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CALCAREOUS NANNOPLANKTON EVOLUTION

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Key words: Evolution, calcareous nannofossils/nannoplankton, extinction events, radiation events, Mesozoic, Cenozoic.

ABSTRACT

Calcareous nannofossils first appeared in the Late Triassic, increased through much of the Jurassic and Cretaceous reaching a diversity peak in the Late Cretaceous. After devastating extinctions at the Cretaceous/Tertiary boundary, nannofossils recovered rapid-

ly to a second diversity peak in the mid Eocene. There followed a decline into the Oligocene, increased diversity in the Miocene and a general decrease into the Pleistocene. Particularly important events in the evolutionary history of the group include their first appearance in the Late Triassic, extinctions at the Triassic/Jurassic boundary, Early and Latest Jurassic evolutionary radiations, Late Cretaceous diversity maximum, Cretaceous/Tertiary boundary extinctions, and Early Tertiary radiation. These events may be explained with reference to driving mechanisms, such as climate, palaeoceanography, nutrient availability, and environmental stability, which in turn may be related to the Icehouse-Greenhouse cycles of FISCHER (1982).

RIASSUNTO

I nannofossili calcarei apparvero la prima volta nel tardo Triassico, aumentarono per buona parte del Giurassico e del Cretaceo raggiungendo un picco di diversità nel Cretaceo superiore. Dopo le massicce estinzioni al limite Cretaceo/Terziario essi raggiunsero rapidamente un secondo massimo di diversità nell'Eocene medio. Seguirono poi un declino nell'Oligocene, un aumento di diversità nel Miocene e una generale regressione nel Pleistocene. Tra gli eventi più significativi della loro storia evolutiva sono da annoverare la prima comparsa nel tardo Triassico, le estinzioni al limite Triassico/Giurassico, la radiazione evolutiva del Giurassico inferiore e superiore, il picco di diversità del Cretaceo superiore, le estinzioni al limite Cretaceo/Terziario e la radiazione del Terziario inferiore. Questi eventi si possono spiegare con riferimento a meccanismi causali, quali il clima, la palaeoceanografia, la disponibilità di nutrienti e la stabilità dell'ambiente, che, a loro volta, possono essere collegati ai cicli "Icehouse" - "Greenhouse" di FISCHER (1982).

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INTRODUCTION

Calcareous nannofossils are the fossilized calcite plates and processes of marine planktonic organisms and include both extant and extinct groups. The most important single group are coccoliths, whose extant counterparts are the coccolithophorid algae. Coccolithophorids are unicellular, marine phytoplankton which precipitate calcite discs (coccoliths) as a cell-wall covering (coccosphere). They provide an excellent living analogue for the palaeontological record, although their relationship with other calcareous nannofossil groups (nannoliths) remains unknown.

While much calcareous nannofossil study has concentrated upon taxonomic, biostratigraphical and palaeoenvironmental aspects, attempts have also been made to understand the phylogenetic relationships within and between the major groups, *e.g.* PRINS (1969, 1971); ROMEIN (1979); PERCH-NIELSEN (1985); BOWN (1987). This paper will present an overview of the evolutionary history of calcareous nannofossils, particularly discriminating significant diversification and extinction events. An attempt will be made to understand the causes underlying these major evolu-

tionary changes and at the same time to assess the extent to which these events in turn influenced the physical (ocean and atmosphere) environment.

Calcareous nannofossils are an ideal fossil group with which to address these questions, having a geological history originating in the early Mesozoic, and representing a primary phytoplankton group and major biogenic, pelagic carbonate producer for much of this time. The details of protistan evolution, complicated by the dominance of asexual reproduction and the uncertainty concerning coccolith/nannolith function, represent a problem when applying classical evolutionary theory to the nannoplankton group. However, at least broad inferences concerning the timing and causes of major periods of evolutionary radiation and extinction can be made, and the effects of these changes can be similarly assessed.

DATA SOURCES AND DATA PROBLEMS

Calcareous nannofossil data have been drawn from the extensive work of the authors together with assimilation of carefully reviewed published data, including AUBRY (1985, 1988, 1989), PERCH-

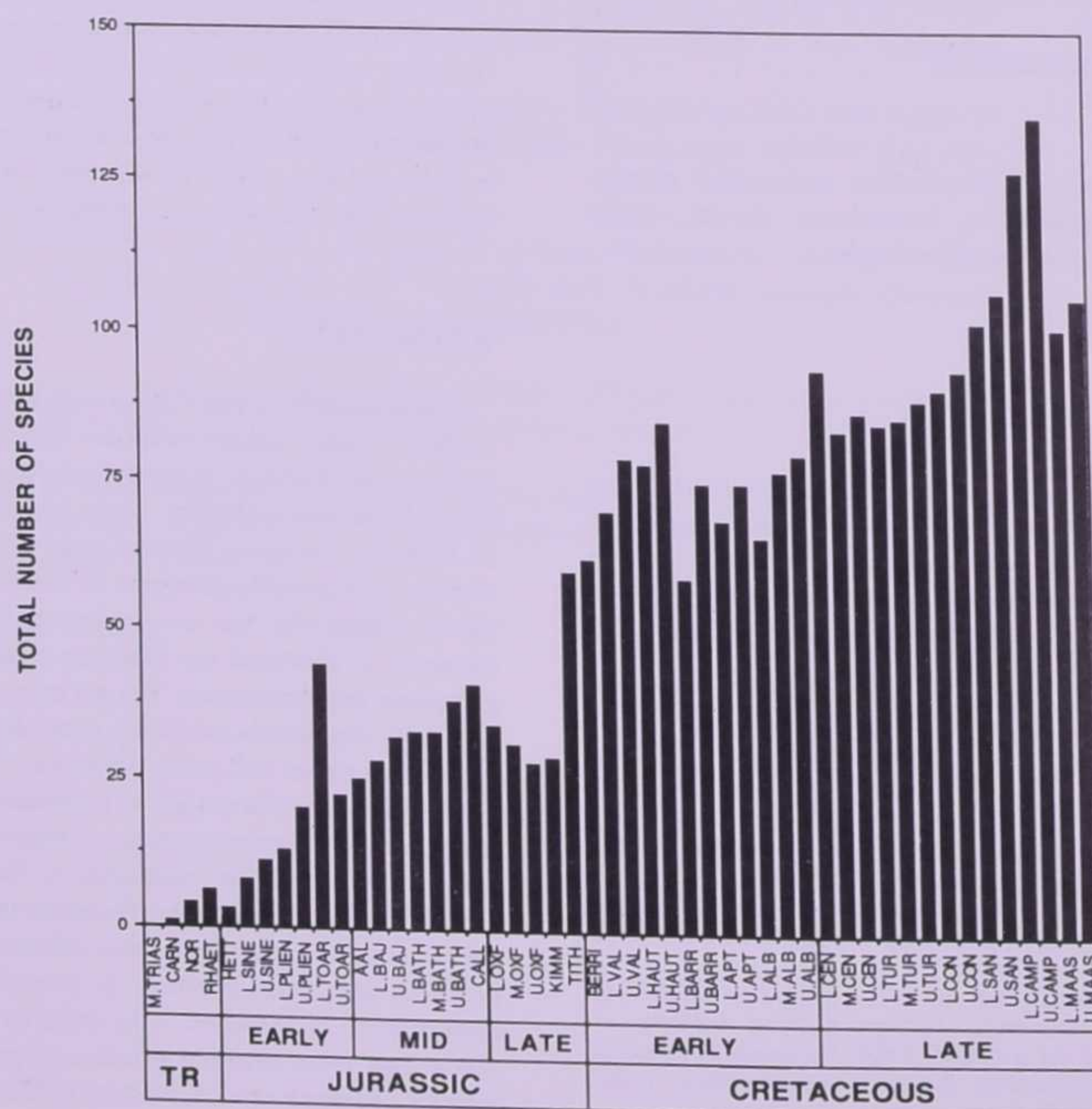


FIG. 1 - Calcareous nannoplankton diversity for the Mesozoic. (Time scale, HAQ *et al.*, 1986).

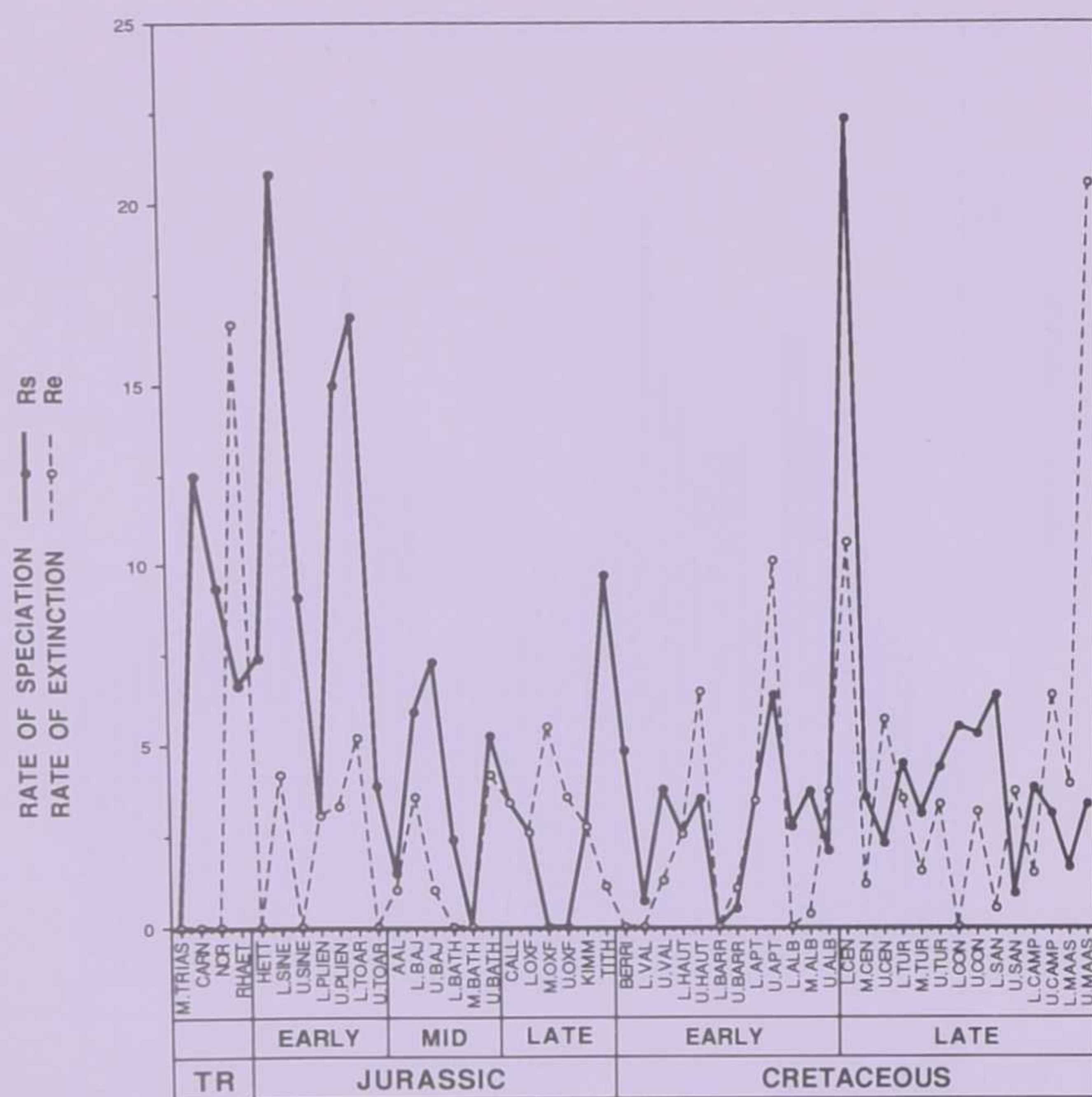


FIG. 2 - Rates of calcareous nannoplankton speciation and extinction for the Mesozoic.

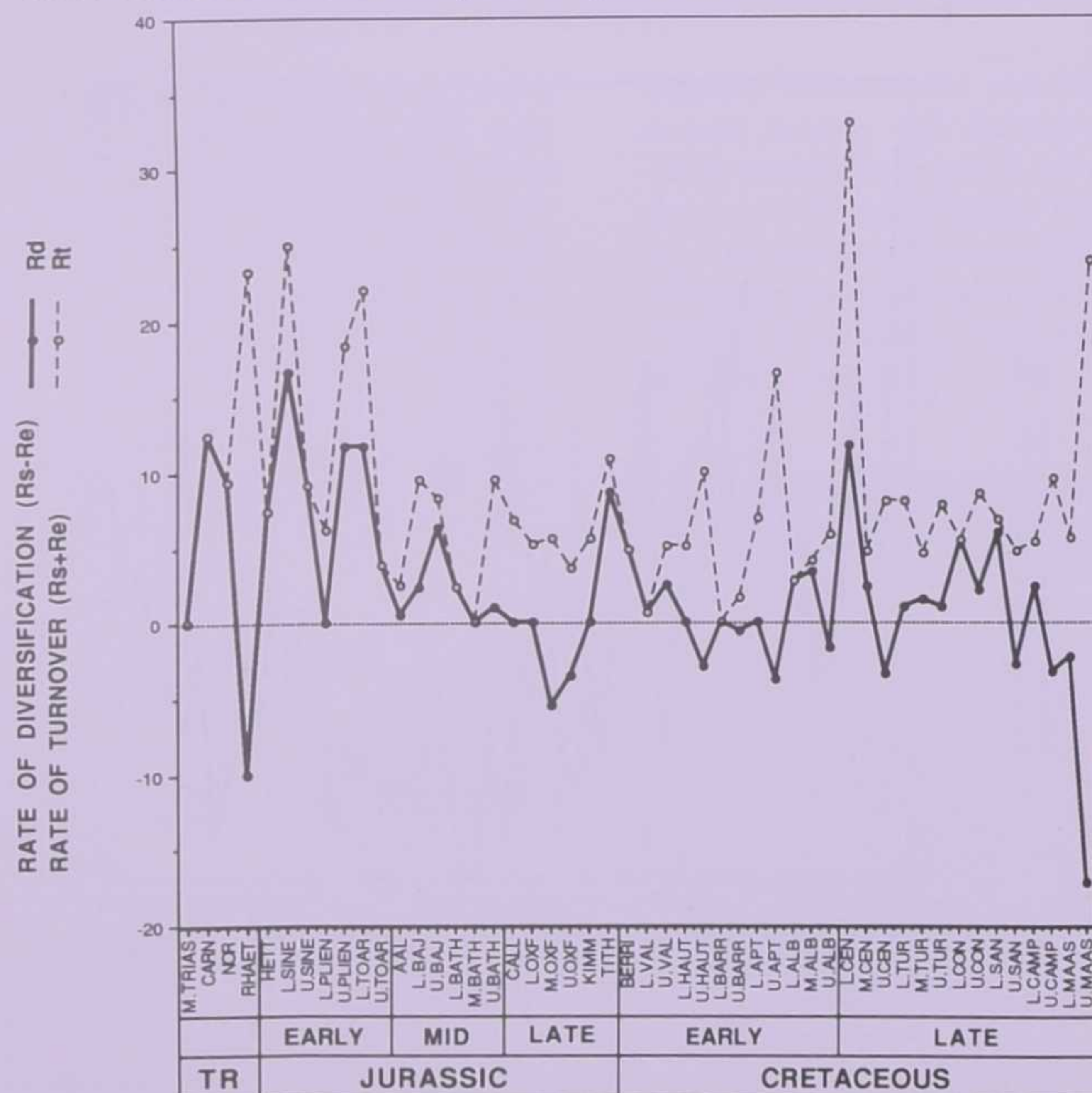


FIG. 3 - Rates of calcareous nannoplankton diversification and turnover for the Mesozoic.

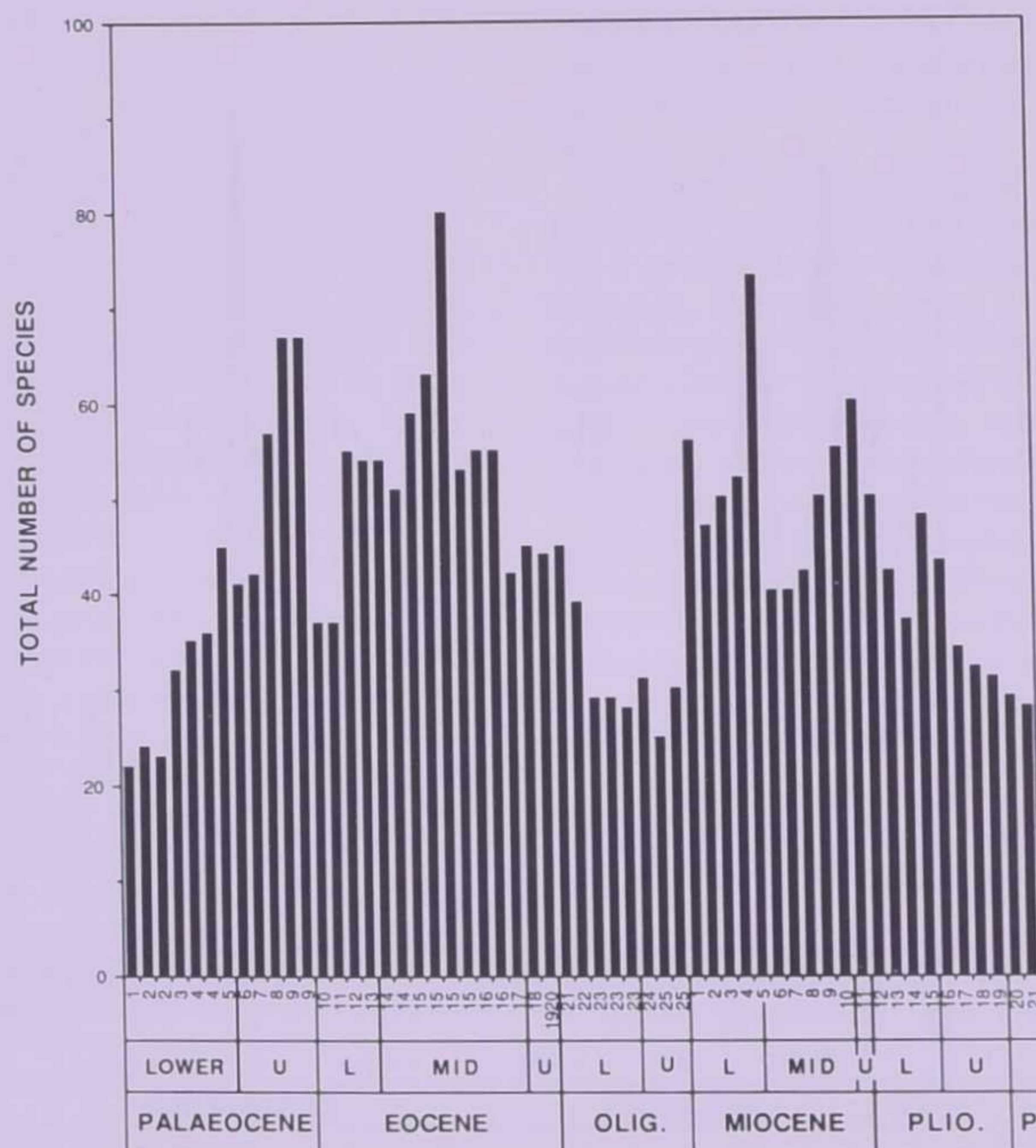


FIG. 4 - Calcareous nannoplankton diversity for the Cenozoic.

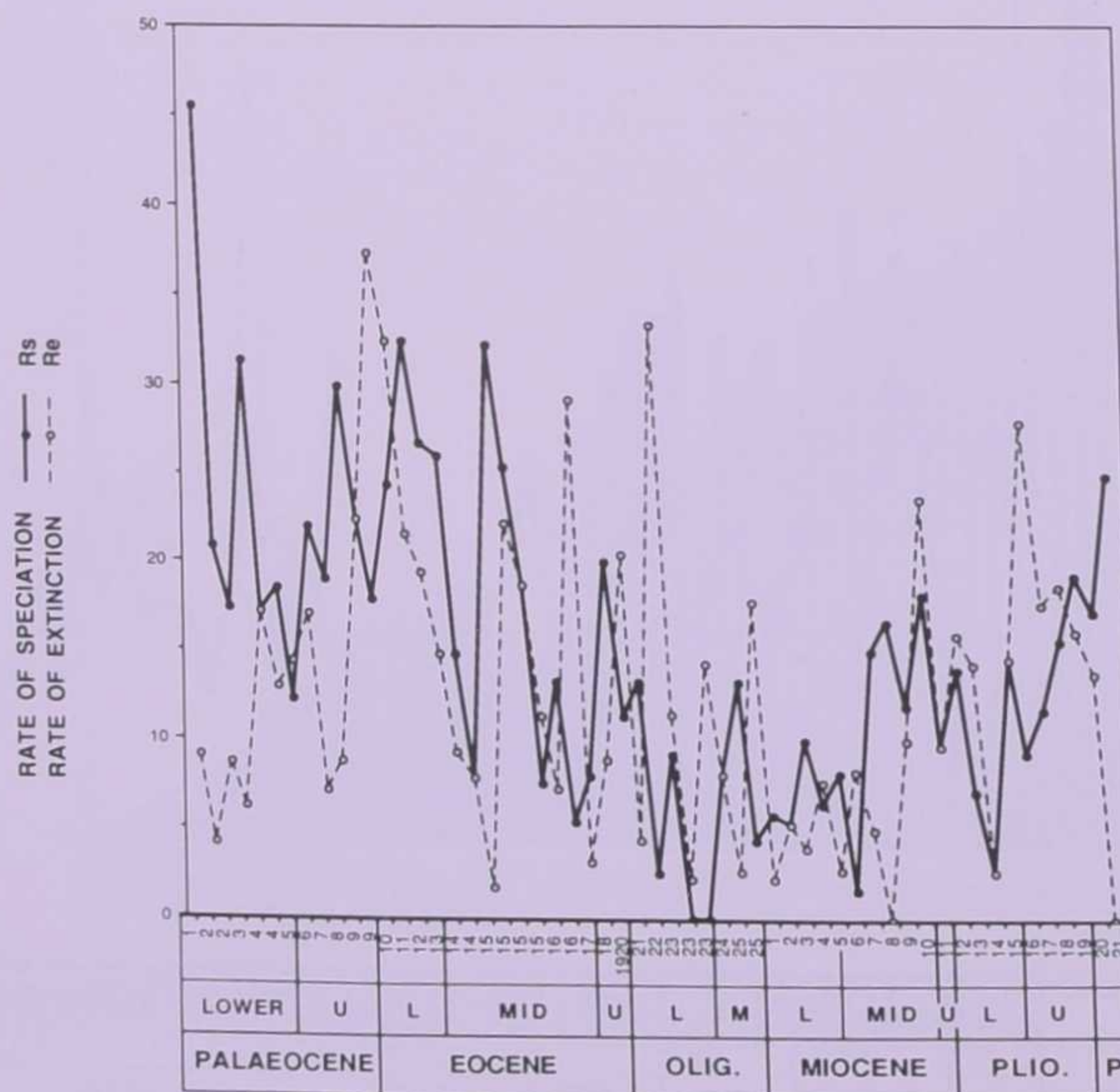


FIG. 5 - Rates of calcareous nannoplankton speciation and extinction for the Cenozoic.

FIG. 7 - Diversity of selected marine microplankton and zooplankton. A - silicoflagellates, B - planktonic foraminifera, C - dinoflagellates, D - acritarchs. After TAPPAN and LOEBLICH, 1973, Figs. 1, 2, 5.

ography, climate, oceanography (chemical and physical), and astronomy must be considered.

At the broadest level, it appears that the marine biota as a whole has been controlled by pandemic forcing factors in the exogenic system. The pattern of development shown by calcareous nannoplankton, *i.e.* Triassic origination, cumulative Mesozoic increase, Late Cretaceous diversity maximum, Cretaceous/Tertiary boundary extinctions, Palaeocene recovery and increase to a maximum in the Eocene, decline into the Oligocene,

increase in the Miocene, general decrease in diversity to the Present Day, is by no means unique but comparable to that of other groups of marine organisms (see TAPPAN and LOEBLICH, 1973, p. 222) (Fig. 7). Such parallel development appears to indicate pervasive causal factors which have controlled the development of marine organisms throughout the Phanerozoic. The broad patterns in diversity and development exhibited by the marine biota are described and discussed in TAPPAN (1968). The cyclicity TAPPAN recognised in

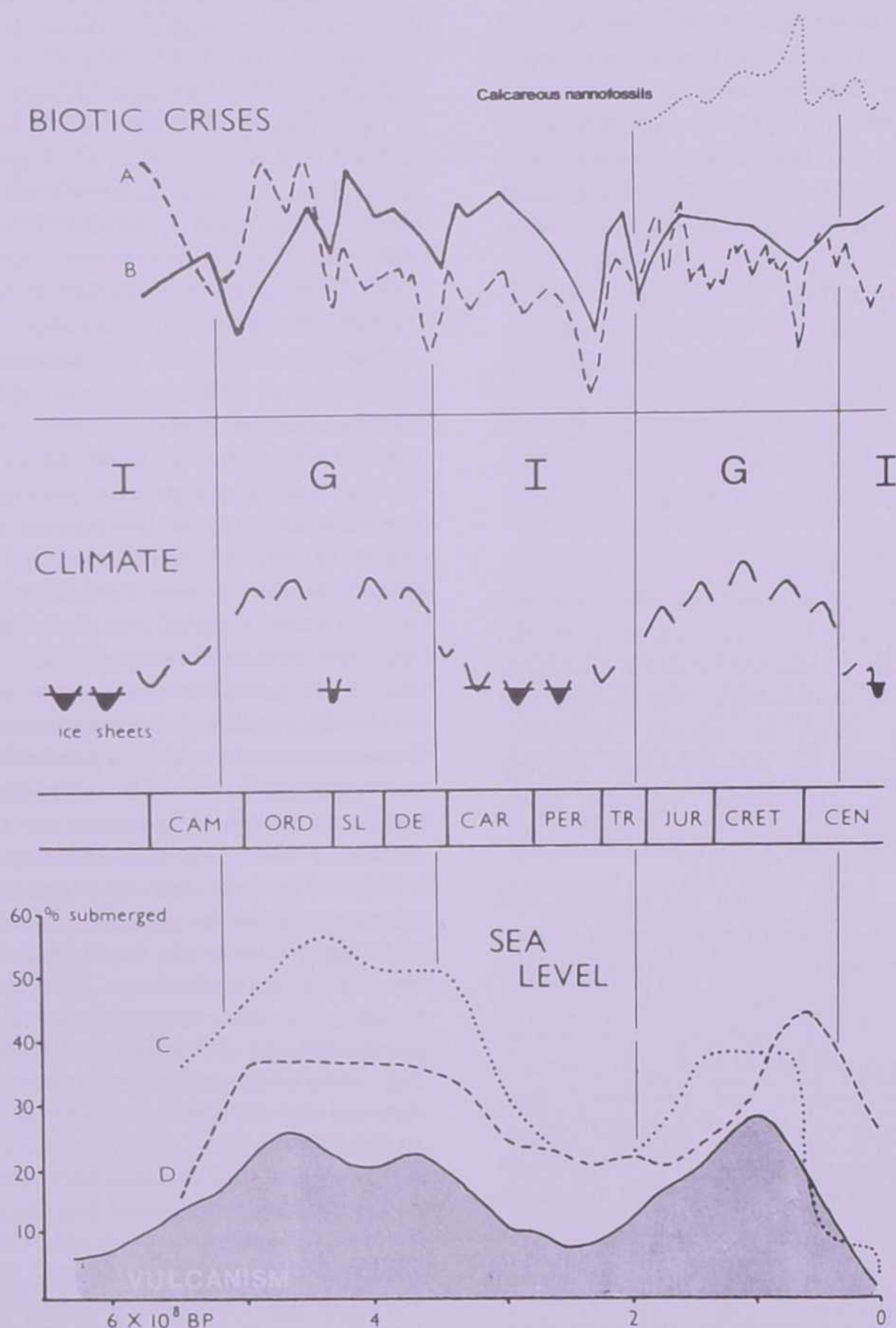


FIG. 8 - The Phanerozoic supercycles of FISCHER. After FISCHER, 1984, Fig. 7-1. Biotic diversity: A - after NEWELL (1967); B - after CUTBILL. Sea-level curves: C - after HALLAM (1977); D - after VAIL *et al.* (1977). Volcanism based on granite emplacement, after ENGEL (1964).

biotic development is also included in discussion of long term cyclicity by FISCHER (1982, 1984). Both authors recognize two broad cycles in the Phanerozoic characterised by coincident trends in biotic diversity, sea-level, physiography, vulcanism, and global temperature.

TAPPAN (1968) recognised two episodes of biotic development, the first, initiated in the Late Precambrian, which saw microfloras (particularly *Achritarcha*) increase through the Early Palaeozoic, reach a maximum during the Ordovician, followed by an extinction event in the Late Devonian. The second cycle began with phytoplankton increasing in the Triassic and Jurassic, reaching a maximum in the Late Cretaceous, and undergoing an extensive extinction event at the Cretaceous/Tertiary boundary. In both cases the maxima in marine microplankton (and other marine groups) coincided with peaks in sea level, volcanic activity, global temperatures and climatic equability. TAPPAN suggested that these microplankton fluctuations were controlled by nutrient availability. Nutrient depletion (and the ensuing extinctions) was caused by reduced atmospheric and oceanic cycling during prolonged periods of equable climate. This was compounded by reduced nutrient input from terrestrial sources due to lowered continental elevations.

FISCHER (1982) recognised similar long-term trends in climate, biotic crises, sea level, and vulcanism, and proposed an all-embracing model driven by mantle convection/seafloor spreading and controlled by atmospheric CO₂ content and sea level. The cycles he named "Icehouse-Greenhouse" cycles, the microplankton maxima occurring during "greenhouse" episodes, when high atmospheric CO₂ induced warm equable climates on a ice-free earth (Fig. 8).

ROTH (1987, 1989) studied the diversity and rates of evolution for Mesozoic calcareous nannofossils and identified a relationship between nannofossil evolution and oceanic circulation/fertility. Roth argued that diversification of nannofossils coincided with periods of high carbon accumulation (anoxic events) and postulated low nutrient conditions which led to increased competition and ensuing speciation. The fundamental driving mechanism was mantle derived; increased seafloor spreading resulting in rising sea-level (and related increase in planetary albedo) and increased atmospheric (volcanogenic) CO₂, which in turn induced climatic equability and water-mass stratification. Conversely, low sea-level stands generated high nutrient conditions and high productivity, leading to lower speciation rates and

possibly extinctions. PERCH-NIELSEN (1986) has also related nannofossil evolution to changes in sea-level.

The relationship between calcareous nannofossils and the exogenic system (including those presented above) will be discussed with reference to particularly significant events in their evolutionary history.

LATE TRIASSIC - FIRST APPEARANCE AND ORIGINS

The earliest confirmed and consistent record of calcareous nannofossils comes from the Upper Triassic (JAFAR, 1983; BOWN and LORD, 1990). Norian and Rhaetian assemblages were composed of nannoliths and small coccoliths (2-3 microns) and were of low diversity (1-6 species) and high abundance. Triassic nannofossils are presently known from Austria, southern Germany, Timor and Australia's northwestern shelf (ODP Leg 122). These occurrences infer at least a complete Tethyan distribution (*i.e.* oceanic) at this time.

The appearance of nannoplankton (the first occurrence of calcareous microplankton in the Phanerozoic fossil record) was an event of considerable significance in terms of both biology/ecology and oceanography/geology. The preceding Palaeozoic period has yielded only sparse evidence of marine microplankton. The organic-walled *Achritarcha* and *Prasinophyceae* alone appear to have occupied the phytoplanktonic niche, and their Palaeozoic record is scant and inconsistent. It is probable that other phytoplanktonic (and microplanktonic) groups were present in the Palaeozoic but left no fossil record due to little or no biomineralization. The only other microplankton known from this period are the zooplanktic radiolaria and tintinnids (TAPPAN and LOEBLICH, 1973). The marine ecosystem, comprising nannoplankton-microplankton-zooplankton, is only recognised in the fossil record following the Permian mass extinctions. The calcareous nannofossils thus take on particular significance, representing one of the first and fundamental building blocks of the oceanic ecosystem which evolved through the Mesozoic and Cenozoic to that seen in the Present Day.

The appearance and rise of nannoplankton also had profound implications for the physical environment, the most obvious of these being their ability to precipitate calcite and to fix CO₂. The widespread and successful exploitation of the marine photic zone by the nannoplankton (and other microplankton groups which arose as the Mesozoic proceeded) must have had an influential role in the ocean/atmosphere system in re-

sponse to their respiration, photosynthesis, nutrient uptake, and carbonate assimilation. Their effect on ocean chemistry, in particular the position of the CCD, is seen by at least the Late Jurassic (e.g. GARRISON and FISCHER, 1969). Any effect on atmospheric composition is less well understood but a significant contribution to atmospheric CO₂ is modelled by VOLK (1989).

The nature and/or existence of causal factors which triggered the first appearance and initial diversification of calcareous nannofossils are not immediately apparent. However, it is interesting to note that an almost identical history is recorded for dinoflagellates (WILLIAMS and BUJAK, 1985). This may indicate that the two events were not coincidental evolutionary episodes, but rather an evolutionary response to change(s) in the physical environment.

The Triassic environment was one of climatic, biotic, and tectonic instability. Climate had begun a long period of warming and drying following a major glacial period in the Late Palaeozoic-Permian (FRANKS, 1979). The biotic system was recovering from the catastrophic Late Permian extinction event; microplankton in particular appear not to have recovered from the Late Devonian extinctions and have an extremely scarce record from the Devonian to Permian (TAPPAN, 1968, p. 205). Tectonically, the breakup of Pangea led to oceanic instability, linked to the formation of many semi-isolated, hypersaline basins (BERGER *et al.*, 1984). In addition, sea-level had begun to rise following a low stand in the Permian. While this instability is perhaps reflected by Norian and Rhaetian extinction events in many marine fossil groups, it is against this background that calcareous nannoplankton first occur. Their appearance may be seen as a response to a recovering environment following a long period of stress, reflected in a number of major extinction events and generally low diversities. This period would correlate with a period of transition from FISCHER's icehouse to greenhouse conditions (FISCHER, 1984, p. 145) (Fig. 8). As climate, and the environment in general, improved and stabilized, the biota began to recover and evolutionary activity re-established older groups and initiated new ones which filled vacant niches. Nannofossils were one of these new groups which developed in response to this relaxation phenomenon.

Continued instability is indicated by nannofossil extinctions at the Triassic/Jurassic boundary, thirteen million years after the first appearance of the group. This significant extinction event removed the dominant nannolith lineages, appar-

ently leaving only one coccolith species (*Crucirhabdus primulus*) which survived into the Jurassic.

EARLY JURASSIC - COCCOLITHOPHORID DIVERSIFICATION

The earliest Jurassic assemblages were composed of the nannolith, *Schizosphaerella punctulata* and the "survivor" coccolith, *Crucirhabdus primulus*. The Hettangian saw low diversity and generally low abundance assemblages, locally abundant due to "blooms" of *Schizosphaerella*. During the Sinemurian, increase became more rapid (speciation rates of 7.5-21%) reflecting diversification of coccolithophorid lineages, and from this time on coccoliths were established as the dominant nannofossil group. The initial Jurassic radiation took place over the Hettangian to Early Toarcian interval (28 m.y.), occurring in two discrete steps; in the Sinemurian, and in the Pliensbachian-Early Toarcian.

The first step involved the coccolith lineage (or lineages) that survived the end-Triassic extinctions. These discolith coccoliths have been divided into two families (BOWN, 1987), Parhabdolithaceae and Zygodiscaceae, both of which were present in the Triassic. The two families diversified in the Hettangian and Sinemurian (rates of speciation between 7 and 21%) but declined in the Late Pliensbachian and Early Toarcian. The Zygodiscaceae continued through the Mesozoic and into the Cenozoic but was generally a conservative lineage of long-ranging taxa, e.g. *Tubirhabdus patulus*, *Zeugrhabdotus embergeri*, and *Z. erectus*. The Parhabdolithaceae declined rapidly in the Early Toarcian and became extinct in the Mid Jurassic, but gave rise to a new family, Stephanolithaceae, which diversified in the Mid and Late Jurassic and continued into the Cretaceous.

The second step saw extinctions in the discolith lineages which coincided with (and were possibly caused by) the appearance of new coccolithophorid lineages, characterised by radically different coccolith morphology, i.e. placoliths. The placolith group diversified rapidly through the Pliensbachian and Early Toarcian, giving rise to six new families by the end of the Early Jurassic (Fig. 9). The placolith families Biscutaceae and Watznaueriaceae were of particular importance.

The Biscutaceae lineage was an evolutionarily active one, diversifying rapidly and including considerable morphological variation. High rates of speciation (15-16%) in the Late Pliensbachian-Early Toarcian largely reflect increases within this group, including two new families, Podor-

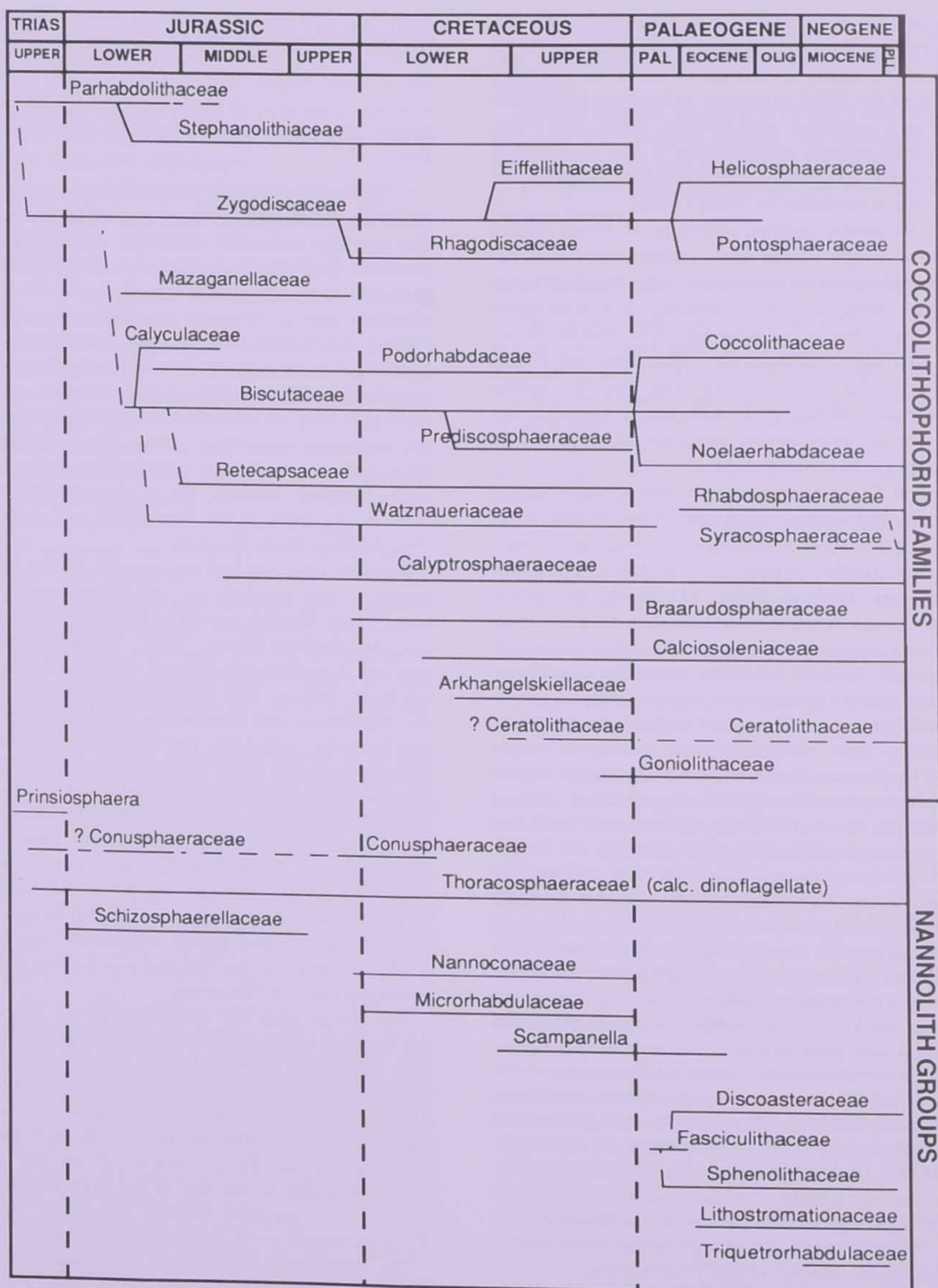


Fig. 9 - Phylogeny of the calcareous nannoplankton.

habdaceae and Calyculaceae. The Biscutaceae lineage continued conservatively through the Mesozoic and became evolutionarily active once again, following the terminal Cretaceous extinctions (Fig. 9).

The Watznaueriaceae was a conservative lineage, in terms of diversity and morphology, but its success in terms of numbers was profound. Numerically the most successful family of the Mesozoic, it dominated assemblages from the Toarcian (Early Jurassic) to the Tithonian (Late Jurassic), and continued into the Cretaceous and earliest Palaeocene.

By the Late Toarcian, nine coccolithophorid families were established (Parahabdolothaceae, Stephanolithaceae, Zygodiscaceae, Biscutaceae, Podorhabdaceae, Calyculaceae, Mazaganellaceae, Watznaueriaceae, Retecapsaceae) defining lineages from which the majority of remaining Mesozoic diversifications can be traced (BOWN, 1987) (Fig. 9).

Throughout this initial period of evolutionary development nannofossils appear to have colonised the marine environment worldwide. They are found throughout Tethys and its adjacent shelf seas, and though information is sparse, they have also been recorded from Pacific margins. Provincialism is apparent during the entire interval.

The location of evolutionary diversification in the Triassic and Early Jurassic appears to have been concentrated in the Mediterranean-Tethys region (BOWN, 1987). Although there was considerable tectonic instability during the Early Jurassic, this area of tropical to subtropical ocean appears to have provided optimum conditions for high abundance and high diversity nannofloras.

The re-establishment and diversification of nannofossils during this period reflects a stabilizing of the Jurassic environment as new ocean basins matured and climate continued to improve as greenhouse conditions became established.

MID JURASSIC

The Mid Jurassic saw the continuation of the trend established in the Early Jurassic for the progressive increase in the total number of species present (25 in the Aalenian increasing to 41 in the Callovian). However, the rate of speciation declined considerably, ranging from 0 to 7%, indicating a "background" type evolutionary rate rather than a continuation of the Early Jurassic radiation. Extinctions, similarly, occurred at back-

ground levels, always less than or equal to the number of new taxa (rate of extinction 0-4%). No new higher taxonomic groups were added (although holococcoliths have their first occurrence) and new appearances represented diversifications within the Stephanolithaceae, Podorhabdaceae, and Watznaueriaceae families. Species of *Watznaueria*, particularly *W. britannica*, numerically dominated assemblages.

LATE JURASSIC - EVOLUTIONARY RADIATION

Following a period of declining diversity in the Oxfordian and Kimmeridgian, a significant evolutionary radiation event was initiated in the Tithonian and continued into the Berriasian. This event coincided with the first occurrence of thick, nannofossil generated pelagic carbonates.

The Oxfordian and Kimmeridgian saw low rates of speciation and increased rates of extinction, which reduced the diversity at this time to around 30 species. Extinctions continued into the Tithonian, but here became masked by rapid speciation. The Late Jurassic extinctions were experienced in all but one coccolith family (Retecapsaceae), but were particularly prevalent in the Podorhabdaceae and Stephanolithaceae. The nanolith *Schizosphaerella* and the Family Mazaganellaceae both became extinct. The only Early Jurassic species to survive into the Cretaceous was *Zeugrhabdotus erectus*. Many genera became extinct including *Crepidolithus*, *Tubirhabdus*, *Lotharingius*, *Ansulasphaera*, *Hexapodorhabdus*, *Podorhabdus*, *Stephanolithion*, and *Triscutum*. The latest Tithonian was also marked by the sharp decline in the watznauerian coccoliths, *W. britannica*, and *W. manivittae*.

This period of extinction coincided with widespread tectonic instability in the Mediterranean-Tethyan region, as the Jurassic carbonate platforms rifted and subsided, and seafloor spreading proceeded (Piemont-Ligurian Ocean). Although the Late Jurassic was a time of regression, the latest Tithonian and earliest Berriasian interval is associated with a period of nannofossil diversification.

The Tithonian-Berriasian diversification was characterised by two main features:

- a) rapid speciation in the coccolith family Retecapsaceae - Early-Mid Jurassic species, *Retecapsa incompta* and *Polypodorhabdus escaigii*, gave rise to the genera *Cretarhabdus*, *Microstaurus*, *Cruciellipsis*, *Speetonia*, and *Grantarhabdus*;
- b) the cryptogenic appearance of many new and apparently unrelated nanolith groups, e.g.

Nannoconus, *Braarudosphaera*, *Conusphaera*, *Polycostella*, *Micrantholithus*, *Lithraphidites*, *Rucinolithus*, and *Hexalithus*.

Nannoconus was particularly successful in terms of both diversity and abundance and the pelagic carbonates seen at this time are mainly attributable to their abundance. Despite the immediate success of nannoconids, their distribution was initially restricted to Mediterranean-Tethys, as were the nannofossil carbonates.

As for the Triassic and Early Jurassic radiations, it appears that the environmental conditions in the Mediterranean-Tethys (and proto-Atlantic) encouraged both diversification and abundance of nannofloras at this time. Speciation may also have resulted from increased biogeographic differentiation which, though weak during the Mid Jurassic, was re-established in the Late Jurassic (COOPER, 1989). The large, zonal Tethys Ocean, and particularly its western termination, was clearly a profound influence on the development of calcareous nannofossils during the Mesozoic. This is particularly well demonstrated in the Tithonian, when many new species evolved in the Mediterranean-Tethys region and remained there, or were not found elsewhere, until considerably later.

The latest Tithonian and Berriasian saw the rejuvenation of many of the Jurassic coccolith lineages, e.g. *Podorhabdaceae* and *Stephanolithiaceae*, and the introduction of new families, such as the *Rhagodiscaceae*.

In the Late Jurassic, a major shift in carbonate production from shallow shelf seas to the open ocean is recorded (the "Kuenen Event" of ROTH (1989)). This event was explained by ROTH (1986) in terms of nannofossil migration from the shelf to open ocean areas. This hypothesis appears counter to available evidence that nannofossils were widely distributed in the marine environment from the earliest Jurassic onward, and that the loci of evolutionary activity at this time was in the more open Mediterranean-Tethys seaway. While the absence of truly oceanic sediments of Early to Mid Jurassic age prevents conclusive proof of this, their presence in shelf and marginal basins worldwide infers their widespread distribution throughout this period. It is more likely that the onset of nannofossil carbonate sedimentation reflected increased productivity, particularly attributable to the successful rise of the new nannolith groups *Nannoconus* and *Conusphaera*. The increased nannofossil productivity also coincided with, and probably resulted in, increasingly favou-

rable conditions for the deposition and preservation of calcite in the deep sea, i.e. lowering of the CCD.

The deposition of pelagic carbonates marked the end of a shift from carbonate deposition concentrated on shelf areas and attributable to benthic invertebrates (typical of the Palaeozoic ecosystem) to pelagic carbonate deposition in more open ocean areas, attributable to planktonic protistan organisms.

EARLY CRETACEOUS

Diversification continued in the Berriasian and speciation was renewed in most of the coccolith lineages (after their Late Jurassic decline) as well as the newly established nannolith groups. Two new loxolith families have first occurrences, *Rhagodiscaceae* and *Eiffelolithaceae*. Speciation dropped down to background levels in the Valanginian but absolute species numbers continued to rise, reaching 85 in the late Hauterivian. A sharp drop in diversity occurred in the early Barremian and numbers were variable until the mid Albian, when steady increase was again the prevalent trend. The Aptian interval saw the first occurrence of the important coccolith family *Arkhangelskiellaceae*, whose ancestry is uncertain, and the *Prediscosphaeraceae*, which is thought to have biscutatean affinities. A number of new nannolith groups also appeared including *Hayesites*, *Scampanella*, and ceratoliths.

LATE CRETACEOUS - DIVERSITY MAXIMUM

The Late Cretaceous was a time of both high diversity and high productivity for calcareous nannoplankton. Steady increases in diversity (variable but low rates of speciation and extinction) were accompanied by the deposition of nannofossil generated pelagic carbonates over large areas (i.e. Europe, North Africa, North America and Australia). A warm, equable, stable climate and high sea-levels appear to have provided optimum conditions for high nannofloral productivity and continued diversity increase. The onset of climatic deterioration, beginning in the latest Cretaceous (Fig. 8), is reflected in increasing rates of extinction, decreasing rates of speciation, and negative values of diversification in the Campanian and Maastrichtian.

Cyclicity in the peaks of speciation and extinction in the Cretaceous has been described by ROTH (1987), but the frequency is quite variable (10-30 m.y. in ROTH; 7-17 m.y. extinctions, 12-14 m.y. speciations, from the present data). ROTH al-

so recognised a relationship between periods of oceanic anoxia (sea-level and nutrients) and increases in rates of speciation. The relationship between transgressions and anoxia, and periods of increased speciation is not particularly confirmed by our results (see also the relationship between sea level and nannofossil evolution presented by PERCH-NIELSEN, 1986).

The high rates of speciation recorded for the Early Cenomanian coincided with the onset of chalk deposition and thus may be partly preservational. However, deposition of the chalk is thought to reflect a transgressional phase and this, along with favourable conditions for increased productivity, may explain the speciation event at this time.

CRETACEOUS/TERTIARY BOUNDARY - EXTINCTIONS

The highest extinction rate in nannofossil history is recorded at the Cretaceous/Tertiary boundary (92%) and diversity dropped from 106 species in the Late Maastrichtian to 14 species in the earliest Palaeocene. Atypical bloom assemblages occurred immediately following the extinction episode and are often characterised by the sequential dominance of *Thoracosphaera*, *Braarudosphaera* and, in high latitude regions, *Cyclagelosphaera*. These occur along with rare coccolithophorid and nannolith "survivors" and new nannolith species, e.g. *Biantholithus sparsus* and *Micrantholithus altus*. The ancestry of most of the new coccolith families can be demonstrated, however they possess morphologies quite different to those seen in the preceding stage.

The nannofossil record from the Maastrichtian and Palaeocene clearly reflects a period of great biotic and physical crisis. High extinction rates and declining diversity occur in the Maastrichtian, followed by a rapid and catastrophic extinction episode at the Cretaceous/Tertiary boundary. The initial decline may be attributed to climatic deterioration which marked the end of the Mesozoic greenhouse phase. However, the dramatic decline at the boundary appears to call for more accelerated change, such as those envisioned by the bolide impact or increased volcanic activity hypotheses (HALLAM, JABLONSKI *in* BRIGGS and CROWTHER, 1990). The earliest Palaeocene bloom assemblages were mostly composed of three long-ranging survivor groups which were probably eurytopic and opportunistic; two of the three normally displaying neritic distribution. The two important coccolith families, which went on to form Cenozoic lineages, were similarly long-ranging

and evolutionarily rather conservative, although the species survivors themselves originated in the Maastrichtian when environmental instability was already apparent. It is likely that the majority of Late Cretaceous species were specialised and stenotopic, having originated during the equable, stable conditions of the late Mesozoic and unable to survive the declining, and ultimately severe, environmental condition which marked the end of the Cretaceous.

EARLY PALAEOCENE - EVOLUTIONARY RADIATION

Following the "bloom" assemblages of the Cretaceous/Tertiary boundary interval, more "normal" nannofloras were re-established and included Mesozoic "survivors" (e.g. *Biscutum*, *Cyclagelosphaera*, *Chiastozygus*, *Placozygus* and *Neocrepidolithus*) and "new" Tertiary forms (e.g. *Prinsius*, *Cruciplacolithus* and *Biantholithus*). Nannoplankton were re-established via an evolutionary radiation of great rapidity and diversity. It appears that three coccolithophorid families (represented by 10 or so species) survived the extinction, along with a number of long-ranging nannolith groups (Fig. 9); around 14 survivor species in all. One hundred and seven new species appeared in the Palaeocene, giving a speciation rate of 8.5 species/m.y. (over 12.5 m.y.). This contrasts with a rate of 1.7 species/m.y. (over 28 m.y.) during the Early Jurassic radiation.

As in the Early Jurassic radiation, it was coccolithophorids that quickly became established as the dominant nannofossil group. The Watznaueriaceae, Zygodiscaceae and Biscutaceae families, which were established in the Early Jurassic, survived the boundary event and the latter two families formed the basis for Early Palaeocene coccolithophorid diversification (Fig. 9).

Biscutaceae. The Biscutaceae formed an evolutionarily active lineage, as it did in the Early Jurassic, and the placolith structure was once more established as the dominant coccolith morphology. In the earliest Palaeocene very small and simple species of *Biscutum* gave rise to the *Prinsius*-*Toweius*-*Reticulofenestra* (Noelaerhabdaceae) lineage (ROMEIN, 1979; GALLAGHER, 1989). This pattern of coccolith evolution comprised progressive increase in structural complexity and increasing shield birefringence (reflecting changing crystallographic orientation). Such a trend is almost identical to that seen in the Early Jurassic, when *Biscutum* gave rise to watznaueriacean coccoliths, whose architecture is similar to the reticu-

lofenestrids. These two lineages were numerically dominant in the Mesozoic and Cenozoic, respectively.

A second lineage of the Biscutaceae saw small *Sollasites*-like coccoliths give rise to *Cruciplacolithus primus* and *Cruciplacolithus inaequalis* in the Early Palaeocene, followed by *Chiasmolithus* and possibly *Ericsonia*.

The genus *Markalius* is here placed within the Biscutaceae due to the direction of suture inclination on the distal shield, the unicyclic nature of the distal shield, and its birefringent properties, i.e. nonbirefringent distal shield and birefringent proximal shield. *Markalius* survived the extinction event and continued through into the Oligocene, but was evolutionarily conservative.

Zygodiscaceae. Three genera of the discolith family Zygodiscaceae crossed the Cretaceous/Tertiary boundary, *Placozygus*, *Chiastozygus* and *Neocrepidolithus*. *Chiastozygus*, represented by the species *C. ultimus*, gave rise to the genus *Neochiastozygus*, with 15 species present by the mid Palaeocene. The genera *Neococcolithes* and *Chiphragmalithus*, which appeared in the Early Eocene, may also be descendants of the *Chiastozygus* lineage. *Placozygus sigmoides* was a common component of boundary interval nannofloras and continued through the Palaeocene. It appears likely that it gave rise to the *Zygodiscus* lineage in the Late Palaeocene. The third zygodiscacean survivor genus, *Neocrepidolithus*, first appeared in the Late Maastrichtian and diversified in the Early Palaeocene.

The survivor families which formed the basis for Tertiary coccolithophorid diversification all stemmed from the Early Jurassic, however, the individual species involved first appeared in the Maastrichtian. It appears likely that these taxa, which originated in a period of increasing environmental stress (e.g. as climate deteriorated at the end of the Mesozoic greenhouse phase), were better able to survive the boundary crisis conditions and to then form new lineages.

Watznaueriaceae. The third coccolith family which survived the crisis, Watznaueriaceae, included very long ranging species which originated during more stable conditions (e.g. *Cyclagelosphaera magerelii*). These species crossed the boundary but were evolutionarily static and became extinct by the end of the Palaeocene.

Nannoliths. In addition to the diversification of survivor Mesozoic coccolithophorid lineages, the Palaeocene radiation also included the appearance of many new, important nannolith groups, e.g. *Fasciculithus*, *Heliolithus*, *Bomolithus*, *Sphenoli-*

thus, and *Discoaster*. The ancestry and relationships between many of these groups is not well understood.

Incertae Sedis and others. A number of long-ranging incertae sedis and atypical coccolithophorid groups also survived the Cretaceous/Tertiary boundary extinction, including *Lapideacassis*, *Scampanella*, *Octolithus*, *Goniolithus*, *Scapholithus* (Calciosoleniaceae), *Semihololithus* (Calyptrerosphaeraceae), *Braarudosphaera/Micrantholithus* and *Thoracosphaera* (calcareous dinoflagellate). With the exception of the latter two groups, these genera have scarce and inconsistent records and are evolutionarily conservative.

PALAEOCENE - RECENT

The Cenozoic nannofossil record generally reveals greater variability in diversity and higher levels of speciation and extinction rates than the preceding Mesozoic. The major evolutionary events following the Palaeocene radiation include a dramatic decline in diversity in the Late Eocene-Oligocene, and a diversity rise in the Early Miocene. Diversity peaks are recorded for the Late Palaeocene (NP9), Mid Eocene (NP15), Early Miocene (NN1, NN5), Late Miocene (NN11), and Early Pliocene (NN15). Diversity troughs are seen in the Early Eocene (NP10-11), Oligocene, Mid Miocene (NN6-7), and Early Pliocene (NN14) (Fig. 4).

Following the Palaeocene radiation, nannoplankton development was characterised by the appearance and rise to dominance of the *Reticulofenestra* group, and the appearance of the families *Helicosphaeraceae*, *Pontosphaeraceae*, and *Ceratolithaceae*. Despite a dip in diversity following NP5, the general trend to the end of the Palaeocene was one of increase, to a peak of 68 species in NP9. The earliest Eocene saw diversities initially lowered, as many Palaeocene stocks became extinct and inceptions were scarce. Increase became rapid in the Early Eocene and diversities were highest in the Mid Eocene, NP15 (rate of speciation 32%), when more first occurrences were observed than at any other time in the Cenozoic (extinctions were also high at this time). Speciation was particularly high in the genera *Reticulofenestra*, *Chiasmolithus*, *Sphenolithus*, *Nannotetrina* and *Rhabdosphaera*. The lowest diversities of the Cenozoic, 27 species, characterised nannofloras in the Oligocene. The Miocene saw a recovery from the Oligocene decline and rejuvenation of many of the existing lineages (e.g. *Sphenolithus*, *Reticulofenestra*, *Discoaster*, *Heli-*

cosphaera and *Scyphosphaera*). Diversity reached 73 species in NN5 but the overall trend following this was one of decrease through the Pliocene and into the Pleistocene.

The increased evolutionary variability through the Cenozoic appears to be related to climatic deterioration, *i.e.* cooling, which occurred throughout this interval, as icehouse conditions became established. Climate was highly variable throughout the Cenozoic with pronounced cooling in the Mid Miocene and Late Pliocene; and warming in the Late Eocene, Late Oligocene to Early Miocene, and Late Miocene (FRAKES, 1979). All of these climatic changes are reflected by nanoplankton diversity changes, the most obvious being the long period of declining diversity from the Mid Eocene to Oligocene, which coincided with the greatest temperature drop of the Cenozoic (FRAKES, 1979). The rise in diversity observed in the Early Miocene is similarly coincident with a period of significant warming. These parallel trends in temperature and diversity may be the best evidence for the role of climate as the major factor controlling the evolution and diversity of oceanic plankton.

The mechanism by which temperature controls nanoplankton diversity is uncertain but may be grossly related to the expansion and contraction of regions of optimum environmental conditions for high diversity. At present, nanoplankton are most diverse in low-latitude, stable, oligotrophic conditions (Jeremy YOUNG *pers. comm.*, 1990) and it is conceivable that such habitats are much reduced as climate deteriorates and oceanic circulation is increased. Such conditions may lead to increased extinction rates and/or reduced speciation and the promotion of high abundance, low diversity assemblages which typify high latitudes and upwelling zones. Reduced sea-level at these times may similarly affect nanoplankton groups with neritic distribution, although this is thought to be a subordinate controlling factor. The impact of climatic variation on nanoplankton groups may be illustrated by low-latitude taxa, *e.g.* Discoasteraceae and Sphenolithaceae, which originated in the Palaeocene and became essentially cosmopolitan in the Eocene, before becoming gradually more restricted in distribution in the Oligocene-Miocene and extinct in the latest Pliocene.

CONCLUSIONS

1. The evolutionary history of calcareous nanofossils is broadly comparable to that of many other marine planktonic groups (TAPPAN, 1968)

and may be related to the mega-cycles of FISCHER (1982). The cycles are fundamentally mantle driven but relate to the biosphere through changes in climate (levels of CO₂, equability, atmospheric/oceanic circulation, nutrients) and tectonics (sea-level, nutrients).

2. The first appearance, Triassic/Jurassic boundary extinctions, and Early Jurassic radiation of calcareous nanofossils occurred during a time of transition from an unstable climatic and tectonic regime to one of progressively greater stability. The establishment and steady increase in diversity and productivity reflected the development of equable, stable, "greenhouse" conditions in the Mesozoic.

3. An evolutionary radiation at the end of the Jurassic included the inception of important new nannolith groups and high levels of productivity. This event completed the shift in carbonate deposition from benthic shelf areas to more open sea and ocean. This trend was further compounded by the diversification of planktonic foraminifera through the Cretaceous.

4. Stable climatic and environmental conditions led to gradually increasing diversities throughout the Cretaceous, reaching peaks in the Cenomanian (coinciding with the onset of chalk deposition) and in the Late Campanian.

5. Decreasing rates of diversification towards the end of the Cretaceous appear to reflect the onset of environmental instability as climatic equability began to break down. Catastrophic extinctions experienced at the Cretaceous/Tertiary boundary were accompanied by bloom assemblages indicating crisis conditions.

6. The species which survived the Cretaceous/Tertiary boundary event and gave rise to evolutionarily active lineages all stemmed from the Late Cretaceous during the regime of increasing environmental instability.

7. The Palaeocene radiation was far more rapid and diverse than the initial Early Jurassic radiation. In both cases the Biscutaceae lineage was the most important in terms of numbers and morphological development. In both cases similarly constructed coccoliths became the dominant forms, watznauerian coccoliths in the Mesozoic, and reticulofenestrid coccoliths in the Cenozoic.

8. The Cenozoic development of calcareous nanofossils does not show the same trend of generally increasing diversity as seen through the Mesozoic. The development was more variable and the levels of diversity seen in the Late Mesozoic were never again attained in the Tertiary. This variability in development reflects environ-

mental instability as climate and sea-level responded to global cooling and warming through this "icehouse" interval.

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REFERENCES

- APPLEGATE J.L. and BERGEN J.A., 1989 - *Cretaceous calcareous nannofossil biostratigraphy of sediments recovered from the Galacia margin, ODP LEG 103*. In G. BOILLOT, E.L. WINTERER *et al.*, Proceedings of the Ocean Drilling Program, Scientific Results, v. 103, pp. 293-326, College Station.
- AUBRY M.P., 1985 - *Handbook of Cenozoic calcareous nannoplankton, Book 1: Ortholithae (Discoasters)*. Micropaleontology handbook series, 266 pp., Micropaleontology Press, New York.
- AUBRY M.P., 1988 - *Handbook of Cenozoic calcareous nannoplankton, Book 2: Ortholithae: holococcoliths, ceratoliths, and others*. Micropaleontology handbook series, 279 pp., Micropaleontology Press, New York.
- AUBRY M.P., 1989 - *Handbook of Cenozoic calcareous nannoplankton, Book 3: Ortholithae (Pentaliths, and others), Heliolithae (Fasiculiths, Sphenoliths, and others)*. Micropaleontology handbook series, 279 pp., Micropaleontology Press, New York.
- BERGER W.H., FUCHTBAUER H., HOLLAND H.D., HOLSER W.T., JENKINS W.J., KULKE H.G., LASAGA A.C., SARNTHEIN M., SEILACHER A., VALETON I., WALLISER O.H. and WEFER G., 1984 - *Short-term changes affecting atmosphere, oceans, and sediments during the Phanerozoic*. In H.D. HOLLAND and A.F. TRENDALL (Eds.), Patterns of Change in Earth Evolution, Dahlem Konferenzen 1984, pp. 171-205, Springer-Verlag, Berlin.
- BOWN P.R., 1987 - *Taxonomy, biostratigraphy and evolution of late Triassic-early Jurassic calcareous nannofossils*. Special Papers in Palaeontology, v. 38, pp. 1-118, Oxford.
- BOWN P.R., COOPER M.K.E., and LORD A.R., 1988 - *A calcareous nannofossil biozonation scheme for the Early to Mid Mesozoic*. Newsletters on Stratigraphy, v. 20 (2), pp. 91-114, Berlin-Stuttgart.
- BOWN P.R. and LORD A.R., 1990 - *The occurrence of calcareous nannofossils in the Triassic/Jurassic boundary interval*. Proceedings of the Triassic/Jurassic Boundary Working Group, Lyon 1988. Cahiers Univ. Catho. sér. Sci., n. 3, p. 127-136, Lyon.
- BRIGGS D.E.G. and CROWTHER P.R., 1990 - *Palaeobiology, a synthesis*. Pp. 1-583, Blackwell Scientific Publications, Oxford.
- COOPER M.K.E., 1989 - *Nannofossil provincialism in the Late Jurassic-Early Cretaceous (Kimmeridgian to Valanginian) period*. In J.A. CRUX and S.E. VAN HECK (Eds.), Nannofossils and their applications, pp. 223-246, Ellis Horwood, Chichester.
- FISCHER A.G., 1982 - *Long-term climatic oscillation recorded in stratigraphy*. In W.H. BERGER and J.C. CROWELL (Eds.), Climate in Earth History, National Academic Press, pp. 97-104, Washington DC.
- FISCHER A.G., 1984 - *The two Phanerozoic supercycles*. In W.A. BERGGREN and J.A. VAN COUVERING (Eds.), Catastrophes and Earth History, Princeton University Press, pp. 129-150, Princeton.
- FRAKES L.A., 1979 - *Climates throughout geologic time*. Elsevier Scientific Publishing Company, 310 pp., Amsterdam.
- GARRISON R.E. and FISCHER A.G., 1969 - *Deep-water limestones and radiolarites of the Alpine Jurassic*. In FRIEDMAN G.M. (Ed.), Depositional Environments in Carbonate Rocks, A. Symposium, Soc. Econ. Paleont. Mineral., Spec. Publ., v. 14, pp. 20-56, Tulsa.
- GALLAGHER L.T., 1989 - *Reticulofenestra: A critical review of taxonomy*. In J.A. CRUX and S.E. VAN HECK (Eds.) Nannofossils and their applications, pp. 41-75, Ellis Horwood, Chichester.
- GOY G., 1981 - *Nannofossiles calcaires des schistes carton (Toarcien inférieur) du Bassin de Paris*. Documents de la RCP 459, éditions BRGM, 86 pp., Paris.
- JAFAR A.S., 1983 - *Significance of Late Triassic calcareous Nannoplankton from Austria and Southern Germany*. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 166 (2), pp. 218-259, Stuttgart.
- LORD A.R. (Ed.), 1982 - *A stratigraphical index of calcareous nannofossils*. British Micropaleontological Society Series, 192 pp., Ellis Horwood, Chichester.
- PERCH-NIELSEN K., 1985 - *Mesozoic calcareous nannofossils*. In H.M. BOLLI, J.B. SAUNDERS and K. PERCH-NIELSEN (Eds.), Plankton Stratigraphy, Cambridge University Press, pp. 329-426, Cambridge.
- PERCH-NIELSEN K., 1986 - *Geologic events and the distribution of calcareous nannofossils - some speculations*. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine, v. 10, pp. 422-432, Pau.
- PRINS B., 1969 - *Evolution and stratigraphy of coccolithinids from the Lower and Middle Lias*. In P. BRONNIMANN and H.H. RENZ (Eds.), Proceedings First International Conference on Planktonic Microfossils, Geneva 1967, v. 2, pp. 547-558, Leiden.

- PRINS B., 1971 - *Speculations on relations, evolution and stratigraphic distribution of discoasters*. In A. FARINACCI (Ed.), *Proceedings II Planktonic Conference*, Roma, 1970, pp. 1017-1037, Edizioni Tecnoscienza, Roma.
- ROMEIN A.J.T., 1979 - *Lineages in early Paleogene calcareous nannoplankton*. *Utrecht Micropaleontological Bulletins*, v. 22, pp. 1-231, Utrecht.
- ROTH P.H., 1986 - *Mesozoic palaeoceanography of the North Atlantic and Tethys oceans*. In C.P. SUMMERHAYES and N.J. SHACKLETON (Eds.), *North Atlantic Palaeoceanography*, Geological Society Special publication, v. 21, pp. 299-320, Blackwell, Oxford.
- ROTH P.H., 1987 - *Mesozoic calcareous nannofossil evolution: relation to paleoceanographic events*. *Paleoceanography*, v. 2, pp. 601-611, Washington.
- ROTH P.H., 1989 - *Ocean circulation and calcareous nannoplankton evolution during the Jurassic and Cretaceous*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 74, pp. 111-126, Amsterdam.
- TAPPAN H., 1968 - *Primary production, isotopes, extinctions and the atmosphere*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 4, pp. 187-210, Amsterdam.
- TAPPAN H. and LOEBLICH A.R., 1973 - *Evolution of the oceanic plankton*. *Earth-Science Reviews*, v. 9, pp. 207-240, Amsterdam.
- VOLK T., 1989 - *Sensitivity of climate and atmospheric CO₂ to deep ocean and shallow-ocean carbonate burial*. *Nature*, v. 337, pp. 637-639, London.
- WILLIAMS G.L. and BUJAC J.P., 1985 - *Mesozoic and Cenozoic dinoflagellates*. In H.M. BOLLI, J.B. SAUNDERS and K. PERCH-NIELSEN (Eds.), *Plankton Stratigraphy*, pp. 847-964, Cambridge.