC
TRIASSIC
20
40
60
80
100
120
140
160
180
200
220
Discoasteraceae
Heliolithaceae
Fasciculithaceae
Sphenolithaceae
Lapideacassaceae
Polycyclolithaceae
Eoconusphaeraceae
Triquetrorhabdulaceae
Ceratolithaceae
Tribrachiatus
Nannotetrina
Braarudosphaeraceae
Ceratolithina Ceratolithoides
Marthasterites
Microrhabdulaceae
Orthogonoides
Lithostromationaceae
Nannoconaceae
Subfamily Calciodinelloideae
Schizosphaerella
Prinsiosphaera

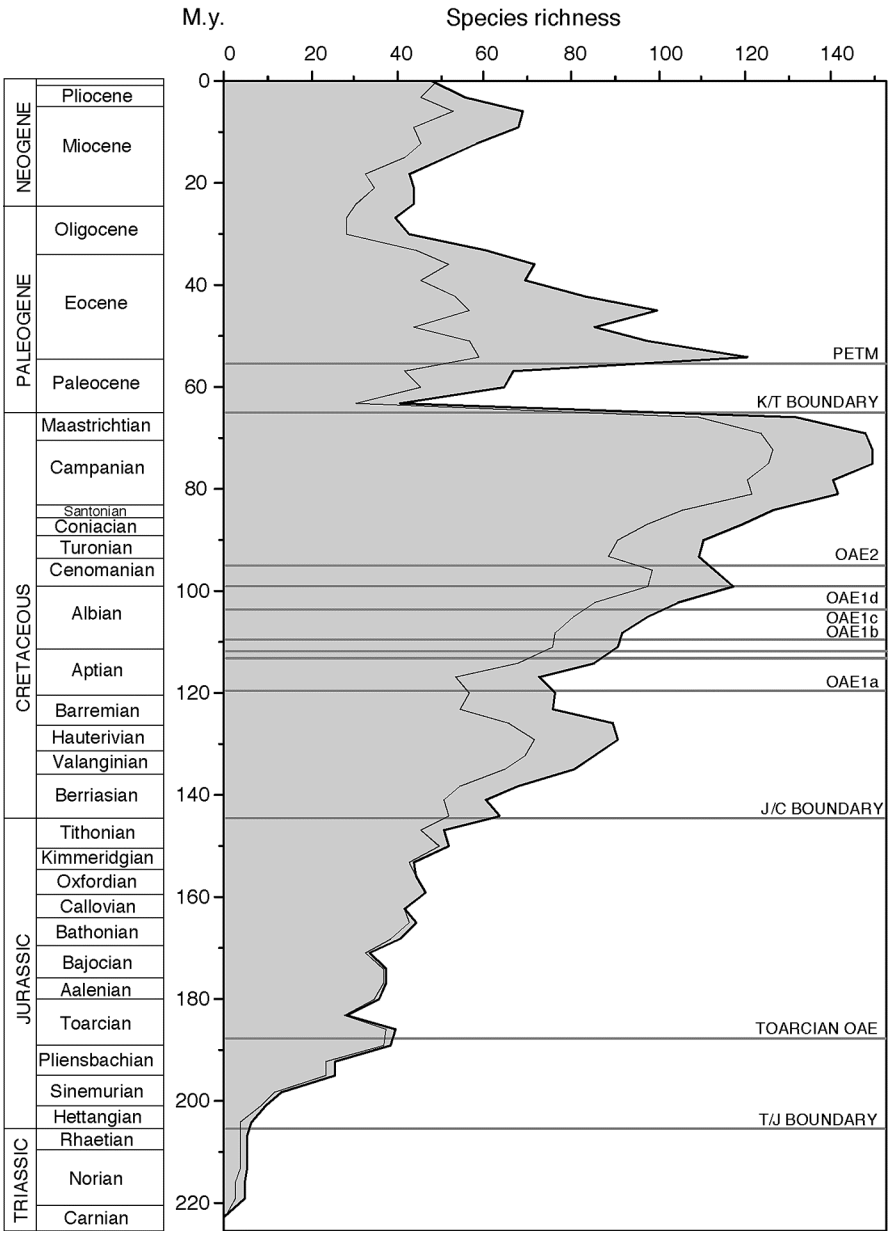


Fig. 2. Coccolithophore (light line) and total nannofossil (dark line) diversity. Data represents species richness for a three million-year interval, plotted at the mid-point. The timescales are from Berggren et al. (1995) and Gradstein et al. (1995). OAE: oceanic anoxic event, PETM: Paleocene/Eocene thermal maximum.

published information has been screened in order to provide a consistent and informed taxonomy, and an attempt was made to reduce monographic and taxonomic-oversplitting effects. Taxa recorded from just one sample have largely been rejected, although this was often restricted to particular families, e.g. Braarudosphaeraceae and Rhabdosphaeraceae. Morphotypes which are thought to represent intraspecific variation, especially within taxa which have living representatives with polymorphic coccospheres, e.g. *Scyphosphaera*, have also been omitted. For

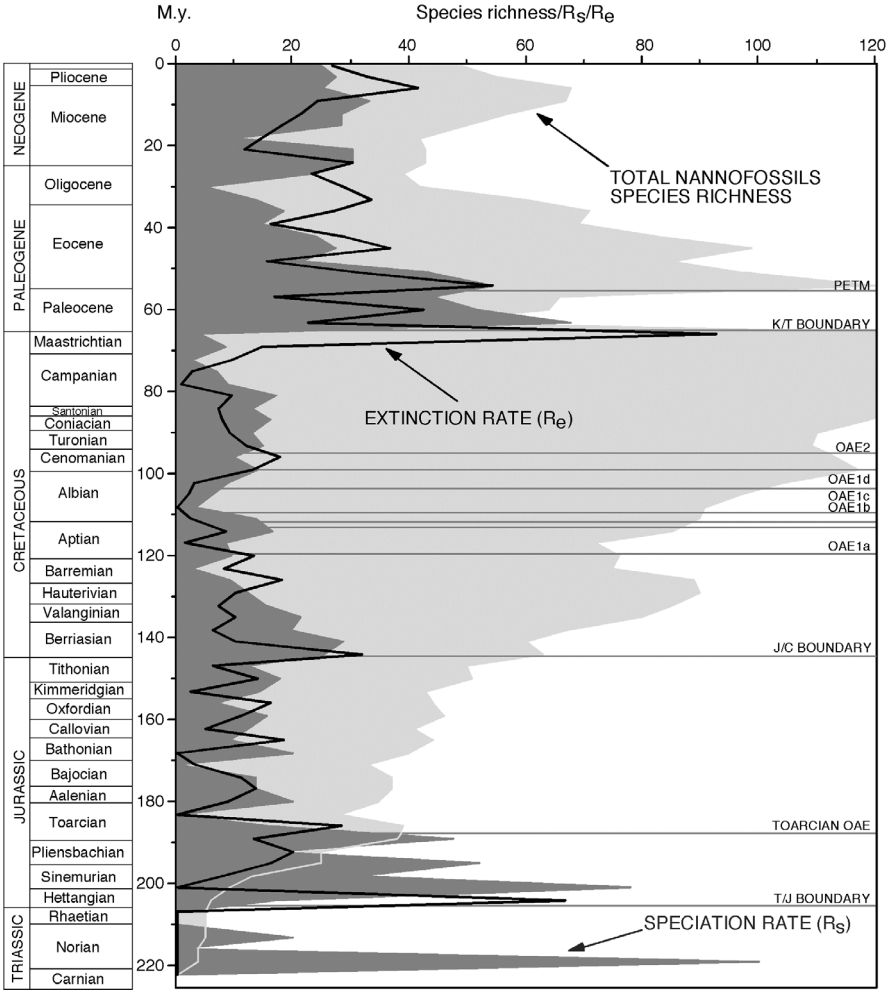


Fig. 3. Nannofossil diversity (pale shading), extinction rate (dark line) and speciation rate (dark shading). R_s/R_e represent % increase/decrease per 3 million year interval. Data plotting, time-scale and abbreviations as in Fig. 2.

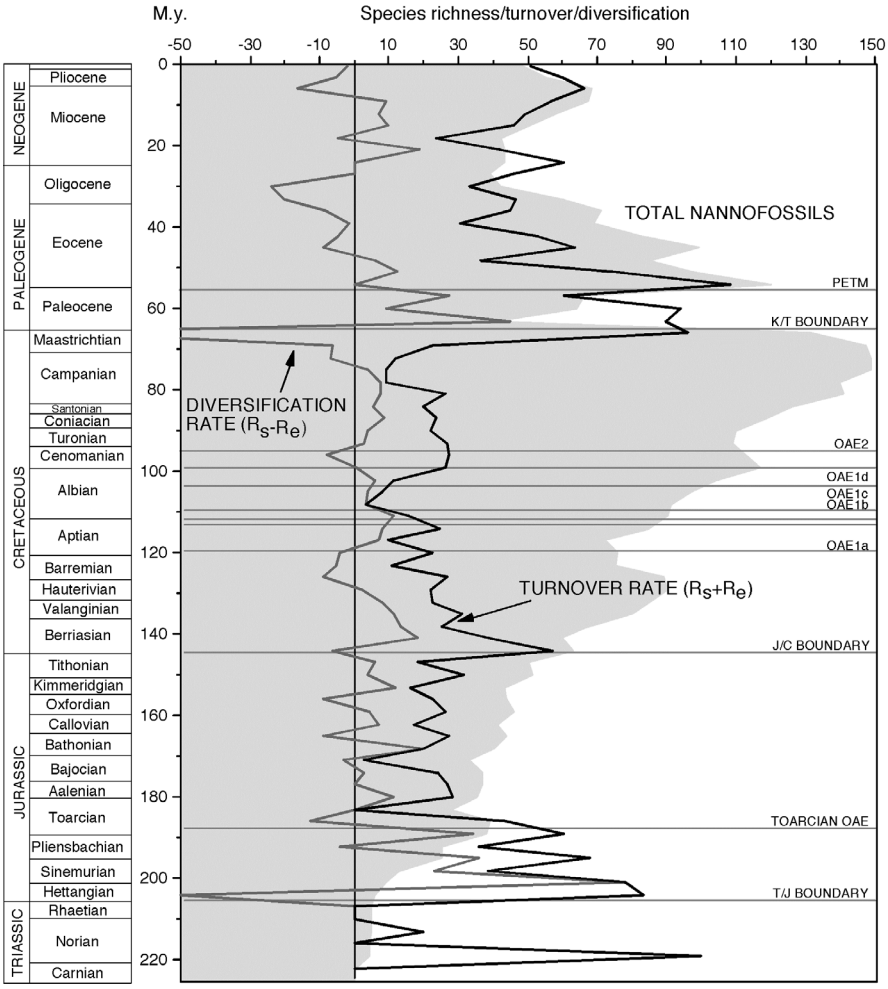


Fig. 4. Nannofossil diversity (pale shading), diversification rate (pale line) and turnover rate dark line). R_d and R_t are measures of % change per 3 million year interval. Data plotting, time-scale and abbreviations as in Fig. 2.

the genus *Scyphosphaera* we have followed the conservative taxonomy of Young (1998) but accept that many more species have been described (around 30 Upper Miocene-Pliocene species, see synthesis of Siesser 1998); however many of these could be considered synonyms, especially when compared to the intraspecific variation displayed on extant coccospheres. Holococcolith taxa are not included, as these have very sporadic fossil records and are likely to represent life-cycle stages which have a corresponding heterococcolith stage (Cros et al. 2000; Billard

and Inouye this volume); their inclusion would thus incorrectly enhance standing diversity.

Diversity is expressed as total species present (species richness) per three million year interval, from 225 million years ago to present day. This interval duration is determined by the stratigraphic resolution at which much of the data was collected but is considered high-resolution enough to reveal real and significant patterns of taxic change (see discussion in Danelian and Johnson 2001). The data were plotted at the mid-point of the time-interval, as estimated from the time-scales of Berggren et al. (1995) and Gradstein et al. (1995) (Fig. 2). We also calculated species richness at Mesozoic substage, and Cenozoic nannofossil biozone, resolution but the trends are nearly identical and they are not included here. Similarly, generic- and family-level diversity trends are closely comparable with those shown by the species data. Both raw counts of numbers of originations and extinctions per stratigraphic interval, and established metrics of evolutionary rates, were calculated. Rates of speciation and extinction were calculated as follows: rate of speciation (R_s) = (1/D)(FO/t)100, rate of extinction (R_e) = (1/D)(LO/t)100, rate of diversification (R_d) = (R_s) – (R_e), and rate of turnover (R_t) = (R_s) + (R_e) (after Roth 1987), where D is total species richness, FO is number of first occurrences, LO is number of last occurrences, and t is the three million-year time-interval.

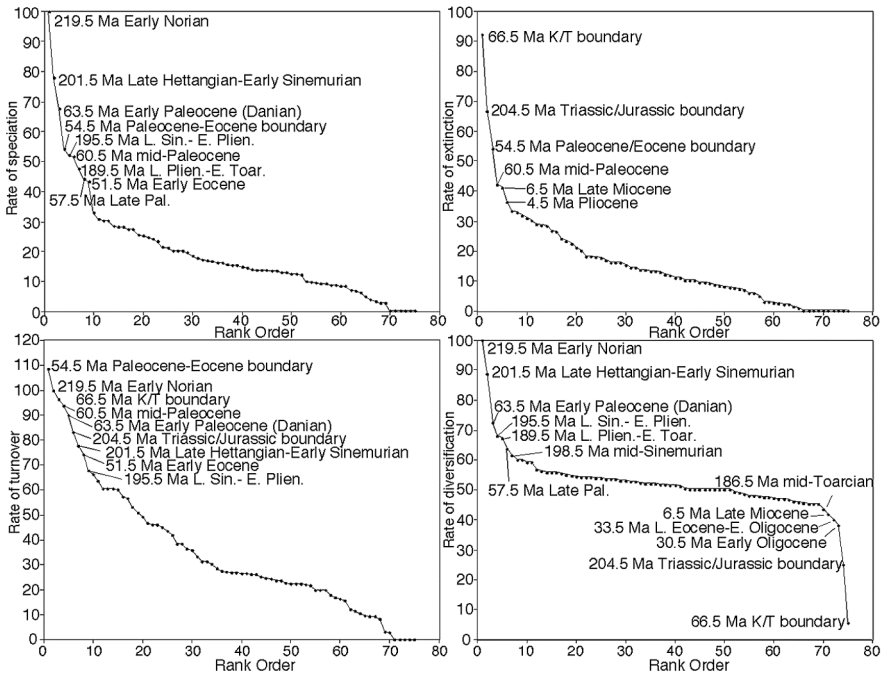


Fig. 5. Nannofossil evolutionary rates: **a.** rate of speciation, **b.** rate of extinction, **c.** rate of turnover, **d.** rate of diversification, ranked by decreasing magnitude. Above-background intervals are identified.

Because the time-interval is constant throughout this data-set the rates have not been divided by three, and R_s and R_e are thus percent increase and decrease (Figs 3 and 4).

The evolutionary rates were plotted as ranked data-sets in order to assess the range of values present and to determine whether there are values which stand out above background (Fig 5).

The diversity data for a number of separate nannoplankton groups have also been plotted. For the Cenozoic, Discoasteraceae, Coccolithales and Isochrysidales (synonym Prinsiales) were chosen in order to represent a range of ecological strategies, from oligotrophic- (Discoasters) to eutrophic-adapted (Isochrysidales) (Aubry 1992; Chepstow-Lusty et al. 1992; Chapman and Chepstow-Lusty 1997) (Fig. 6). In the Mesozoic, where nannoplankton paleoecologies have yet to be clearly identified, diversity was compiled for taxa which show a degree of biogeographical restriction (Fig. 7).

Quality of nannoplankton diversity data

Despite our contention that nannoplankton have a fossil record of outstanding quality, there are a number of provisos which must be considered when using and interpreting diversity data per se, and specific issues relating to nannoplankton data in particular, e.g. selective preservation, polymorphism and cryptic species.

While it may be argued that diversity patterns simply represent stochastic trends in time, with no predominant controlling mechanism, they have nevertheless proven to be extremely useful in identifying periods of significant global change, e.g. many stage boundaries, mass extinction events, etc., and there is strong support for the robustness and biological reality of diversity data at different scales and taxonomic levels (Miller 2000). The significance of the nannoplankton data is supported by the presence of parallel trends in taxonomically disparate protistan plankton groups, such as dinoflagellates and planktic foraminifera (Fig. 8), which, in turn, suggests the possibility of an overarching abiotic control which is responsible for such changes. In addition, the strength of the nannoplankton data is demonstrated by the consistency at which the main trends have been identified by studies spanning three decades, despite great changes in classification concepts and the introduction of significant numbers of new taxa. Time series diversity data for calcareous nannoplankton have previously been presented by Tappan and Loeblich (1973 – low resolution), Lipps (1970 – low resolution), Perch-Nielsen (1986 – Cretaceous and Cenozoic), Roth (1986, 1987, 1989 – Jurassic and Cretaceous), Knoll (1989 – Upper Cretaceous to Oligocene), and Bown et al. (1991, 1992 – Mesozoic to Cenozoic). Most of these studies are relatively low in stratigraphic resolution, using substages or nannofossil biozones as sample intervals.

Other, non-biological explanations for apparent parallel diversity trends have been discussed widely in the literature and include age-related sample availability (see discussion in Miller 2000) and sea-level and environment-related sampling

and preservational biases (e.g. MacLeod et al. 1997; Gale et al. 2000). These arguments do not generally apply to nannoplankton records, as discussed above, as the data is broadly global in distribution, near-continuous stratigraphically, and from across the range of marine environments.

However, there are a number of potential preservational biases which are particularly relevant to nannoplankton, namely those introduced by size and life-cycle coccolith poly- or dimorphism. Only a small proportion of modern nannoplankton are large enough, or robustly calcified enough, to be routinely preserved or observable in the geological record (Young et al. 1994). This results in a significant disparity between Quaternary diversity values (49 species) and diversity estimates for extant taxa (~220 species). A proportion of this disparity is accounted for by holococcolith diversity (~66 morphospecies), almost all of which are less than 3 µm long and none of which have a consistent fossil record, both because of their small size and delicacy. Holococcoliths do become consistent components of nannofossil assemblages in the Upper Cretaceous and, to a lesser extent, in the

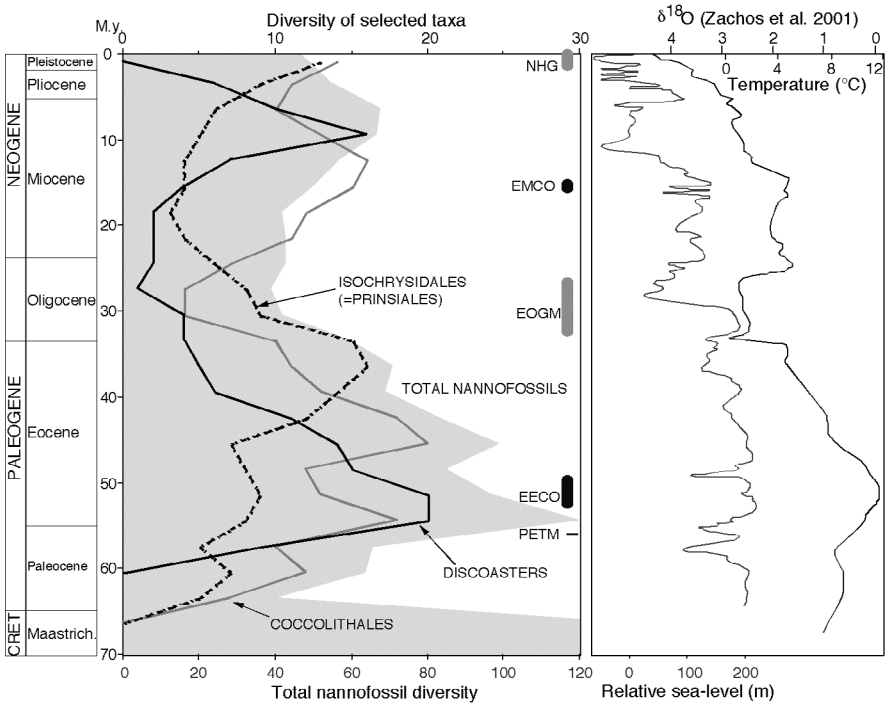


Fig. 6. Cenozoic nannofossil diversity (pale shading) with diversity for the Discoasteraceae (dark line), Isochrysidales (dashed line) and Coccolithales (pale line). Deep-sea oxygen isotope record (dark line) after Zachos et al. (2001). Relative sea-level curve (pale line) after Haq et al. (1987). PETM: Paleocene/Eocene thermal maximum, EECO: Early Eocene climatic optimum, EOGM: Early Oligocene glacial maximum, EMCO: Early Miocene climatic optimum, NHG: Northern Hemisphere glaciation.

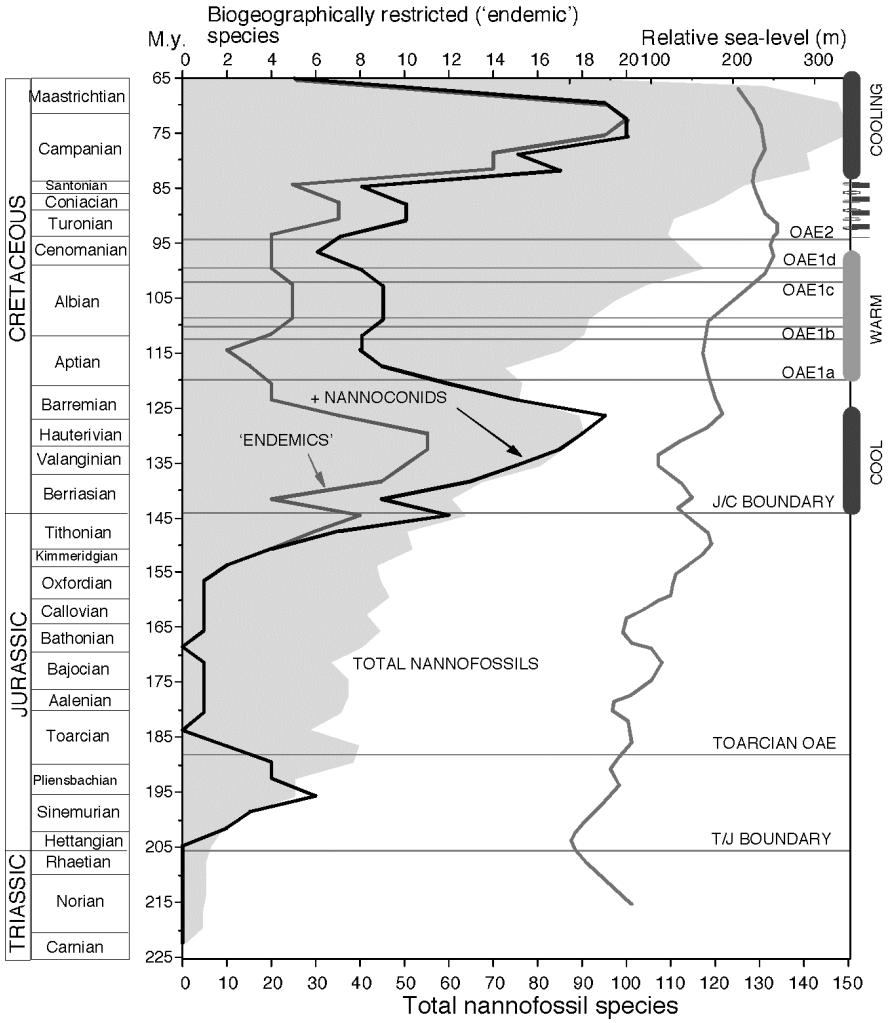


Fig. 7. Mesozoic nannofossil diversity (pale shading) with diversity for biogeographically-restricted species (pale line) and for biogeographically-restricted species plus nannoconids (dark line). Relative sea-level curve after Haq et al. (1987).

Paleogene, but these are generally larger forms. We suspect that holococcoliths have been abundant throughout the history of coccolithophores but are rarely preserved, and have avoided the potential problem by excluding them from our data, and assume that they, in any case, contribute to the diversity data via their heterococcolith counterparts.

There are also a number of living families which contribute significantly to global diversity but are only sporadically found as fossils, again due to size and

delicacy, most notably the Syracosphaeraceae (~51 extant species). However, most of the living clades have good fossilization potential, and comparison of Quaternary and extant diversities within these groups shows perfect representation. We therefore concede that not all clades may have been represented well in the fossil record, however those that are present are likely to have left a meaningful record of their evolution and diversity through time.

A qualitative survey of size distribution through time suggests at least one of the high-diversity nannoplankton episodes, in the Campanian (Upper Cretaceous), broadly coincides with increases in general coccolith size, however this relationship is not obvious elsewhere on the diversity curve.

Finally, the rapid progress in genetic characterization of extant plankton taxa has revealed the existence of cryptic species in both coccolithophore and planktic foraminifera, and this phenomenon has clear implications for diversity records. The coccolithophore 'species' *Emiliania huxleyi*, *Calcidiscus leptoporus* and *Coccolithus pelagicus* are currently the best understood in terms of genetics, coccolith biometrics and life-cycle, and may include four, three and two cryptic species, respectively (de Vargas et al. this volume; Geisen et al. this volume; Quinn et al. this volume). However, these species have been classified relatively conservatively by algologists and this inclination has been followed by those dealing with their fossil counterparts. In contrast, much paleontological nanno

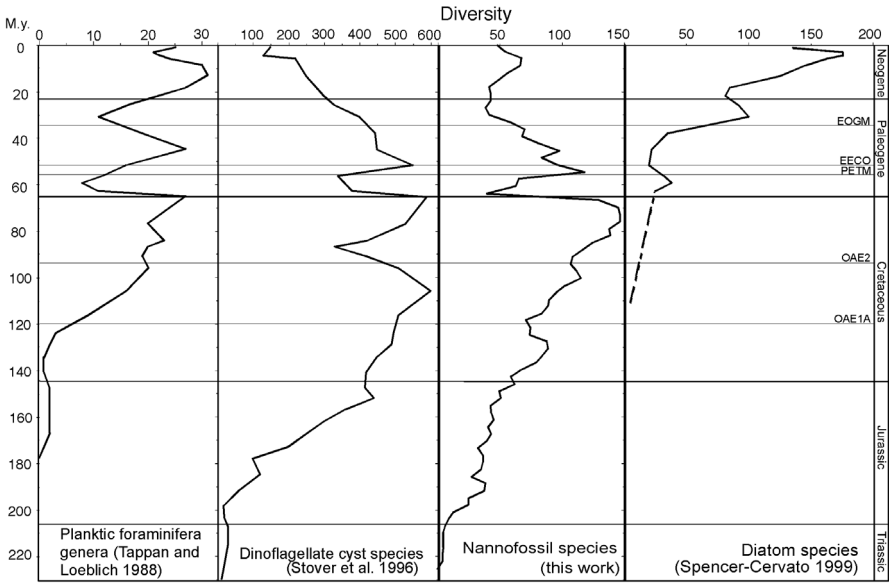


Fig. 8. Diversity of planktic foraminifera genera (after Tappan and Loeblich 1988), dinoflagellate cyst species (after Stover et al. 1996), nannofossil species (this work) and marine diatom species (Spencer-Cervato 1999). The data are collected at different stratigraphic resolutions but nevertheless provide some indication of trends in diversity between the different plankton groups. Abbreviations as in Figs 2 and 6.

plankton taxonomy has erred on the side of 'oversplitting', often subdividing similar nannofossils based on fine-scale morphological differences, in many cases driven by the desire to enhance biostratigraphic resolution. The finely-divided paleontological taxonomy is thus supported by observations of extant cryptic species and may not be greatly underestimating diversity in the fossil record, and while absolute numbers may be affected, the trends may well be the same.

Major events in nannoplankton evolution

By means of introduction to the evolution of nannoplankton, we present a brief review of the major events in their history.

225 Ma First appearance

Calcareous nannofossils first occur in the fossil record in Carnian sediments from the Southern Alps, Italy (Janofske 1992; Bown 1998b). These earliest forms are nannoliths and calcareous dinoflagellates. Coccoliths and non-dinoflagellate nannoliths are present from the Norian, but Triassic assemblages, while reasonably abundant, are of low diversity (maximum five species) and were possibly restricted to low latitudes (Bown 1998b). Triassic coccoliths are simple murolith morphologies (i.e. having narrow, wall-like rims) of very small size (2–3 μm) and show clear V/R-mode biomineralisation style.

Claims for pre-Triassic calcareous nannofossils are unsubstantiated and usually based on misidentification of inorganic calcareous objects or clear cases of contamination (reviewed in Bown 1987).

205.7 Ma Triassic/Jurassic boundary extinctions

Continuous, nannofossil-bearing boundary sections have not yet been documented, but there is strong evidence that four of the five Late Triassic nannofossil species became extinct at, or close to, the boundary (Bown 1998b). This coincides with a mass extinction event documented in invertebrate and vertebrate faunas (Hallam and Wignall 1997). One coccolith species, *Crucirhabdus primulus*, survived. Recovery following the extinctions appears to have been rather slow, although this may also reflect the paucity of productive Early Hettangian sections.

205–188 Ma Early Jurassic evolutionary radiation

The radiation of coccolithophores following the Triassic/Jurassic extinctions is one of the most important diversification events in the group's history. In just over 10 million years, nine out of a total of 16 Mesozoic families originated, repre-

senting a significant proportion of the Mesozoic and Cenozoic taxic and morphologic diversity. Coccoliths became the dominant nannofossil group, and coccolith size increased significantly. The radiation can be viewed as two separate episodes: the first saw re-establishment and radiation of the surviving Triassic coccolith group (muroliths) during the Late Hettangian–Sinemurian; the second, the appearance and radiation of new and innovative coccolith morphologies (notably placoliths) in the Pliensbachian–Early Toarcian. Holococcoliths are also first recorded at this time, but may be missing from earlier records due to preservation bias (Bown 1993).

146–140 Ma Jurassic/Cretaceous boundary turnover

The Tithonian–Berriasian saw a turnover of coccoliths at species level (17 extinctions, 15 originations) and the appearance of three important nannolith families: the Nannoconaceae, Braarudosphaeraceae and Microrhabdulaceae (see Fig. 1). It is also an interval often cited as recording the first occurrence of nannofossil-generated pelagic carbonates, an observation based on the switch from radiolaria-dominated siliceous sediments to nannofossil-dominated carbonates (Maiolica Formation) in western Tethys (Baumgartner 1987). However, earlier nannofossil-carbonates are not uncommon, e.g. the stone bands of the Kimmeridge Clay Formation, UK (Gallois 1976; Gallois and Medd 1979), and the earliest oceanic sediments, of Bathonian–Callovian age, are rather rich in calcareous nannofossils, described as marly limestones and claystones with up to 75% nannofossils (Sheridan et al. 1983). The significance of this interval in terms of nannofossil-carbonate sedimentation is, therefore, yet to be rigorously analyzed, as is the hypothesis that nannoplankton originated in shelf environments and only later migrated into oceanic habitats (e.g. Roth 1986).

80–68 Ma mid-Campanian–mid-Maastrichtian diversity maximum

The Campanian supported the highest global diversity (149 species) of fossilized nannoplankton in the evolutionary history of the group. This maximum coincided with large coccolith size and widespread distribution of nannofossil chalks.

65 Ma Cretaceous/Tertiary extinction event

The catastrophic, instantaneous and synchronous extinction of nannoplankton at the K/T boundary was a unique event in the group's evolutionary history. Of 131 Late Maastrichtian species, only nine survived: a species extinction rate of 93%, a generic extinction rate of 85%. Moreover, none of the nine survivors were common members of Late Cretaceous assemblages.

65–53 Ma Paleocene recovery and radiation

Post-K/T-extinction nannoplankton assemblages are characterized by high dominance of species which are traditionally thought of as survivor-opportunists. Interestingly, in a re-run of the Late Triassic nannofloras, small calcispheres dominated alongside the survivor coccoliths and nannoliths, and incoming Cenozoic coccoliths were initially diminutive (~2 µm). New Cenozoic taxa appeared rapidly and were dominant in some areas within 50 kyr (Pospischal 1996). The evolutionary radiation that followed was both rapid and morphologically diverse. The new coccolith morphologies differed significantly from the Mesozoic architectures, and the later Paleocene was also characterized by nannolith groups (*Sphenolithus*, *Fasciculithus*, *Heliolithus*, *Discoaster*) whose radial structure almost certainly arose from coccolithophore ancestors. Evolutionary relationships between survivor lineages and new Cenozoic taxa have been conceived, but are somewhat inconclusive, largely because of problems associated with the observation of small coccoliths (Romein 1979; Perch-Nielsen 1985b; MacLeod et al. 1997).

The Paleocene radiation saw 62 species added in 10 my, compared with 32 species added in 13 my during the initial Early Jurassic radiation.

29–26 Ma Oligocene diversity minimum

Following a diversity maximum of 120 species in the Late Paleocene–Early Eocene, diversity declined rapidly through the Middle to Late Eocene, to a minimum of 39 species (10 species at nannofossil zone level) in the Oligocene. Extinctions occurred throughout the familial diversity of the group but were near-terminal in the Coccolithaceae (two species) and Discoasteraceae (two species).

11–0 Ma Miocene recovery and late Neogene decline

Nannoplankton diversity rallied in the Late Miocene (11–5 Ma), with diversification particularly in the Discoasteraceae and Ceratolithaceae. However, the trend through the Pliocene and Quaternary has been one of diversity loss.

Nannoplankton diversity patterns

The diversity plot in Fig. 2 shows data for both coccoliths and total nannofossils, and the two records show closely parallel trends. These data support the assertion that most nannolith taxa are either non-coccolith morphologies produced by haptophytes, as seen in the extant genus *Ceratolithus* (Sprengel and Young 2000), or objects produced by biologically distinct, but ecologically similar phytoplankton groups. The larger discrepancy between coccoliths and nannofossils in the Eocene

is due to high diversities in the Discoasteraceae and Braarudosphaeraceae, and both may be coccolithophores.

Rates of speciation, extinction, diversification and turnover were plotted as ranked data-sets in order to assess the range of values present and, particularly, to determine whether there are values which stand out above background (Fig. 5). For all four metrics there is a discontinuous distribution, and a clear distinction can be made between the majority of values, which broadly fall on line and represent background rates, and more extreme values, which represent above-background events.

The Mesozoic diversity record is characterized by a dominant trajectory of increasing diversity (Fig. 2). Above-background rates of speciation (R_s >35) were restricted to the Late Triassic and Early Jurassic, during the first appearance and primary radiation of nannoplankton, respectively (Fig. 3). Above-background extinction rates (R_e >35) were confined to the Triassic/Jurassic and K/T boundary intervals. Speciation and extinction rates are relatively uniform through the remainder of the Jurassic and the Cretaceous, but are slightly higher at the Jurassic/Cretaceous boundary, producing a peak in rate of turnover (Fig. 4). The Cretaceous diversity increase is interrupted by minima in the Barremian–Early Aptian and Cenomanian–Turonian, and a diversity fall into the Maastrichtian. The timing of taxonomic innovation is best shown in the phylogenetic trees (Fig. 1) and, as previously discussed, clustering of suprageneric-level change is restricted to the Early Jurassic and Jurassic/Cretaceous boundary intervals.

Cenozoic diversity patterns are markedly more variable than those of the Mesozoic, and rates of speciation and extinction are consistently higher throughout the interval (Figs 2, 3). These elevated rates are particularly clear in the turnover data (Fig. 4). The Paleocene evolutionary radiation was initiated soon after the K/T boundary extinctions and proceeded rapidly, with the majority of taxonomic innovation introduced within 10 my. Diversity close to that of the Campanian Mesozoic maximum was achieved by the Early Eocene (120 species) but this was followed by rapid diversity decline to a minimum in the Oligocene (39 species). Diversity rose again through the Miocene but was followed by decline through the Pliocene and Quaternary, and the Neogene in general was characterized by lower standing diversities. Above-background evolutionary rates occurred through much of the early Paleogene, and high extinction rates were recorded in the late Neogene. The introduction of major taxonomic innovation was largely restricted to the Paleocene radiation.

The taxon-specific diversity data reveal patterns that are clearly distinct from global diversity. The Mesozoic biogeographically-restricted taxa display strong diversity peaks in the Early Jurassic, Early Cretaceous (Berriasian–Barremian) and Campanian (Fig. 7). The main Cenozoic nannofossil groups each show somewhat similar trends, with diversity peaks in the Paleogene and Neogene, separated by Oligocene minima, but there is a consistent offset between each record (Fig. 6). The Discoasteraceae show peaks in the Early Eocene and Late Miocene, and near-extinction and extinction in the Oligocene and latest Pliocene, respectively. The Coccolithales show peaks in the Middle Eocene, Middle Miocene and Late Neogene. The Isochrysidales peak in the Late Eocene and Late Neogene.

Explaining diversity patterns in the fossil record

Diversity patterns in the fossil record have been attributed to a raft of causal factors, ranging from biotic causes such as competition and ecological replacement to, more commonly, abiotic causes such as environmental stability, climate change, sea-level variation (and consequent area effects), plate tectonic configurations and nutrient supply or productivity of oceanic water-masses. In reality, these factors may all play a role in controlling global diversity and many of them are inexorably interrelated. Two models in particular have been championed in recent years. In simple terms, the energy-bound model of Vermeij (1995) suggests that increasing nutrient supply results in diversification, as population growth-rates increase and ecological constraints on innovation decrease. Conversely, Hallock (1987) argues that the nutrient-controlled expansion and contraction of a continuum of oceanic trophic resources leads to diversification during intervals of reduced nutrient supply and extinctions during periods of increased nutrients. Observations on the biogeography and ecology of extant nannoplankton (McIntyre and Bé 1967; Okada and Honjo 1973; Winter et al. 1994; Thierstein et al. this volume) suggest that the Hallock model best explains present day nannoplankton diversity distribution. Extant coccolithophore diversity is strongly influenced by high-diversity but low standing-crop, K-mode-dominated communities living in stable, oligotrophic, subtropical ocean-gyre water-masses. Areas of high, and usually pulsed, nutrient delivery (high latitude and upwelling sites) support low-diversity, high standing-stock populations dominated by one or more r-mode taxa and, in extreme cases, monospecific blooms. The diversity patterns of fossil nannoplankton can thus be interpreted by analogy with their living counterparts: increased diversity reflecting expansion of oligotrophic habitats, and extinctions caused by reduction of oligotrophic habitats and expansion of eutrophic areas.

Mesozoic nannoplankton evolution and diversity

The Mesozoic diversity data is plotted against sea-level and a limited number of paleoclimate observations (Fig. 7). Broad inferences can be drawn concerning the Mesozoic climate-ocean system: for example, it is thought to have been characterized by globally-warm greenhouse conditions with little or no polar ice and low pole-to-equator thermal gradients. However, more detailed records of change within this framework remain enigmatic (see reviews by Frakes et al. 1992; Frakes 1999; Gale 2000; Burnett et al. 2000). Most workers now agree that the mid-Cretaceous supported climates of exceptional warmth and that this was followed by Late Cretaceous cooling which varied in structure and timing with latitude. The isotope records of Jenkyns et al. (1994 – English Chalk) suggest that long-term cooling was initiated in the Turonian, whereas those of Huber (1998 – Southern Ocean) support continued high-latitude warming in the Early Turonian and sustained warmth into the earliest Campanian followed by long-term cooling through the Maastrichtian.

The broadly-increasing diversity pattern of the Mesozoic (excluding Triassic/Jurassic boundary extinctions) is suggestive of long-term stability and widespread oligotrophy in photic-zone environments. This supports the generalized inferences described above but does not preclude the existence of fluctuations in the Jurassic–Cretaceous ocean-climate system, rather indicating that such fluctuations were not as great, rapid or sustained as those of the Cenozoic.

The appearance of nannoplankton in the Late Triassic, and the near-coincident appearance of dinoflagellates, has been attributed to evolutionary opportunity following ecosystem clearance during the end-Permian mass extinction (Bown et al. 1991). Nevertheless, the time-lag between the mass extinction and the appearance of nannofossils is almost 30 my. Molecular analysis shows that the two phytoplankton groups have much longer histories, probably stretching back to the Proterozoic (Medlin et al. 1997). The appearance of coccoliths in the Triassic is therefore almost certainly a biomineralisation innovation, but possibly linked with a secondary symbiotic event.

The initial evolutionary radiation of nannoplankton was interrupted by extinctions at the Triassic/Jurassic boundary, which were part of a mass extinction event which has been variously related to impacts (Olsen et al. 2002), igneous activity (Wignall 2001), sea-level (Hallam and Wignall 1997) and global carbon-cycle perturbation (Hesselbo et al. 2002). This event may yet prove comparable to the K/T boundary event but the real significance of the event for nannoplankton is difficult to judge due to the low Triassic diversities involved. The survival of just one species, however, suggests it may well have been a catastrophic reduction and raises the possibility that wholesale extinction of nannoplankton may have been involved in marine ecosystem collapse in both Mesozoic mass extinctions.

The Early Jurassic evolutionary radiation was initiated following these extinctions and by the Early Toarcian most major innovations had been introduced. Consequently, speciation and diversification rates fell to levels which were broadly maintained through the remainder of the Mesozoic (background levels). This pattern of initial evolutionary experimentation followed by long-term stability is shown by many groups of organisms (Gould et al. 1987) and has been termed evolutionary equilibrium (Sepkowski 1978) or diversity equilibrium (Wei and Kennett 1986).

Slightly elevated rates of speciation, extinction and turnover occurred around the Jurassic/Cretaceous boundary, and species-level turnover was high, as discussed above. This interval is associated with substantial faunal changes (hence the position of the system boundary) but is rather poorly understood in terms of environmental change. High rates of diversification in radiolaria, and a shift from radiolaria- to nannofossil-dominated sedimentation, have been explained by a climate-forced reduction of nutrient delivery to the western Tethys and Atlantic Oceans in the Tithonian (Danelian and Johnson 2001). This may also explain nannoplankton speciation at this time, particularly as western Tethys appears to have been a locus of evolutionary activity during the Jurassic (Bown 1987). However, the Tithonian also saw the introduction of considerable biogeographic differentiation, and diversification within separate nannofloral provinces may well have significantly contributed to global biodiversity.

Cretaceous nannoplankton evolutionary history was characterized by overall diversity increase but bracketed by more dramatic events at the base and top of the period. Diversity rise was not uniform, rather three intervals of increase were interrupted by minima spanning the Barremian–Early Aptian and Early Cenomanian–Turonian, and a slight fall into the Maastrichtian.

The Berriasian–Barremian and Turonian–Campanian periods of diversity increase broadly correlate with putative cooler climate intervals (Huber 1998; Frakes 1999), and the Campanian diversity maximum may have been related to the onset of late Mesozoic high-latitude cooling. Both intervals are clearly accompanied by significant peaks in diversity of biogeographically-restricted taxa at both high and low latitudes, and this is particularly clear in the Campanian, with the development of a well-defined and diverse Austral province (Watkins et al. 1996; Lees 2002). These observations strongly suggest that cooler Mesozoic climate intervals led to increased heterogeneity within photic zone environments, greater biogeographic partitioning, and hence diversity maxima. The mid-Cretaceous interval, considered a time of exceptional warmth, saw significantly reduced numbers of endemic taxa and this may explain the diversity minimum which preceded it; diversity nevertheless continued increasing through the Late Aptian and Albian. Similarly, biogeographic reorganization in response to climate amelioration may explain the reduction of diversity in the mid-Maastrichtian (Huber and Watkins 1992; Watkins et al. 1996; Lees 2002).

One of the most interesting features of the Cretaceous phylogenetic and diversity data is the lack of a clear relationship between nannoplankton evolution and the Oceanic Anoxic Event (OAE) intervals. These events are widely believed to represent significant regional or global perturbations of the marine environment, characterized by rapid carbon burial and incorporating aspects of extreme warmth, widespread oceanic stagnation and anoxia, and possibly enhanced primary productivity (Leckie et al. 2002), and they have been widely cited as significant events in nannoplankton history (Roth 1987, 1989; Bralower et al. 1994; Leckie et al. 2002). Our data show that rates of evolutionary change never rose above Mesozoic background levels during the OAEs, and the intervals are not characterized by significant taxonomic loss or innovation. It is notable that the global OAEs, 1a and 2, both occurred within the diversity minima noted above, but decrease occurred substantially prior to their onset. Although taxon-specific nannoplankton abundance fluctuations are associated with OAE1a (e.g. Erba 1994), and links between planktic foraminifera evolution and OAEs appear to be strong (Leckie et al. 2002), there is no case for major turnovers in the case of calcareous nannoplankton.

Nannoplankton, more than any other fossil group, have informed our detailed understanding of the timing, magnitude, and geography of extinctions at the K/T boundary, and subsequent recovery and radiation. Worldwide, high-resolution studies have consistently reported rapid (i.e. geologically instantaneous), synchronous, near-terminal extinctions across the biodiversity of the nannoplankton group accompanied by a collateral crash in pelagic carbonate sedimentation (Thierstein 1981; Pospichal 1994, 1996; Gartner 1996; MacLeod et al. 1997; Burnett 1998). Our data corroborates previous observations, with nine out of 14 coccolithophore

families terminated at the boundary and 93% extinction rate at species level. Recovery following the extinctions was rapid, and the rather atypical survivor groups (see MacLeod et al. 1997) were soon joined by new Cenozoic taxa whose origins were rather cryptic.

Cenozoic nannoplankton evolution and diversity

The Cenozoic nannoplankton data is plotted against paleoclimatological information, including long-term climate trends and intervals of particular interest, e.g. the Paleocene/Eocene Thermal Maximum, Early Eocene climatic optimum, etc. (Fig. 6). Broadly, there is good correlation between nannoplankton diversity and climate trends: diversity generally increased during periods of climate warming (e.g. Paleocene–Early Eocene, Miocene) and decreased as climate cooled (e.g. Middle Eocene–Oligocene, Pliocene–Recent). The Paleocene radiation occurred during a period of warm greenhouse climate, probably comparable to that of the late Mesozoic. The Cenozoic diversity maximum in the Late Paleocene–Early Eocene corresponded to a climatic optimum and maximum dispersal of warm-water taxa (Pospichal and Wise 1990). Diversity decline through the Eocene closely parallels climatic deterioration marked by falling surface- and deep-water temperatures (Zachos et al. 1994, 2001). The Cenozoic diversity minimum occurred during the Oligocene glacial maximum, which saw the initial establishment of significant Antarctic glaciation. We acknowledge that these correlations are of low resolution, however, they appear to be significant events in terms of long-term change, especially since parallel trends are seen in other plankton groups (see below).

The correlation between diversity and climate is particularly striking in the Paleogene, but the relationship contrasts with the Mesozoic observations, described above. This suggests that the magnitude of climate cooling in the Eocene did not support diversification through biogeographic partitioning but rather reduction of diversity due to the contraction of stable oligotrophic habitats and the suppression of diversity at temperate and high latitudes: high diversity at high latitudes was a feature of the Mesozoic. This interpretation is further supported by the taxon-specific diversity records, and particularly the diversity history of the warm-water, oligotrophic-adapted Discoasteraceae. Maximum discoaster diversity coincided with the group maximum and then declined precipitously through the Eocene to near-extinction in the Oligocene. The mesotrophic-adapted Coccolithales peaked in diversity in the Middle Eocene, coinciding with a short recovery in group diversity (the Cenozoic maximum at nannofossil zone resolution), and echoing Mesozoic observations of diversity increase accompanying cooling. The cooler-water, meso-eutrophic-adapted Prinsiales increased in diversity through the Eocene but declined sharply in the Oligocene. The records of these taxa reveal contrasting responses to climate change which can be explained by their different ecological strategies, but underlines the importance of the K-selected groups, in this case discoasters, in terms of global diversity.

These global and taxon-specific diversity records are remarkably similar to patterns observed in planktic foraminifera, which show declining diversity but successive peaks in warm-, temperate- and cool-adapted groups through the Eocene (Boersma and Premoli Silva 1991; Hallock et al. 1991). These authors also observed high Middle Eocene diversity, attributing it to the coexistence of older, 'warm-world' biotas with new, 'cooling-world' biota, describing this as a temporal or evolutionary ecotone (Hallock et al. 1991), an observation which is also applicable to the nannoplankton record.

The similar evolutionary histories of these two biologically and ecologically distinct plankton groups is strong evidence of abiotic, and specifically climatic, control on their evolution at this time. However, it should be noted that the marked decline in nannoplankton diversity in the Late Eocene and Oligocene was accompanied by exponential rise in marine diatom diversity (Spencer-Cervato 1999), although this may well reflect an expansion of habitats conducive to diatom diversification, i.e. cool high-latitude water-masses, rather than direct competition between the two phytoplankton groups (Fig. 8).

These diversity patterns conform to the Hallock hypothesis, with K-selected taxa proliferating during warming and warm intervals, as stable oligotrophic habitats and the trophic resource continuum expanded, creating more potential habitat space, and the increased importance of meso- and eutrophic-adapted groups during periods of cooling.

The Neogene record is less straightforward. Nannoplankton diversity recovered through the Middle to Late Miocene, and the Discoasteraceae underwent a renewed period of radiation culminating in the Late Miocene diversity maximum. This is suggestive of an expansion of warm, stable oligotrophic habitats during the Miocene but does not correlate particularly well with our current understanding of Miocene climates and oceans, coming soon after a significant cooling event in the deep-water oxygen isotope record (Zachos et al. 2001). However, oxygen isotope records from planktic foraminifera suggest that, while cooling proceeded relatively rapidly at high latitudes (and ice built up on Antarctica), surface-water temperatures were stable, or even warmed, in temperate, subtropical and tropical regions (Savin et al. 1985).

As in the Eocene, the Isochrysidales showed diversity increase through the Pliocene and Pleistocene, against a general background of declining diversities. The terminal decline of discoasters occurred during a time of cooling and onset of glaciation in the Northern Hemisphere, however, the correlation is not exact, and in fact extinctions of the final species *Discoaster brouweri* and *D. triradiatus* are recorded in an interglacial (Chapman and Chepstow-Lusty 1997).

High rates of speciation and extinction throughout the Cenozoic suggest a level of evolutionary stability ('equilibrium') was not attained in the last 65 my. High speciation and turnover rates were initially associated with the post-K/T recovery and radiation, but the high extinction rates, which are recorded relatively consistently, appear to be associated first with the Paleocene/Eocene boundary event, and second the Eocene–Oligocene climatic deterioration associated with the onset of Cenozoic glaciations. The rapid and high-amplitude climate changes appear to have consistently maintained evolutionary rates at levels significantly higher than

those seen in the Mesozoic, and resulted in an overall pattern of diversity decline from the Eocene to present. These statistical observations are supported by qualitative comparisons of nannoplankton assemblages, with far greater differences seen between the Cenozoic epochs compared with for example the Cretaceous stages. Either abiotic or biotic factors forced higher turnover in the Cenozoic or there is a fundamental difference in the nannoplankton which evolved following the K/T boundary extinctions.

Conclusion

The combined information from nannoplankton phylogenetic trees and diversity data provide us with an outstanding record of evolutionary history for this phytoplankton group. Although not all extant clades have been well represented in the fossil record, those that are present are likely to have left a representative and meaningful record of their evolution and diversity through time. The existence of cryptic species and life-cycle dimorphs (holococcoliths) may not greatly affect the diversity trends we have observed.

There is good correlation between previously-documented extinction data and the nannoplankton record, with the two major post-Paleozoic mass extinction events shown clearly by significantly above-background evolutionary rates. In fact, it is conceivable that extinction in the marine realm may have been abetted by eradication of the primary-producer phytoplankton during these events. Although the primary extinction mechanism is yet to be identified, it could possibly have been due to impact-induced darkness or hyperthermal-induced calcification crises. The two major nannoplankton evolutionary radiation events occurred directly following these extinction events.

Coccolithophores and associated nannoplankton showed a pattern of broadly increasing diversity through the Mesozoic, suggesting long-term stability and widespread oligotrophy in photic-zone environments. Jurassic/Cretaceous boundary turnover and taxonomic innovation may have been linked to reduced nutrient cycling in western Tethys and/or biogeographic differentiation, but may also reflect more profound ocean-climate changes at this time, which we have yet to identify. Two important Cretaceous periods of diversity increase (Neocomian and Turonian–Campanian) were both associated with increased levels of biogeographic differentiation, most likely linked to climate cooling. Reduced biogeographic partitioning in the mid-Cretaceous, linked to warm climates, may explain the diversity decline which preceded it. The two major Cretaceous OAEs (OAE1a and OAE2) fall within intervals of reduced diversity but are not obviously associated with above-background evolutionary rates or significant taxonomic loss or innovation.

Cenozoic diversity records are closely correlated with climate change, increasing diversity associated with climate warming and decreasing diversity with cooling. This contrasts with Mesozoic diversity patterns and indicates that the magnitudes, rates and duration of Cenozoic cooling prevented diversification through

biogeographic differentiation and, instead, saw suppression of diversity at temperate and high latitudes. Warm intervals supported high diversities of warm, K-selected taxa, such as discoasters, whereas cool and cooling climates saw increases in meso- and eutrophic-adapted groups, such as the Coccolithales and Isochrysidales (synonym Prinsiales). Miocene diversities are not well correlated with paleoclimate trends but suggest that, while cooling proceeded at high latitudes, particularly associated with ice-sheet growth in Antarctica, warmer, oligotrophic habitats were sustained or expanded at low latitudes, supporting high global diversity and the diversification of the K-selected discoasters. As bipolar glaciation was established in the late Neogene, discoasters declined to extinction, the Prinsiales group increased, but diversity decreased overall. High rates of speciation and extinction were sustained throughout the Cenozoic, and evolutionary equilibrium was never achieved. The overall pattern of diversity decline from the Eocene to present suggests onset and evolution of the icehouse-mode climate-ocean system resulted in higher extinction rates, lowered diversity in temperate and high latitudes, and global diversity minima during the Oligocene and Pliocene–Holocene.

References

Aubry M-P (1984) Handbook of Cenozoic calcareous nannoplankton, Book 1: Ortholithae (Discoasters). Micropaleontology Press, American Museum of Natural History, New York

Aubry M-P (1988) Handbook of Cenozoic calcareous nannoplankton, Book 2: Ortholithae (Holococcoliths, Ceratoliths and others). Micropaleontology Press, American Museum of Natural History, New York

Aubry M-P (1989) Handbook of Cenozoic calcareous nannoplankton, Book 3: Ortholithae (Pentaliths, and others), Heliolithae (Fasciculiths, Sphenoliths and others). Micropaleontology Press, American Museum of Natural History, New York

Aubry M-P (1990) Handbook of Cenozoic calcareous nannoplankton, Book 4: Heliolithae (Helicoliths, Cribriliths, Lopadoliths and others). Micropaleontology Press, American Museum of Natural History, New York

Aubry M-P (1992) Late Paleogene calcareous nannoplankton evolution: a tale of climatic deterioration. In: Prothero DR, Berggren WA (eds) Eocene–Oligocene Climatic and Biotic Evolution, Princeton University Press, pp 272–309

Aubry M-P (1998) Early Paleogene calcareous nannoplankton evolution: a tale of climatic amelioration. In: Aubry M-P, Lucas SG, Berggren AW (eds) Late Paleocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records. Columbia University Press, pp 158–203

Aubry M-P (1999) Handbook of Cenozoic calcareous nannoplankton, Book 4: Heliolithae (Zygoliths and Rhabdoliths). Micropaleontology Press, American Museum of Natural History, New York

Baumgartner PO (1987) Age and genesis of Tethyan Jurassic radiolarites. Eclogae Geol Helv 80: 831–879

Berggren WA, Kent DV, Swisher III CC, Aubry M-P (1995). A revised Cenozoic chronology and chronostratigraphy. In: Berggren WA, Kent DV, Hardenbol J (eds) Geo-

chronology, Time-Scales, and Global Stratigraphic Correlation: Framework for an Historical Geology. SEPM Spec. Publ. 54: 129–212
Boersma A, Premoli Silva I (1991) Distribution of Paleogene planktonic foraminifera – analogies with the Recent? Palaeogeogr Palaeocl 83: 29–48
Bown PR (1987) Taxonomy, biostratigraphy, and evolution of late Triassic–early Jurassic calcareous nannofossils. Spec Pap Palaeontol 38: 1–118
Bown PR (1993) New holococcoliths from the Toarcian–Aalenian (Jurassic) of northern Germany. Senckenbergiana Lethaea 73: 407–419
Bown PR (1998a) Calcareous nannofossil biostratigraphy. Kluwer Academic Publishers, pp 1–315
Bown PR (1998b) Triassic. In: Bown PR (ed) Calcareous nannofossil biostratigraphy, Kluwer Academic Publishers, pp 29–33
Bown PR, Young JR (1997) Mesozoic calcareous nannoplankton classification. J Nannoplankton Res 19: 21–36
Bown PR, Burnett JA, Gallagher LT (1991) Critical events in the evolutionary history of calcareous nannoplankton. Historical Biology 5: 279–290
Bown PR, Burnett JA, Gallagher LT (1992) Calcareous nannoplankton evolution. Memorie di Scienze Geologiche XLIII: 1–17
Bralower TJ, Arthur MA, Leckie RM, Sliter WV, Allard DJ, Schlanger SO (1994) Timing and paleoceanography of oceanic dysoxia/anoxia in the Late Barremian to Early Aptian (Early Cretaceous). Palaios 9: 335–369
Burnett JA (1998) Upper Cretaceous. In: Bown PR (ed) Calcareous nannofossil biostratigraphy. Kluwer Academic Publishers, pp 132–199
Burnett JA, Young JR, Bown PR (2000) Calcareous nannoplankton and global climate change. In: Culver SJ, Rawson PF (eds) Biotic Response to Global Change: The last 145 million years. Cambridge University Press, pp 35–50
Chapman MR, Chepstow-Lusty AJ (1997) Late Pliocene climatic change and the global extinction of the discoasters: an independent assessment using oxygen isotope records. Palaeogeogr Palaeocl 134: 109–125
Chepstow-Lusty AJ, Shackleton NJ, Backman J (1992) Upper Pliocene *Discoaster* abundance variations from the Atlantic, Pacific and Indian Oceans: the significance of productivity pressure at low latitudes. Memorie di Scienze Geologiche XLIV: 357–373
Cros L, Kleijne A, Zeltner A, Billard C, Young JR (2000) New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. Mar Micropaleontol 39: 1–34
Danelian T, Johnson KG (2001) Patterns of biotic change in Middle Jurassic to Early Cretaceous Tethyan radiolaria. Mar Micropaleontol 43: 239–260
Erba E (1994) Nannofossils and superplumes: The early Aptian "nannoconid crisis". Paleoceanography 9: 483–501
Frakes LA (1999) Estimating the global thermal state from Cretaceous sea surface and continental temperature data. In: Barrera E, Johnson CC (eds) Evolution of the Cretaceous Ocean-Climate System. Geol Soc Am Spec Pap 332: 49–57
Frakes LA, Francis JE, Syktus JI (1992) Climate Modes of the Phanerozoic. Cambridge University Press, pp 1–274
Gale AS (2000) The Cretaceous World. In: Culver SJ, Rawson PF (eds) Biotic Response to Global Change: The last 145 million years. Cambridge University Press, pp 4–19
Gale AS, Smith AB, Monks NEA, Young JA, Howard A, Wray DS, Huggett JM (2000) Marine biodiversity through the Late Cenomanian–Early Turonian: palae-

oceanographic controls and sequence stratigraphic biases. J Geol Soc London 157: 745–757
Gallois RW (1976) Coccolith blooms in the Kimmeridge Clay and the origin of North Sea Oil. Nature 259: 473–475
Gallois RW, Medd AW (1979) Coccolith-rich marker bands in the English Kimmeridge Clay. Geol Mag 116: 247–334
Gartner S (1996) Calcareous nannofossils at the Cretaceous–Tertiary boundary. In: MacLeod N, Keller G (eds) Cretaceous–Tertiary mass extinctions: biotic and environmental changes. W.W. Norton & Company, pp 27–47
Gould SJ, Gilinsky NL, German R (1987) Asymmetry of lineages and the direction of evolutionary time. Science 236: 1437–1441
Gradstein FM, Agterberg FP, Ogg JG, Hardenbol J, Van Veen P, Thierry J, Huang Z (1995) A Triassic, Jurassic and Cretaceous time-scale. In: Berggren WA, Kent DV, Hardenbol J(eds.), Geochronology, Time-Scales, and Global Stratigraphic Correlation: Framework for an Historical Geology. SEPM Spec Publ 54: 95–126
Hallam A, Wignall PB (1997) Mass extinctions and their aftermath. Oxford University Press, pp 320
Hallock P (1987) Fluctuations in the trophic resource continuum: A factor in global diversity cycles? Paleoceanography 2: 457–471
Hallock P, Premoli Silva I, Boersma A (1991) Similarities between planktonic and larger foraminiferal evolutionary trends through Paleogene paleoceanographic changes. Palaeogeogr Palaeocl 83: 49–64
Haq BU, Hardenbol J, Vail PR (1987) Chronology of Fluctuating Sea Levels Since the Triassic. Science 235: 1156–1167
Hesselbo SP, Robinson SA, Surlyk F, Piasecki S (2002) Terrestrial and marine extinction at the Triassic–Jurassic boundary synchronized with major carbon-cycle perturbation: a link to initiation of massive volcanism? Geology 30: 251–254
Huber BT (1998) Tropical paradise at the Cretaceous poles? Science 282: 2199–2200
Huber BT, Watkins DK (1992) Biogeography of Campanian–Maastrichtian calcareous plankton in the region of the Southern Ocean: paleogeographic and paleoclimatic implications. The Antarctic Paleoenvironment: a perspective on global change. Antarctic Research Series 56: 31–60
Janofske D (1992) Calcareous nannofossils of the Alpine Upper Triassic. In: Hamrsmîd B, Young JR (eds) Nannoplankton Research, Vol. 1, Knihovnicka ZPZ, 14a, 1: 87–109
Jenkyns HC, Gale AS, Corfield RM (1994) Carbon- and oxygen-isotope stratigraphy of the English Chalk and Italian Scaglia and its palaeoclimatic significance. Geol Mag 131: 1–34
Knoll A (1989) Evolution and extinction in the marine realm: some constraints imposed by phytoplankton. Phil Trans R Soc London B 325: 279–290
Leckie MR, Bralower TJ, Cashman R (2002) Oceanic anoxic events and plankton evolution: biotic response to tectonic forcing during the mid-Cretaceous. Paleoceanography, 17: 1041
Lees JA (2002) Calcareous nannofossil biogeography illustrates palaeoclimate change in the late Cretaceous Indian Ocean. Cretaceous Res 23: 537–633
Lipps JH (1970) Plankton evolution. Evolution 24: 1–22
MacLeod N, Rawson PF, Forey PL, Banner FT, Boudagher-Fadel MK, Bown PR, Burnett JA, Chambers P, Culver S, Evans SE, Jeffery C, Kaminski MA, Lord AR, Milmer AC,

Milner AR, Morris N, Owen E, Rosen BR, Smith AB, Taylor PD, Urquhart E, Young JR (1997) The Cretaceous–Tertiary biotic transition. J Geol Soc London 154: 265–292

McIntyre A, Bé AWH (1967) Modern Coccolithophoridae of the Atlantic Ocean. I. Placoliths and cyrtoliths. Deep-Sea Res 14: 561–597

Medlin LK, Kooistra WHCF, Potter D, Saunders JB, Andersen RA (1997) Phylogenetic relationships of the "golden algae" (haptophytes, heterokont chromophytes) and their plastids. Plant Syst Evol Supplementum 11: 187–219

Miller A (2000) Conversations about Phanerozoic global diversity. Paleobiology 26 (4) supplement, Deep Time: Palaeobiology's Prespective, pp 53–73

Okada H, Honjo S (1973) The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea Res 20: 355–374

Olsen PE, Kent DV, Sues H-D, Koeberl C, Huber H, Montanari A, Rainforth EC, Fowell SJ, Szajna MJ, Hartline BW (2002) Ascent of dinosaurs linked to an iridium anomaly at the Triassic–Jurassic boundary. Science 296: 130–133

Perch-Nielsen K (1985a) Mesozoic calcareous nannofossils. In: Bolli HM, Saunders JB, Perch-Nielsen K (eds) Plankton Stratigraphy. Cambridge University Press, pp 329–426

Perch-Nielsen K (1985b) Cenozoic calcareous nannofossils. In: Bolli HM, Saunders JB, Perch-Nielsen K (eds) Plankton Stratigraphy. Cambridge University Press, pp 427–554

Perch-Nielsen K (1986) Geologic events and the distribution of calcareous nannofossils – some speculations. Bull Cent Rech Elf E 10: 421–432

Pospichal JJ (1994) Calcareous nannofossils at the K-T boundary, El Kef: No evidence for stepwise, gradual, or sequential extinctions. Geology 22: 99–102

Pospichal JJ (1996) Calcareous nannoplankton mass extinction at the Cretaceous/Tertiary boundary: an update. In: Ryder G, Fastovsky D, Gartner S (eds) The Cretaceous–Tertiary event and other catastrophes in Earth history. Geol Soc Am Spec Paper 307: 335–360

Pospichal JJ, Wise SW Jr. (1990) Paleocene to Middle Eocene calcareous nannofossils of ODP Sites 689 and 690, Maud Rise, Weddell Sea. Proc Ocean Drill Prog Sci Results 113: 613–638

Romein AJT (1979) Lineages in early Paleogene calcareous nannoplankton. Utrecht Micropaleontological Bulletins 22: 1–230

Roth PH (1986) Mesozoic palaeoceanography of the North Atlantic and Tethys Oceans. In: Summerhayes CP, Shackleton NJ (eds) North Atlantic Palaeoceanography. Geol Soc Spec Pub 21: 299–320

Roth PH (1987) Mesozoic calcareous nannofossil evolution: relation to paleoceanographic events. Paleoceanography 6: 601–611

Roth PH (1989) Ocean circulation and calcareous nannoplankton evolution during the Jurassic and Cretaceous. Palaeogeogr Palaeocl 74: 111–126

Savin SM, Abel L, Barrera E, Hodell D, Keller G, Kennett JP, Killingley J, Murphy M, Vincent E (1985) The evolution of Miocene surface and near-surface marine temperatures: oxygen isotopic evidence. In: Kennett JP (ed) The Miocene Ocean: paleoceanography and biogeography. Geol Soc Am Mem 163: 49–82

Sepkowski Jr. JJ (1978) A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. Paleobiology 4: 223–251

Sheridan RE, Gradstein FM et al. (1983) Init. Repts. DSDP, 76. Washington (US Govt. Printing Office)

Siesser WG (1998) Calcareous nannofossil genus *Scyphosphaera*: structure, taxonomy, biostratigraphy, and phylogeny. Micropaleontology 44: 351–384

Smith A (1994) Systematics and the fossil record. Blackwell, 223pp
Spencer-Cervato C (1999) The Cenozoic Deep Sea Microfossil Record: Explorations of the DSDP/ODP Sample Set Using the Neptune Database. Palaeontologica Electronica, 2: art. 4
Sprengel C, Young JR (2000) First direct documentation of associations of *Ceratolithus cristatus* ceratoliths, hoop-coccoliths and *Neosphaera coccolithomorpha* planoliths. Mar Micropaleontol 3: 39–41
Stover LE, Brinkhuis H, Damassa SP, de Verteuil L, Helby RJ, Monteil E, Partridge AD, Powell AJ, Riding JB, Smelror M, Williams GL (1996) Mesozoic–Tertiary dinoflagellates, acritarchs and prasinophytes. In: Jansonius J, McGregor DC (eds) Palynology: principles and applications, vol 2. American Association of Stratigraphic Palynologists Foundation, pp 641–750
Tappan H, Loeblich Jr. AR (1973) Evolution of the Oceanic Plankton. Earth-Sci Rev 9: 207–240
Tappan H, Loeblich Jr. AR (1988) Foraminiferal evolution, diversification and extinction. J Paleontol 62: 695–741
Thierstein HR (1981) Late Cretaceous calcareous nannoplankton and the change at the Cretaceous-Tertiary boundary. In: Douglas RG, Warme J, Winterer EL (eds) The Deep Sea Drilling Project: a decade of progress. SEPM, Spec Pub 32: 355–394
Vermeij GJ (1995) Economics, volcanoes, and Phanerozoic revolutions. Paleobiology 21: 125–252
Watkins D, Wise S, Pospichal 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
Wei W, Kennett JP (1986) Taxonomic evolution of Neogene planktonic foraminifera and paleoceanographic relations. Paleoceanography 1: 67–84
Wignall PB (2001) Large igneous provinces and mass extinctions. Earth-Sci Rev 53: 1–33
Winter A, Jordan RW, Roth P (1994) Biogeography of living coccolithophores in ocean waters. In: Winter A, Siesser WG (eds) Coccolithophores. Cambridge University Press, pp 161–177
Young JR (1998) Neogene. In: Bown PR (ed) Calcareous nannofossil biostratigraphy. Kluwer Academic Publishers, pp 225–265
Young JR, Bown PR (1997) Cenozoic calcareous nannoplankton classification. J Nannoplankton Res 19: 36–47
Young JR, Didymus JM, Bown PR, Prins B, Mann S (1992) Crystal assembly and phylogenetic evolution in heterococcoliths. Nature 356: 516–518
Young JR, Bown PR, Burnett JA (1994) The Haptophytes: Palaeontological perspectives. In: Green JC, Leadbeater BSC (eds) The Haptophyte Algae. The Systematics Association Special Volume No. 51, pp 379–392
Zachos JC, Stott LD, Lohmann KC (1994) Evolution of early Cenozoic temperatures. Paleoceanography 9: 353–387
Zachos JC, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292: 696–693