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SOME FEATURES OF NANNOFLORA DEVELOPMENT IN THE CENOZOIC ATLANTIC AND INDIAN OCEANS

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Palabras clave: Paleógeno, Neógeno, Cuaternario, Nannofósiles calcáreos (variaciones), Paleocéanografía.

ABSTRACT: Specific and generic compositions of Cenozoic Calcerous Nannoplankton from bottom sediments of the Atlantic and Indian oceans are analyzed, based on deep-waters drilling data. Eleven stages in the development of the Nannoflora are recognized, based on changes in generic composition through time. Rates of evolution in the Paleogene, Neogene and Quaternary periods were counted. It was found that rates of evolution of Calcareous Nannoplankton varied: the intervals between 60-45 and 20-4

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million years ago (m.a) were characterized by accelerated evolution, indicating favorable conditions for the development of nannoplankton. The marked worsening of conditions, retarded rates of evolution and reduced tempo of evolution were 65 and 40-15 m.a. The most abrupt changes in species and genus composition occurred 65 and 1,8 m.a. and less pronounced changes occurred 18-17, 15-14 and 5-4 m.a.

RESUMEN: Se analizan las composiciones específica y genérica del Nannoplancton calcáreo del Cenozoico en muestras de los océanos Atlántico e Índico. Se reconocen 11 etapas en el desarrollo de la Nannoflora, deducidas a partir de los cambios en la composición genérica a lo largo del tiempo. Se muestran etapas de la evolución el Paleógeno, Neógeno y Cuaternario. Se deduce que estas etapas de evolución del Nannoplancton Calcáreo ha variado en el intervalo entre 60 y 45 millones de años (m.a.) y entre 20 y 4 m.a., caracterizándose por una evolución acelerada, que indica condiciones favorables para el desarrollo del nannoplancton. Se produjeron fuertes empeoramientos de las condiciones, etapas de evolución retardadas, y tiempos reducidos de evolución en los 65 y entre 40 y 15 m.a. Los cambios más drásticos en la composición de especies y géneros ocurrieron hace 65 y 1,8 m.a., y los menos pronunciados entre los 18 y 17, 15 y 14 y los 5 y 4 m.a..

INTRODUCTION

The determination of the stages in the history of the Earth implies study of many different abiotic and biotic factors. Now a great amount of paleontological data are available about the development of different organisms in time. They were developing fast or slow, in great or little abundant of forms, species and genera. These parameters correlate very strong with biological productivity, with carbonate production, with very many properties of the biotic and abiotic nature. The boundaries of the development stages usually correlate with changes in litology, tectonics, stratigraphy, climate, and others. The researches of rates of the evolution rates and stages in the development of different organisms help to determine their synchronicity and work out more accurate stratigraphy relationships.

The major change of calcareous nannoflora species and genera took place across the Danian-Maastrichtian boundary. A marked reduction in the abundance and species diversity of the calcareous nannoplankton has been shown in the Danian and Paleocene. Only not many species went through the Maastrichtian to Danian (BRAMLETTE, 1965; HAQ, 1973; POSPICHAL & WISE, 1990, etc.).

PREVIOUS WORKS

BUKO (1979) after STEHLI *et al.*(1969) and STEHLI & WELLS (1971) worked out the thesis about the close connection between taxonomic diversity, high temperatures and high rates of the appearence of new species. BUKO suggested the following definitions:

1) the taxonomic evolution is the change of the number of taxa;

2) the rate of evolution is the common number of new taxa in a specifical time interval;

3) the rate of speciation is the number of new species in a unit of time;

4) the rate of the extinction is the number of the species extinction in a unit of time.

ROTH (1987) used the following indices: species diversity, rate of speciation, rate of extinction, rate of diversification, rate of turnover, survivorship and species accretion. The positive diversification rates are those where the rate of speciation exceeds the rate of extinction.

The corellation of evolutionary tempos and number of taxa with temperature was noted by STRELNIKOVA (STRELNIKOVA, 1991) for marine Cretaceous and Paleogene diatoms, and by NEVESSKAJA & AMITROV (Oral presentation, PALEONTOLOGY INSTITUTE AC. SCI. RUSSIA, 1993) for Cenozoic marine molluscs. The number of species and genera of bivalvia and gastropoda, and their rate of appearance and extinction are higher in the Paleogene than in the later epochs.

The stages in the development of Paleogene nannoflora were studied by MUSILEV (1978) and KOSHKARLY (1981). They distinguished up to 5 stages, and we used their results in this work.

MATERIAL AND METHODS

Deep Sea Drilling records (INIT. REPTS. OF THE DSDP, 1969-1983) show that there were more than 500 species of Nannofossils in the Atlantic and Indian oceans during the Cenozoic. These species and genera compositions were analyzed within 9 intervals at 5 Ma spacing for the Paleogene, and within 10 time intervals in the Neogene and Quaternery periods, following the scales of MARTINI and BUKRY (MARTINI, 1970; BUKRY, 1978; OKADA & BUKRY, 1980; Table 1 in DMITRENKO, 1992). Eleven species of more than 100 living during the Cretaceous continued through the Maastricht-Danian boundary in two oceans. New genera and species of the Cenozoic develop during the different periods of time: from several hundred Ma up to more than 60 Ma.

The stages in the development of Cenozoic nannoflora were studied by analysis of nannoplankton genera composition change. The phylogenetic lineages were reconstructed for many genera of nannoplankton, but the relationship connections between different genera and families were not studied. Consequently we are establishing the differente changes from one genus to another, but the genera do not belong in the same phylogenetic branch. We were able to use only a change of phylogenetic line in the *Discoaster* morphotypes. We distinguish 5 major stages and 11 minor ones in the development of the Cenozoic Nannoflora on the basis of the changes in generic associations.

The study of evolutionary tempos is based on common abundance of fossils, on the number of different taxa, and especially generic and specific diversity. The number of appearances and extinctions of taxa defines the rates of evolution. The rate of speciation (of origination) is the number of species appearance in a million years. The rate of extinction is the number of species disappearances in a million years.

The sum of these rates is the rate of the taxonomic composition change (NEVESSKAYA & AMITROV, 1993). The difference of these rates is the rate of diversification (ROTH, 1987). This difference can be positive or negative. Evolution is positive if the rate of speciation exceeds the rate of extinction. Evolution is negative, if the rate of disappearance exceeds the rate of origination.

RESULTS

Figure 1 shows taxonomic evolution of the nannoflora — the development of different genera in the Cenozoic. On this basis 11 stages were evaluated in the Cenozoic..

The Early Paleocene, 65 Ma, was unique in the development of calcareous nannoplankton. B.HAQ (1973) noted that it lasted until the end of Early Paleocene. The first *discoaster*s appeared in the Atlantic and Indian oceans during the Paleocene: 65-60 Ma, there were three to four species. Later, towards the end of the Paleocene epoch, *discoaster*s underwent rapid speciation. The Paleocene is characterized by the presence of species of *Hornibrookina, Toweius, Fasciculithus, Heliolithus, Cruciplacolithus* and also *Marthasterites* and genera of the **Zygodiscaceae** family, some of which continued their evolution from the Mesozoic. Most of these genera survived into the Early Eocene (see fig. 1).

The Eocene was the apogee of the diversification of the Cenozoic calcareous nannoflora. During this time species diversity and evolutionary rates were at their highest levels. During the Eocene the development of the family **Zygodiscaceae** continued, though the number of species declined sharply, and toward the Oligocene the family became extinct. *Heliolithus* underwent pronounced changes, becoming rare and losing its stratigraphic importance. *Fasciculithus* and *Marthasterites* continued to exist, and in the Early Eocene *Toweius* was also present, although it became extinct towards the Middle Eocene. Species of *Calcidiscus* and *Cyclicargolithus* appeared, and *Helicosphaera, Discolithina, Chiasmolithus* and *Sphenolithus* achieved high diversities. The highest species diversities were achieved by *Discoaster* and *Coccolithus.*

Beginning 40 Ma and continuing into the Oligocene, a sharp deterioration of environmental conditions brought about a rapid decline in species diversity and a reduction in rates of evolution. Toward the Oligocene species of *Fasciculithus, Zygolithus* and *Zygodiscus* became extinct, and the species diversities of *Ericsonia, Chiasmolithus, Discoaster, Coccolithus* and *Braarudosphaera* decreased. The number of *Pontosphaera, Sphenolithus* and *Reticulofenestra* increased. The maximum of the *Discoaster* species number took place at 10 Ma, and the number

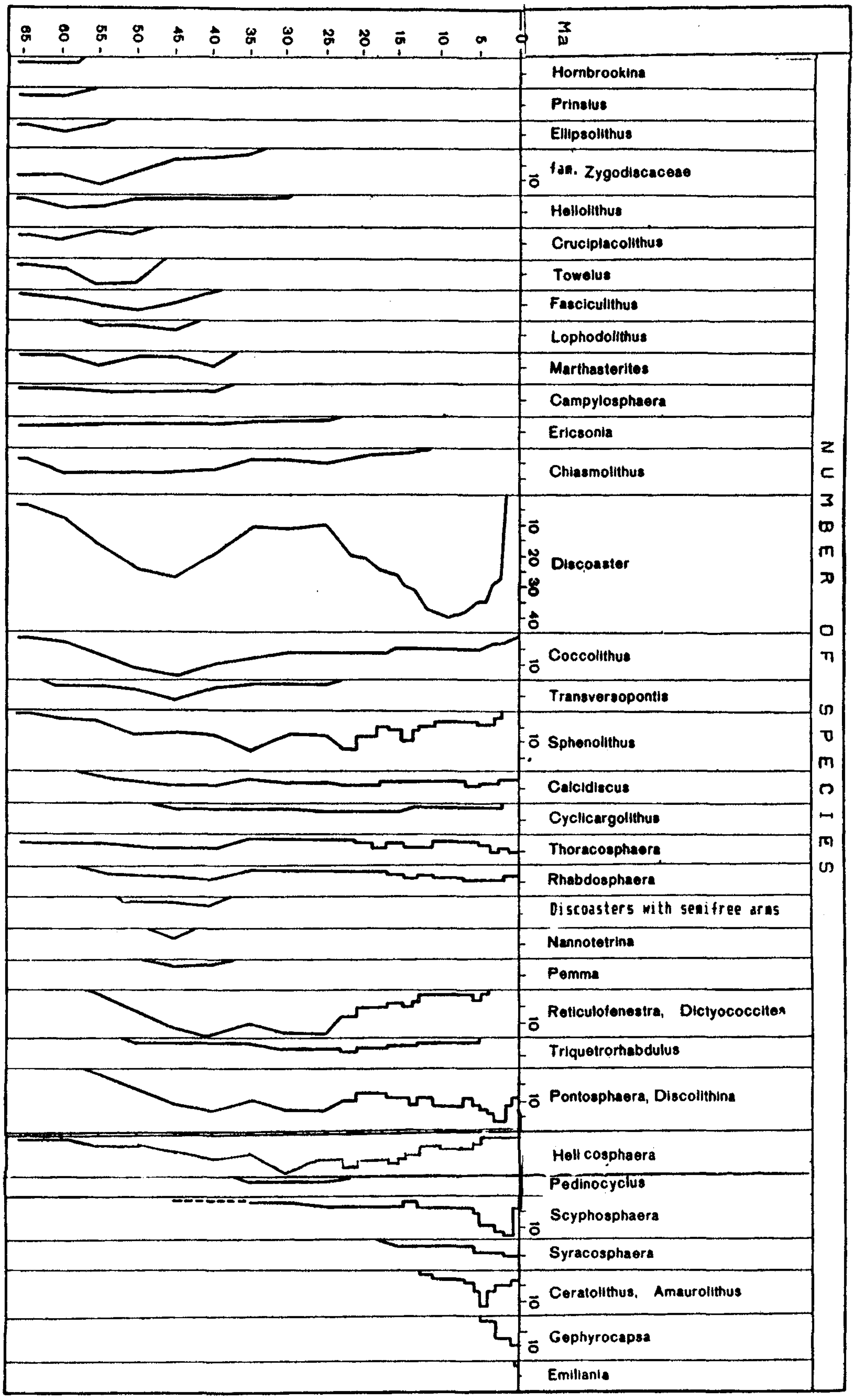

Fig.1. Changes in the relative abundance of species of calcareous nannoplankton during the Cenozoic.

of *Helicosphaera, Sphenolithus* and *Reticulofenestra* species increased in this direction.

Thus, even through forms of **Zygodiscaceae** (some of which survived from the Mesozoic) and also *Heliolithus* and *Fasciculithus* continued to be significant in Paleocene times, in the Eocene the most important forms were *Discoaster, Helicosphaera, Reticulofenestra* and *Coccolithus. Chiasmolithus* continued to develop, and *Fasciculithus,* which became less important, also existed. During the Oligocene *Chiasmolithus, Discoaster* and *Coccolithus* decreased in importance, while the development of the species of genera *Sphenolithus, Reticulofenestra, Helicosphaera* and *Discolithina* increased.

In the Paleocene and Eocene the "rosette" *discoaster*s had very important significance. *Discoaster*s with arms (rays) took their place in the Late Oligocene, Miocene and Pliocene. In the Oligocene and Miocene *discoaster*s had robust arms, in the Pliocene they had very delicate arms. *Discoaster*s are not present in the Quaternary period.

The big stages were distinguished in the Cenozoic on the basis of the change of generic associations and change of *discoaster* morphotypes:

1) The Paleocene-Early Eocene are characterized by *Heliolithus, Cruciplacolithus, Fasciculithus, Toweius*, "rosette" *discoaster*s;

2) The Middle-Late Eocene has abundant "rosette" *discoaster*s, *Reticulofenestra, Sphenolithus;*

3) The Oligocene-Miocene has *discoaster*s with arms, *Reticulofenestra, Sphenolithus, Triquetrorhabdulus*;

4) The Pliocene has *discoaster*s with delicate arms, *Reticulofenestra, Scyphoshaera* and family **Ceratolithaceae;**

5) The Quaternary has very small placoliths.

Minor stages of nannoplankton evolution also can be indentified in the Cenozoic.

Two stages were distinguished in the Paleocene. The first is the Early Paleocene. It included Mesozoic elements of Nannoflora with very low species diversity and genus *Hornibrookina.* The genera *Transversopontis* appeared also at that time.

The second stage is the Late Paleocene. Here the species diversity of the genera *Discoaster, Heliolithus, Fasciculithus, Toweius* and *Cruciplacolithus* strongly increased. *Lophodolithus, Reticulofenestra* and *Pontosphaera* appeared at that time.

Three stages were recognized in the Eocene.

The Early Eocene stage included the diminished genera *Heliolithus, Marthasterites* and later very sharp reduced *Fasciculithus.* The genera *Cyclicargolithus* and *Triquetrorhabdulus* appeared in this stage. The species diversity of the genera *Reticulofenestra, Pontosphaera, Sphenolithus* and *Discoaster* increased.

The Middle Eocene stage included the diminished Late Paleocene flora with very rare *Heliolithus,* absence of *Toweius, Ellipsolithus* and *Cruciplacolithus*, but with a further increase in the species diversity of the genera *Transversopontis, Helicosphaera, Pontosphaera, Chiasmolithus*. In the Middle Eocene new genera appeared, including *Pemma* and *Nannotetrina.* The latter one existed only during this stage.

The Late Eocene stage is connected with the further increase in the species diversity of genera *Helicosphaera, Pontosphaera, Chiasmolithus, Reticulofenestra,* and with declining species diversity of the genera *Coccolithus, Discoaster* and *Transversopontis.* The genera *Nannotetrina, Lophodolithus* and *Discoaster* with semifree arms disappeared, while the genus Isthmolithus existed only at this stage.

The next stage is the Early Oligocene. The Eocene-Oligocene boundary is very important. The remaining *Transversopontis, Isthmolithus, Tribrachiathus, Campylosphaera, Pemma* and *discoaster*s with semifree arms disappeared. The new genus *Pedinocyclus* appeared nearly 35 Ma. The upper boundary of this stage is within the Early Oligocene. About 33 Ma the change of morphotype of *discoaster*s took place: the rosette shape *discoaster*s were replaced by star shape *discoaster*s in number of the species and in abundance. Further increasing of the species diversity in the genera *Reticulofenestra, Pontosphaera* and *Triquetrorhabdulus* took place.

In the next stage, from the end of Early Oligocene to the end of Early Miocene, no new genera appeared. There were species of the star shape *discoaster*s with thick arms, *Sphenolithus, Reticulofenestra* and above everything many *Cyclicargolithus floridanus* (Roth, Hay) Bukry.

The Oligocene-Miocene boundary does not correspond to a sharp change of nannoplankton associations, but the species diversity of the genera *Reticulofenestra, Pontosphaera, Sphenolithus* and *Discoaster* is reduced.

Next stage is the Middle-Late Miocene. The *discoaster*s with delicate arms and with ornamentation or thickening of their central knobs, *Triquetrorhabdulus, Sphenolithus* and *Cyclicargolithus floridanus* were reduced in number at this stage.

Two stages were distinguished in the Pliocene. During the Pliocene the further formation of species with delicate arms *discoaster*s took place; *Amaurolithus* and *Ceratolithus* also are present. The Early Pliocene stage is distinguished from the Late Pliocene by the abundant *Reticulofenestra* represented by a small number of species.

The Late Pliocene did not contain "typical" (large and middle) *Reticulofenestra,* but *Gephyrocapsa* appeared in it and the number of *Scyphosphaera* species increased.

The last stage is the Quaternary period. The Pliocene - Pleistocene boundary is very important. Great changes were taking place at that time in the compositions of

Nannoflora, but they were not as important as at the Mesozoic-Cenozoic boundary. The genera *Discoaster, Cyclicargolithus* and others ended their existence, and *Sphenolithus* disappeared almost totaly. *Scyphosphaera* and *Pontosphaera* were reduced in number of species. Very small placoliths of new genera dominated in the Quaternary. No genus had great species diversity, except *Gephyrocapsa* had 10 species.

Changes in species diversity during the Cenozoic occured at varying rates. Graphs of this change (Fig. 2) show the presence maximum diversity during the Eocene and diminished from the Early Paleocene to the end of the Oligocene. During Neogene-Quaternary time two time-intervals - the Miocene, 15-14 Ma, and the Early Pliocene, 5-4 Ma - were comparable in number of species of calcareous nannoplankton with intervals in the Paleogene: the Middle Miocene - with the end of the Oligocene, 27 Ma, and the Early Pliocene- with the Late Paleocene, 56 Ma, and with the Late Eocene, 40 Ma.

Based on studies of calcareous nannoplankton species compositions, graphs of changes in numbers of species during the Cenozoic were constructed (Fig. 2b,c). These graphs show the rates of development of the calcareous nannoflora. In the Paleogene the maximum origination of new species (see fig. 2b) occured between 50 and 45 Ma, from the middle of Early to the end of Middle Eocene. A decrease in species diversity occurred at 60 Ma (at the end of the Early Paleocene), and a pronounced decrease occured at the end of the Eocene. Also, minimal rates of origination of new species occured at 35 and 25 Ma, in the Oligocene, only to the end of Early Oligocene, 30 Ma, there was a brief increase in the number of species. Species extinction rates increased from 65 to 40 Ma (Fig. 2c), then slowed toward 35 Ma and increased somewhat toward the close of the Paleogene period. In general, the fastest rates of evolutionary changes occured during the Eocene; however, during the Early and Middle Eocene high rates of extinction were exceeded by even higher rates of speciation. Toward the end of the epoch the extinction rates exceeded origination rates, due probably to decreasing temperatures. During the Oligocene rates of evolution of the nannoplankton sharply decreased.

The greatest increase in speciation during Neogene-Quaternary times occurred during the Early Miocene, at 23-21 Ma, the Middle Miocene, at 18-17 Ma, and the Early Pliocene, at 5-4 Ma (see fig. 2b). The highest extinction rates occurred during the Middle Miocene, 15-14 Ma, the Early Pliocene, at 5-4 Ma, nearly the Pliocene-Pleistocene boundary, 1.8 Ma (essential), and toward the close of the Early Pleistocene, 0,9 Ma (see fig. 2c). All of these time intervals were evidently associated with the most marked changes in nutritional conditions for the calcareous nannoplankton, with such changes being due primarily to temperature variations in the near-surface ocean waters. The rate of speciation, which was at its lowest levels from 35-10 Ma (see fig. 2b), increased somewhat during the last 5 Ma. The rate of species extinction (see fig. 2c), which generally decreased between 40 and 20 Ma, when abundance was at its minimum during the Cenozoic, increased gradually but slightly from 15 to 5 Ma, then sharply in the last 5 Ma, due in part to the intensive extinction occuring towards the Pliocene-Pleistocene boundary: **Coccolithaceae** underwent a marked decrease in size, and discoasters and various

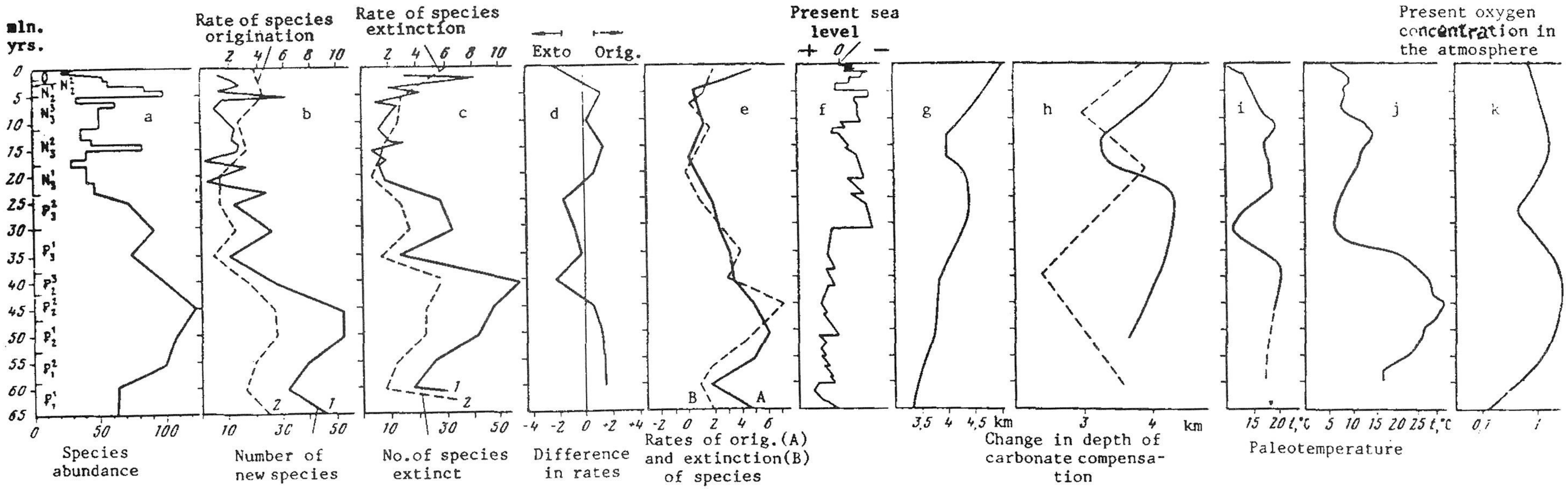

Fig.2. Rates of evolutionary development of calcareous nannoflora in the Cenozoic. Correlation with several environmental parameters: a) Changes in species diversity of calcareous nannoplankton during the Cenozoic; b) Changes in rates of speciation: 1) Curve of number of species present, 2) curve of changes in rate of speciation (number of species/million years); c) changes in rates of species extinction: 1) number of species, 2) changes in rate of extinction (number of species/million years); d) changes in balance between rates of species origination and species of extinction; e) rates of speciation (solid line) and extinction (dashed line) of species of nannoplankton in epicontinental seas (HAQ, 1973); f) eustatic sea level changes (from the book by HARLEND et al., 1985); g,h) changes in the carbonate compensation depth during ihe Cenozoic: g) in eastern part of the Indian ocean (LOUTIT & KENNETT, 1981), h) in the Atlantic ocean: solid line — North Atlantic ((BERGER & ROTH, 1975), dashed lines — South Atlantic ((MALGUEN, 1978); i) changes in paleotemperature in the near-surface waters of the coral reef in the vicinity of New Zealand (DEVEREUX, 1967); j) changes in temperature of near-surface waters in the North Sea (isotope data, BUCHARDT, 1978); k) changes in acidity of the atmosphaere during the Cenozoic (TAPPAN, 1968).

nannoliths went extinct. The diversification curve represents the relationship between the rates of species origination and their extinction. Fig. 2d shows that from 65 to 45 and 20 to 4 Ma rates of origination exceeded rates of extinction, indicating accelerated rates of evolution (positive evolution). Reduced evolutionary rates characterized the intervening periods from 40 to 25 Ma and since 4 Ma (negative evolution). During Cenozoic time the least favorable period for the diversification of calcareous nannoplankton was the Quaternary, when there was a marked reduction in rates of speciation and a failure to survive the crisis that occurred on the boundary between the Pliocene and the Pleistocene.

Comparing the graphs for changes in species diversity during the Cenozoic (see fig. 2 a-d) with graphs for rates of evolution through time, one sees a single trend for two oceans (see fig 2b,c) and for the epicontinental seas (see fig 2e, by HAQ, 1973). The decline in species diversity and in rate of evolution during the Oligocene may be linked to global regression, depicted in the graph of eustatic sea level change (Fig. 2f, HARLEND *et al*, 1985; VAIL *et al.*, 1977), with shoaling of the carbonate compensation depths (Fig. 2g, LOUTIT, and KENNETT, 1981; fig. 2h, BERGER & ROTH, 1975; MALGUEN, 1978), and with variations in near-surface water temperatures during the Cenozoic (Fig. 2i, DEVEREUX, 1967; fig. 2j, BUCHARDT, 1978). Some correlation with atmospheric oxygen content is also apparent (Fig. 2k, TAPPAN, 1968). The data represented above permit better resolution of changes in calcareous nannoflora evolution, its changes correlate best of all with changes in paleotemperatures of the near-surface waters:

1) 60-45 and 20-4 Ma were times of high rates of evolution, hence of suitable conditions; 2) 65 and 40-15 Ma and last 4 Ma were characterized by marked by retarded rates of evolution and reduced tempo of evolution, and marked by worsening of conditions;

3) the most pronounced changes in nannoflora species and genera composition took place 65 Ma and towards the end of the Pliocene, and less pronounced changes occured 18-17, 15-14 and 5-4 Ma;

4) in the evolutionary development of the Cenozoic calcareous nannoflora one can discern 11 stages dominating by different groups of genera: 1) Early Paleocene, 2) Late Paleocene, 3) Early Eocene, 4) Middle Eocene, 5) Late Eocene, 6) Early Oligocene, 7) stage of Early Oligocene-Early Miocene, 8) Middle-Late Miocene stage, 9) Early Pliocene, 10) Late Pliocene, 11) the stage of the Quaternary period.

DISCUSSION

Some authors recognised 5 different stages in the Paleogene. KOSHKARLY, 1981 distinguished Early, Middle and Late-Eocene stages; MUSILEV, 1978 gave Early, Middle Eocene and Late Eocene-Early Oligocene (?) stages. We recognised Early, Middle and Late Eocene stages. The boundary between the Eocene and the Oligocene stages was carried out in the above study. It was proved by the fact of the sharp diversity decline and by the changes in the rates of speciation and extinction. This rates were low jast like in the Early Paleocene. This minimum took place jast before the sharp change of the sea level (see fig. 2e). The environmental parameters on fig. 2 correlate well with each other and prove the Cenozoic stages.

CONCLUSION

The greatest change occured with the Nannoflora during the Cenozoic. The number of species was reduced to one fourth from Eocene to Late Pleistocene and the average sizes of the Coccoliths has shrunk by more than half.

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