

FAUNAL TURNOVER AND DEPTH STRATIFICATION: THEIR RELATIONSHIPS TO CLIMATE AND PRODUCTIVITY EVENTS IN THE EOCENE TO MIOCENE PELAGIC REALM

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ABSTRACT—A new approach to the study of evolution based on quantitative faunal analysis and the spatial distribution of taxa in the oceanic water column is presented. Middle Eocene to Miocene planktonic foraminiferal turnovers have been examined based on the numerical abundances of species and their relative depth habitat as inferred from oxygen isotope ranking of species. Results indicate that most turnovers occur in the surface and intermediate water faunas, that all but one of the faunal turnovers coincide with accelerated global cooling, and that all faunal turnovers occur during intervals of increased productivity in the $\delta^{13}\text{C}$ record. This apparent correlation implies that faunal turnover dynamics are mediated by intrinsic changes in the thermal structure of the oceanic surface waters over time. Nevertheless, there is no obvious linkage of specific environmental parameters to the proliferation or decline of specific faunal elements. The incorporation of these types of data into the story of the evolution of the planktonic foraminiferal fauna promises to yield new insight into the nature of both biotic and abiotic factors that have played a role in the origin and maintenance of planktonic foraminiferal diversity.

Key words: Faunal turnover, depth stratification, oxygen isotopic ranking of species.

INTRODUCTION

Evolutionary patterns of taxonomic diversity in planktonic foraminifera have been studied by many workers (*e.g.*, Thunell, 1981; Corliss *et al.*, 1984; Wei and Kennett, 1986; Stanley *et al.*, 1988) who have reached the consensus that these data provide evidence for a close link between the major features of planktonic foraminiferal evolution and changes in global climate and eustatic sea level. However, despite the fact that taxonomic data sets like those used in previous investigations have proven to be quite valuable for examining the general pattern of these correspondences, such an actuarial approach to evolutionary analysis is insufficient for determining the specific nature of the interrelationships between patterns of organismic diversification and changes in the surrounding environment in that they lack the requisite ecological dimension. Obviously, each species has its own unique pattern of distribution and relative abundance, one that is determined by the intrinsic limits of its environmental tolerance as well as by coeval patterns in the distribution of predator and prey organisms. Thus, the employment and analysis of data that explicitly treat all entities as ecological equivalents cannot help but provide a seriously biased picture of the true complexity of these interactions as well as preclude all but the most optimistic hope of rigorous causal analysis.

Among modern marine plankton, assemblages of approximately 5 to 6 species generally dominate the fauna and may constitute up to 80% of the total number of individuals present. The remaining species are, of course, numerically rare, and for the most part lacking in ecological significance such that their disappearance from (or appearance in) the local fauna is likely to be ecologically inconsequential. Moreover, since first and last appearances of taxa at particular locations usually occur at times when these species are comparatively rare, these may also be relatively minor ecological events

irrespective of their importance in biostratigraphic analyses and the fact that they serve as the basis for taxonomic compendia. In contrast, changes in the relative abundance of the dominant species directly reflect changes in the physical and biological character of the local environment. Consequently, it is only through the quantitative analysis of microfossil assemblages that data sufficiently sensitive to examine the relationships between environmental change and planktonic foraminiferal faunal turnover can be obtained.

In this study, we explore relationships between faunal turnovers among planktonic foraminifera as assessed by changes in the relative abundance of the dominant species groups and changes in climate and nutrient supply. Additional detail is provided by subdivision of the standing foraminiferal fauna into those species groups which predominantly inhabit surface, intermediate and deep water sectors within the upper part of the oceanic water column. This depth stratification is based on a qualitative oxygen isotopic ranking of individual species (as discussed below) and permits the grouping together of taxa that share a common set of specific environmental tolerances thus allowing them to be regarded as a coherent ecological unit. Relative abundance changes in each depth sector imply changes in water mass stratification and the physical expansion or contraction of particular habitats which are presumably driven by external factors such as variations in ocean water temperature and density.

Based on this analysis, five major planktonic foraminiferal faunal turnovers are identified between the Late Eocene and Late Miocene and a generalized picture of faunal decline and replacement during this interval is developed. This type of approach to the analysis of evolutionary dynamics within the planktonic foraminiferal fossil record has the potential to correlate directly faunal turnovers with changes in the physical environment as observed in the historical record of stable

isotopic fluctuations and changes in oceanic water mass stratification through time. In addition, such studies will permit identification of the sources of major taxonomic radiations in the planktonic foraminiferal fauna through time in terms of the physical location of ancestral faunas, provide new data and characters for use in determining patterns of planktonic foraminiferal ancestry and descent, and ultimately address questions concerning the precise role of abiotic and biotic factors in the creation and maintenance of historical patterns in planktonic foraminiferal diversity.

DEPTH STRATIFICATION OF PLANKTONIC FORAMINIFERA AND THE ^{18}O RECORD

Planktonic foraminifera live in the upper portion of the oceanic water column with the highest density of individuals in the upper 100 m. Below 400 m depth living foraminifera are rare (Bé and Tolderlund, 1971; Bé *et al.*, 1971). Plankton tow studies have indicated that living planktonic foraminifera are depth stratified with many species remaining at constant depths and others migrating downward during their life cycle (Bé and Tolderlund, 1971; Lidz *et al.*, 1968; Berger, 1969; Bé and Hemleben, 1970; Bé and Tolderlund, 1971; Williams *et al.*, 1979; Fairbanks *et al.*, 1980, 1982). It has also been observed that most shallow-dwelling species are spinose and most deeper-dwelling species are nonspinose although these patterns may change on a seasonal basis. This distributional relationship appears to have been reversed during the Paleogene (Shackleton *et al.*, 1985).

Among living foraminifera, Fairbanks *et al.* (1980, 1982) noted that nonspinose species calcify their tests in oxygen isotopic equilibrium with the surrounding water-mass whereas spinose species seem to undergo non-equilibrium calcification (by 0.3 to 0.4‰ in $\delta^{18}\text{O}$ values). They also found that within the Gulf Stream many species appear to calcify within the photic zone, or upper 100 m of the water column, and subsequently migrate to greater depths. Williams and coworkers, however, noted a good agreement between depth stratification of species from plankton tows in the Indian Ocean and inferred depths from oxygen isotope data (Williams *et al.*, 1979; Williams and Healy-Williams, 1980). Thus, regardless of non-equilibrium isotopic fractionation, seasonal temperature variations and vital effects, depth rankings of species based on oxygen isotope data exhibit a general agreement with the vertical stratification observed from plankton tow studies. This temperature-depth relationship is based on the relative values of ^{18}O with the lightest O^{18} values being indicative of warmer, surface waters, while the heavier O^{18} values are indicative of species that live either at greater depths or in cooler surface waters (Williams *et al.*, 1979; Williams and Healy-Williams, 1980; Fairbanks *et al.*, 1980, 1982). Although the depth stratification of species is currently interpreted largely as a function of temperature, the vertical separation of species may be closely related to the thermohaline-induced density stratification of sea water (Emiliani, 1954; Hecht and Savin, 1972; Savin and Douglas, 1973; Douglas and Savin, 1978). This relation-

ship, however, has not been fully investigated.

Oxygen isotopic analyses of Tertiary and Cretaceous planktonic foraminifera display a consistent isotopic ranking indicating that species were depth stratified throughout this time period (Douglas and Savin 1978; Boersma and Shackleton, 1981; Boersma and Premoli Silva, 1983; Savin *et al.*, 1985; Keller, 1985b; Shackleton *et al.*, 1985). While it is reasonable to assume that ancient oceans were also depth stratified, the assignment of species to relative depth habitats based on oxygen isotope values is not without its difficulties. Apart from species calcifying out of isotopic equilibrium, vertical migration, seasonal variations, secretion of gametogenic calcite at reproductive rather than living depths, and diagenetic alteration of foraminiferal shells can greatly affect isotopic values. Nevertheless, these difficulties can be overcome and a consistent depth ranking for species achieved through isotopic analysis of the individual species in coeval faunal assemblages at multiple locations (Keller, 1985b; Savin *et al.*, 1985). Therefore, while the isotopic ranking of species is not necessarily representative of the depth range within which these organisms spend the major part of their life cycle, it does provide a relative ranking of individual species with respect to one another. Once species have been isotopically ranked, it is possible to construct vertical temperature profiles and to determine where in the water column species extinctions and originations occurred.

In this study we have attempted to use oxygen isotope ranking of planktonic foraminifera in Middle Eocene through Miocene deep-sea sections to understand the evolutionary changes underlying major faunal assemblage turnovers. We have provided a preliminary ranking of most common planktonic foraminifera based on both published and unpublished data, but further isotopic ranking of species is still necessary. Despite these limitations, however, the data presented here are sufficient to demonstrate the potential of this tool for understanding the general pattern of planktonic foraminiferal evolution and its relationship to variations in both abiotic and biotic aspects of the pelagic marine environment.

MIDDLE EOCENE—MIOCENE $\delta^{18}\text{O}$ SPECIES RANKING

Middle Eocene to Oligocene depth stratification of planktonic foraminifera must rely entirely on oxygen isotope ranking because none of these species are extant. In contrast, many Miocene species are still living today and their depth habitat is known from plankton tows. We have collected stable isotope data from published reports by Saito and Van Donk (1974), Douglas and Savin (1973, 1975, 1978), Boersma and Premoli Silva (1983, 1989), Keller (1985b) Shackleton *et al.* (1985), Savin *et al.* (1985), Keigwin and Corliss (1986) and Corliss and Keigwin (1986) and our own unpublished data. Based on this composite data set we have compiled a preliminary depth stratification of species grouped into surface, intermediate and deep water dwellers as listed in Tables 1 and 2. By analogy with present oceanic conditions, it is assumed that the isotopically lightest species

Table 1. Depth ranking of Middle Eocene to Oligocene planktonic foraminifera based on oxygen isotope variations.

| Middle Eocene | Late Eocene | Oligocene |
|--------------------------------------|--|---------------------------------------|
| | Surface: | |
| <i>Acarinina bullbrooki</i> | <i>Chilouembelina cubensis</i> | <i>Globigerina ampliapertura</i> |
| <i>A. broedermanni</i> | <i>Truncorotaloides rohri</i> | <i>Pseudohastigerina barbadoensis</i> |
| <i>A. planodorsalis</i> | <i>Globigerinatheka semiinvoluta</i> | <i>Globigerina officinalis</i> |
| <i>Muricoglobigerina senni</i> | <i>Globigerinatheka index</i> | <i>G. ouachitaensis</i> |
| | <i>Turborotalia cerroazulensis</i> | <i>G. angustiumbilitata</i> |
| | <i>T. cumialensis</i> | <i>Globorotalia siakensis</i> |
| | <i>Hantkenina alabamensis</i> | <i>Gl. pseudokugleri</i> |
| | <i>Pseudohastigerina barbadoensis</i> | <i>Gl. mendacis</i> |
| | <i>Globigerina ampliapertura</i> | |
| | <i>G. officinalis</i> | |
| | <i>G. ouachitaensis</i> | |
| | <i>G. angustiumbilitata</i> | |
| | Intermediate: | |
| <i>Morozovella lehneri</i> | <i>Subbotina linaperta</i> | <i>Subbotina linaperta</i> |
| <i>M. spinulosa</i> | <i>S. angiporoides</i> | <i>S. angiporoides</i> |
| <i>M. aragonensis</i> | <i>S. utilisindex</i> | <i>S. utilisindex</i> |
| <i>Truncorotaloides rohri</i> | <i>Globigerina eoacaena</i> | <i>Globigerina eoacaena</i> |
| <i>Globigerinatheka semiinvoluta</i> | <i>G. galavisi</i> | <i>G. galavisi</i> |
| | <i>G. euapertura</i> | <i>G. praebulloidis</i> |
| <i>G. index</i> | <i>G. medizai</i> | <i>Pseudohastigerina micra</i> |
| | <i>Pseudohastigerina micra</i> | <i>Globoquadrina dehiscens</i> |
| | <i>Globorotaloides carcoselleensis</i> | <i>Globorotalia opima opima</i> |
| | | <i>Globorotalia opima nana</i> |
| | Deep: | |
| <i>Globigerinatheka</i> spp. (large) | <i>Globoquadrina venezuelana</i> | <i>Globoquadrina venezuelana</i> |
| | <i>Gq. pseudovenezuelana</i> | <i>Gq. pseudovenezuelana</i> |
| | <i>Gq. tripartita</i> | <i>Gq. tripartita</i> |
| | <i>Catapsydrax</i> spp. | <i>Gq. praedehiscens</i> |
| | | <i>Catapsydrax</i> spp. |

Table 2. Depth ranking of Miocene planktonic foraminifera based on $\delta^{18}\text{O}$ variations.

| Early Miocene (21 Ma) | Middle Miocene (16 Ma) | Late Miocene (8 Ma) |
|--------------------------------------|------------------------------------|---------------------------------------|
| | Surface: | |
| <i>Globigerinoides</i> mixed spp. | <i>Globigerinoides</i> mixed spp. | <i>Globigerinoides</i> mixed spp. |
| <i>G. trilobus</i> | <i>G. trilobus</i> | <i>G. trilobus</i> |
| <i>G. sacculifer</i> | <i>G. sacculifer</i> | <i>G. sacculifer</i> |
| <i>G. subquadratus</i> | <i>G. subquadratus</i> | <i>G. obliquus</i> |
| <i>Globorotalia kugleri</i> | <i>Globoquadrina altispira</i> | <i>Globoquadrina altispira</i> |
| <i>Globorotalia siakensis</i> | <i>Globorotalia siakensis</i> | <i>Orbulina universa</i> |
| <i>Globorotalia mayeri</i> | <i>Globorotalia mayeri</i> | <i>Globigerinita glutinata</i> |
| <i>Globigerinita glutinata</i> | <i>Globigerinita glutinata</i> | |
| <i>Globigerina angustiumbilitata</i> | | |
| | Upper intermediate: | |
| | <i>Globorotalia peripheroronda</i> | <i>Globorotalia menardii</i> group |
| | <i>Gl. fohsi</i> group | <i>Globorotalia continuosa</i> |
| | <i>Globorotalia continuosa</i> | <i>Globorotalia acostaensis</i> |
| | | <i>Sphaeroidinellopsis seminulina</i> |
| | | <i>Globigerina nepenthes</i> |
| | | <i>Globigerina druryi</i> |
| <i>Globoquadrina dehiscens</i> | <i>Globoquadrina dehiscens</i> | <i>Globoquadrina dehiscens</i> |
| | Lower intermediate: | |
| <i>Globorotalia miozea</i> | <i>Globorotalia miozea</i> | <i>Globorotalia conoidea</i> |
| <i>Globigerina woodi</i> | <i>Globigerina woodi</i> | <i>Globigerina woodi</i> |
| <i>Globigerina bulloides</i> | <i>Globigerina bulloides</i> | <i>Globigerina bulloides</i> |
| <i>Globigerina praebulloidis</i> | | <i>Neogloboquadrina pachyderma</i> |
| | Deep: | |
| <i>Globoquadrina venezuelana</i> | <i>Globoquadrina venezuelana</i> | <i>Globoquadrina venezuelana</i> |
| <i>Globoquadrina tripartita</i> | <i>G. pseudovenezuelana</i> | |
| <i>Gq. praedehiscens</i> | | |
| <i>Catapsydrax</i> spp. | | |

live in the mixed surface water layer comprising the uppermost 50 m to 100 m of the water column. Intermediate dwellers are inferred to occupy the interval at or above the thermocline and below the mixed surface layer from approximately 100 m to 250 m depth. Deep water dwellers are assumed to live below the thermocline, or below 250 m depth (Berger, 1969; Bé and Tolderlund, 1971; Williams *et al.*, 1979; Williams and Healy-Williams, 1980; Fairbanks *et al.*, 1980, 1982). Ranking of species relative to generalized low latitude $\delta^{18}\text{O}$ values is listed in Tables 1 and 2 and illustrated in Figs. 1 to 4.

Middle Eocene

Middle Eocene oxygen isotopic values of planktonic foraminifera show a clustering of most species at the isotopically light end of the spectrum indicating little variation in the temperature and density conditions of the upper portion of the water column. Isotopically light or surface dwelling species include the spinose *Acarinina bullbrooki*, *A. broedermanni*, *A. planodorsalis* and *Muricoglobigerina senni*. Intermediate dwellers with slightly heavier isotopic values are observed in *Morozovella lehneri*, *M. spinulosa*, *M. aragonensis* and *Truncorotaloides rohri*. Only large *Globigerinatheka* spp. were observed to have significantly heavier oxygen

isotope values and are therefore classified as relatively deep water dwellers. All of the spinose surface dwellers become extinct during the climatic cooling towards the end of the Middle Eocene (Keller, 1983a, 1985a).

Late Eocene

Compared with the Middle Eocene there is greater variation in oxygen isotope values among Late Eocene planktonic foraminifera indicating increased water mass stratification. With the extinction of the warm water spinose Middle Eocene species, a cooler water fauna dominates the surface mixed layer during the Late Eocene. This new surface group consists of the Middle Eocene survivor *Globigerinatheka semiinvoluta* and *G. index*, *Turborotalia pomeroli*, *T. cerroazulensis*, *T. cunialensis*, *Hantkenina alabamensis* and *Chiloguembelina cubensis* (Figs. 1 and 2). With the exception of *Chiloguembelina cubensis* all of these surface dwellers disappear by the end of the Late Eocene. New surface dwellers evolving at this time and continuing into the Oligocene are generally small globigerine forms including *Globigerina officinalis*, *G. ouachitaensis*, *G. angustum-bilicata* and *G. ampliapertura*.

Isotopically heavier or intermediate water forms include the small taxa *Pseudohastigerina micra*, *Globo-*

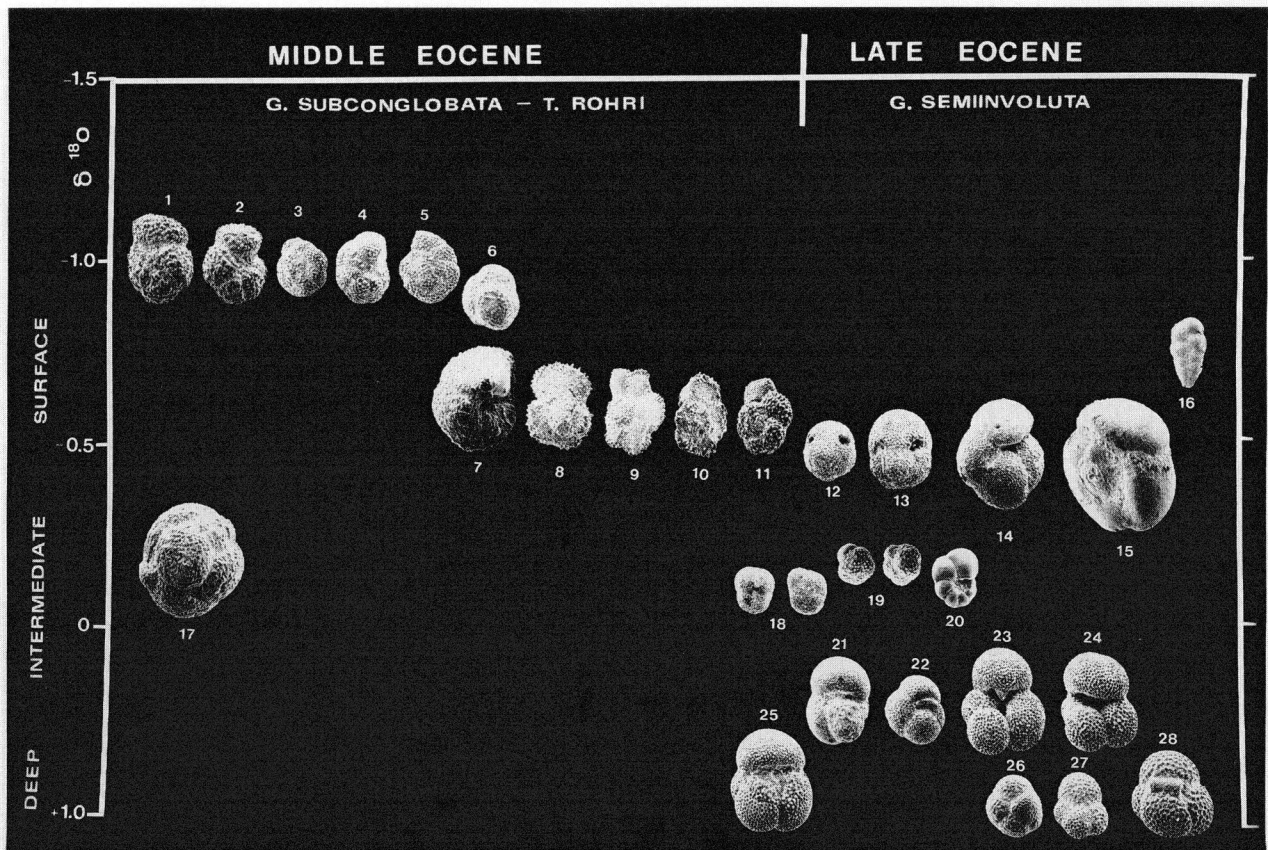


Fig. 1. Preliminary oxygen isotope ranking of Middle Eocene to Late Eocene planktonic foraminifera. All species are illustrated at the same magnification to show relative size differences. 1, 2. *Acarinina bullbrooki*, 3. *Gl. broedermanni*, 4, 5. *Gl. planodorsalis*, 6. *Muricoglobigerina senni*, 7. *Gl. aragonensis*, 8. *A. spinulosa*, 9, 10. *A. lehneri*, 11. *Truncorotaloides rohri*, 12. *Globigerinatheka semiinvoluta*, 13. *Globigerinatheka index*, 14, 15. *Turborotalia cerroazulensis*, 16. *Chiloguembelina* sp., 17. *Globigerinatheka* sp., 18. *Globorotaloides carcoselleensis*, 19. *Globigerina medizai*, 20. *Pseudohastigerina micra*, 21. *Subbotina linaperta*, 22. *S. angiporoides*, 23. *Globigerina eocaena*, 24. *G. galavisi*, 25. *Globoquadrina venezuelana*, 26. *Catapsydrax unicava*, 27. *Catapsydrax* sp., 28. *Catapsydrax dissimilis*.

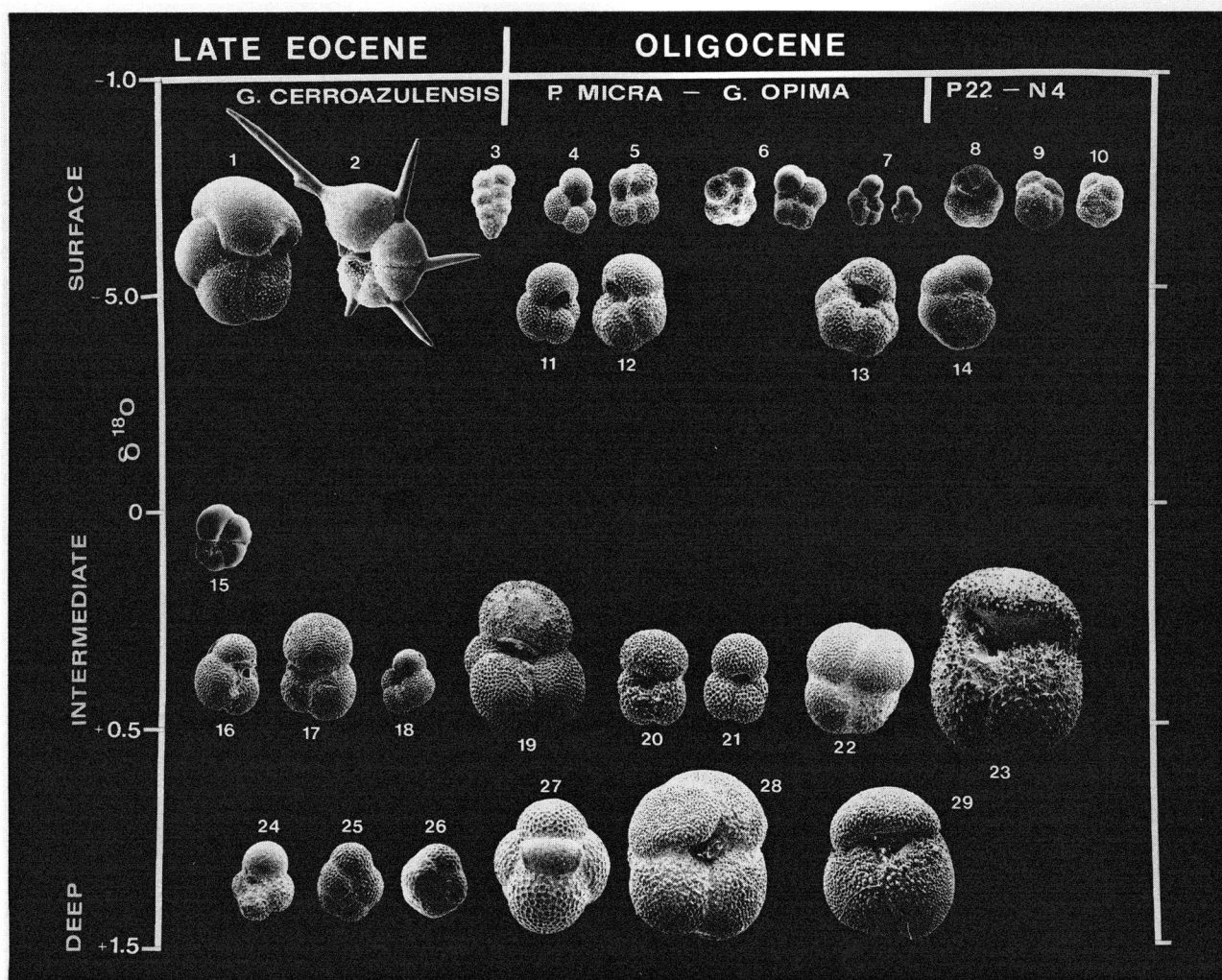


Fig. 2. Preliminary oxygen isotope ranking of Late Eocene to Oligocene planktonic foraminifera. All species are illustrated at the same magnification to show relative size differences. 1. *Turborotalia cerroazulensis*, 2. *Hantkenina alabamensis*, 3. *Chilguembelina cubensis*, 4. *Globigerina officinalis*, 5. *G. ouachitaensis*, 6. *G. angustum-bilicata*, 7. *Pseudohastigerina barbadoensis*, 8. *Globorotalia pseudokugleri*, 9. *Gl. mendacis*, 10. *Gl. kugleri*, 11, 12. *Globigerina ampliapertura*, 13. *G. ciperoensis*, 14. *Gl. siakensis*, 15. *Pseudohastigerina micra*, 16. *Subbotina angiporoides*, 17. *S. linaperta*, 18. *S. minima*, 19. *Globigerina eocaena*, 20. *G. galavisi*, 21. *G. praebulloides*, 22. *Globorotalia opima*, 23. *Globoquadrina dehiscens*, 24. *Catapsydrax* sp., 25, 26. *Catapsydrax unicava*, 27. *Catapsydrax dissimilis*, 28. *Globoquadrina venezuelana*, 29. *Globoquadrina tripartita*.

rotaloides carcoselleensis and *Globigerina medizai* (Fig. 1). Slightly heavier intermediate depth values characterize larger globigerine forms including *Subbotina linaperta*, *S. angiporoides*, *Globigerina eocaena* and *G. galavisi* while *Catapsydrax* and *Globoquadrina* taxa exhibit the heaviest oxygen isotope values.

Oligocene

The Oligocene shows a broad distribution of $\delta^{18}\text{O}$ values among planktonic foraminifera indicating a narrow surface mixed layer and a broad cool intermediate and deep water layer (Fig. 2). The small globigerine morphotypes that evolved during the latest Eocene dominate the Early Oligocene surface layer. Most of these species disappear in the *Globorotalia opima* Zone and a new group of small globigerine and globorotaliid taxa evolve including *Globorotalia pseudokugleri*, *Gl. mendacis*, *Gl. siakensis*, *Globigerina ciperoensis* and *G. angustum-*

bilicata (Table 1). These species continue to dominate the surface mixed layer into the earliest Miocene.

Among the isotopically heavier intermediate dwellers all but one species (*Globoquadrina dehiscens*) are Eocene survivors which become extinct during the Middle Oligocene. Isotopically heavy or deep water dwellers continue to be representative of *Globoquadrina* and *Catapsydrax* (Table 1, Fig. 2).

Miocene

Oxygen isotope ranking of Miocene planktonic foraminifera in three Miocene time intervals (8 Ma, 16 Ma and 21 Ma) was discussed in an earlier paper (Keller, 1985b) and is briefly summarized here. The isotope depth ranking is based on stable isotope analysis of individual species in multiple deep-sea sections across low to middle latitudes (see also Savin *et al.*, 1985). Consistency in the relative isotopic ranking among various taxa is inter-

puted to reflect depth ranking in the water column. Table 2 lists the relative depth ranking of species for each Miocene time slice with species grouped into the same surface, intermediate and deep water sectors.

Early Miocene

The Early Miocene surface group consists of the small globorotaliid and globigerine Oligocene survivors, most of which disappear at the top of Zone N.4 or in Zone N.5, and the newly evolving *Globigerinoides* group and *Globoquadrina altispira*. *Globigerinoides* taxa dominate tropical surface waters through the Miocene and to the Recent (Table 2, Fig. 3). Intermediate dwellers include globoquadrinids (*Gq. dehiscens*, *Gq. praedeheiscens*), small globorotaliids and globigerinids. *Catapsydrax* and *Gq. venezuelana* continue to be the only deep water dwellers, with *Catapsydrax* going extinct by the late Early Miocene.

Middle and Late Miocene

Greater $\delta^{18}\text{O}$ variation is evident among Middle and Late Miocene planktonic foraminifera implying increased water mass stratification as compared with the Early Miocene ocean (Table 2, Fig. 4; Keller, 1985b; Savin *et al.*, 1985). Among low latitude surface dwellers the *Globigerinoides* group continues to dominate along with *Globorotalia siakensis* which disappears at the Middle/Late Miocene boundary. Few new species evolve in the surface mixed layer (e.g., *Orbulina*, *Pulleniatina*) and most evolutionary activity appears to occur at intermediate depths. A relatively large-sized group of globorotaliids evolves (*Gl. fohsi*-*Gl. peripheroronda* group, *Gl. menardii*-*Gl. tumida* group) as well as a small-sized, isotopically heavier group of globigerinids (*G. druryi*-*G. nepenthes*) and globorotaliids (*Gl. continua*-*Gl. acostaensis*). *Globoquadrina venezuelana* remains isotopically the heaviest or deepest dwelling species.

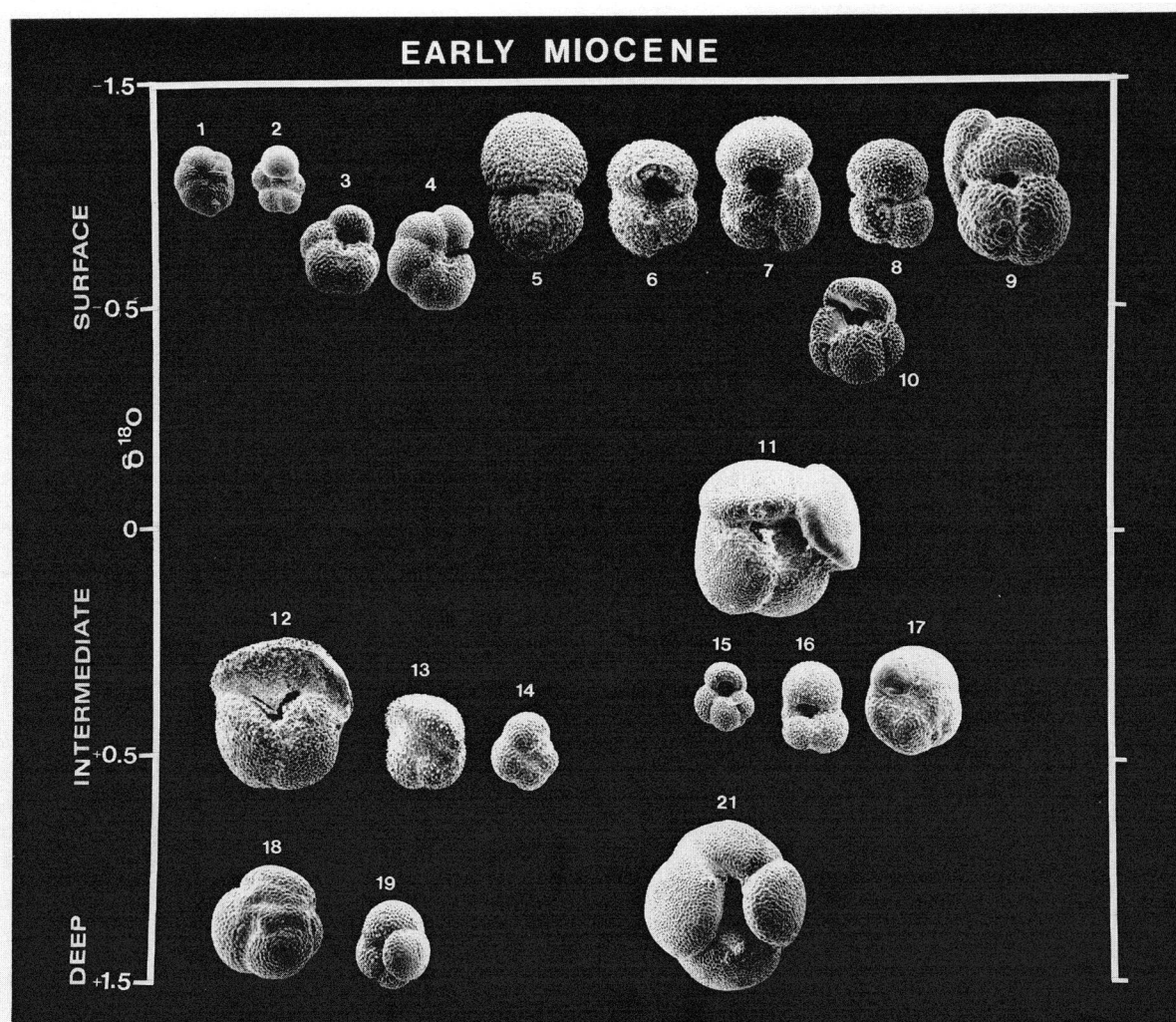


Fig. 3. Isotopic ranking of Early Miocene planktonic foraminifera illustrated in relation to general low latitude $\delta^{18}\text{O}$ values. All species are illustrated at the same magnification to show relative size differences. Key to taxa: Surface: 1 *Globorotalia kugleri*, 2 *Globigerina angustiumbilitata*, 3 *G. ciproensis*, 4 *Gl. siakensis*, 5 *Globigerinoides trilobus*, 6 *G. subquadratus*, 7 *G. altiapertura*, 8 *Globigerinoides parawoodi*, 9 *G. sacculifer*, 10 *Globoquadrina altispira*. Intermediate: 11 *Globoquadrina dehiscens*, 12 *Gq. praedeheiscens*, 13 *Globigerina binaiensis*, 14 *Globorotalia continua*, 15 *Globigerina woodi*, 16 *G. bulloides praebulloides*, 17 *Gl. miozea*. Deep: 18 *Catapsydrax dissimilis*, 19 *C. unicava*, 20 *Globoquadrina tripartita*, 21 *Gq. venezuelana*.

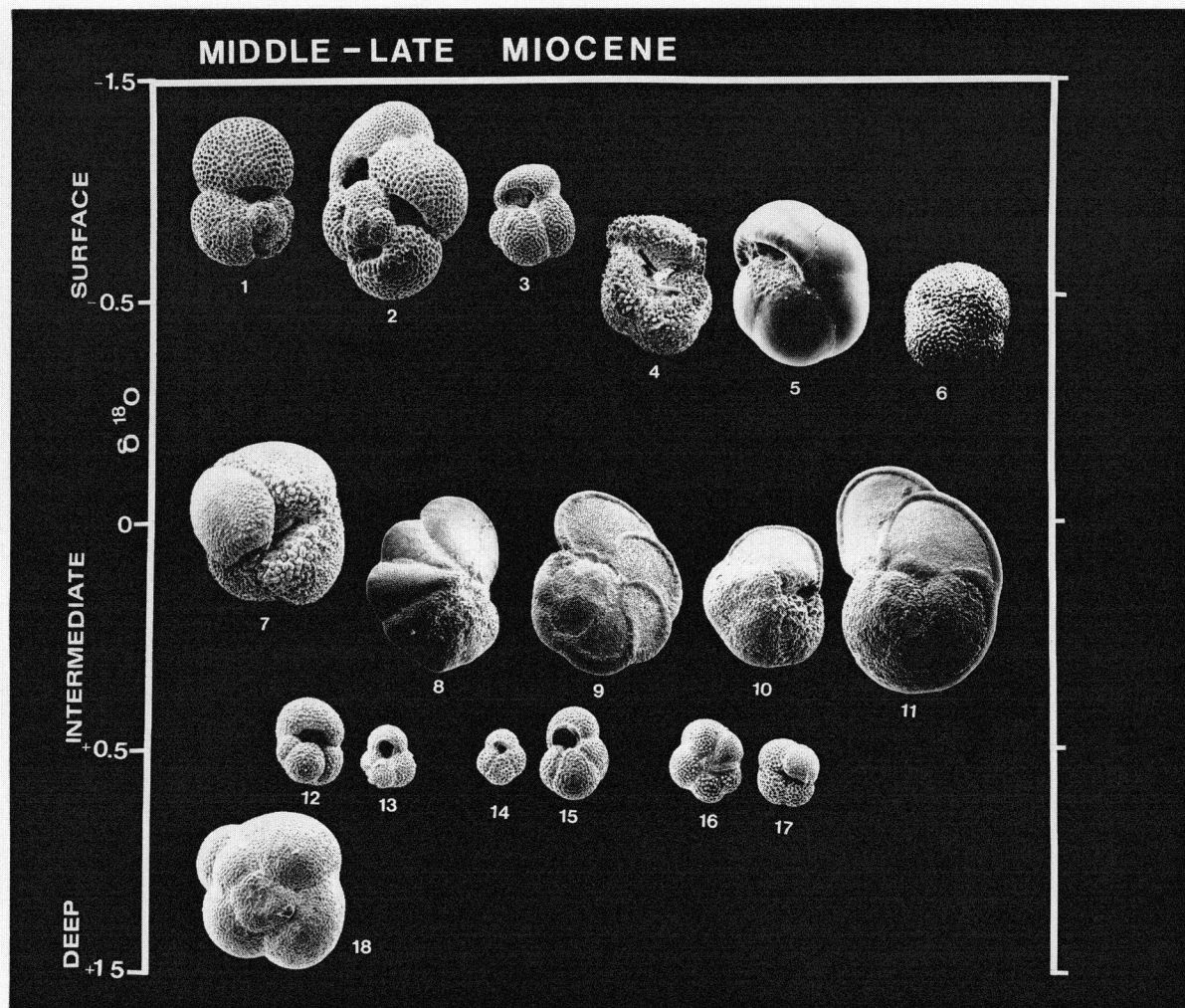


Fig. 4. Isotopic ranking of Middle to Late Miocene planktonic foraminifers illustrated in relation to general low latitude $\delta^{18}\text{O}$ values. All species are illustrated at the same magnification to show relative size differences. Key to taxa: Surface: 1. *Globigerinoides trilobus*, 2. *G. sacculifer*, 3. *G. obliquus*, 4. *Globoquadrina altispira*, 5. *Pulleniatina primalis*, 6. *Orbulina*. Intermediate: 7. *Globoquadrina dehiscens*, 8. *Globorotalia fohsi*, 9. *Gl. menardii*, 10. *Gl. conomiozea*, 11. *Gl. tumida*, 12. *Globigerina bulloides*, 13. *G. woodi*, 14. *G. druryi*, 15. *G. nepenthes*, 16. *Gl. acostaensis*. Deep: 17. *Globoquadrina venezuelana*.

MIDDLE EOCENE—MIOCENE DEPTH STRATIFICATION

The relative abundance of dominant species groups in surface, intermediate and deep water habitats is illustrated in Fig. 5 based on data from the equatorial Pacific DSDP Site 77B for the Oligocene-Miocene interval and Indian Ocean DSDP Site 219 for the Eocene interval. Within each depth habitat species have been grouped by common evolutionary trends. For example species that evolved during the same time span are grouped together and followed through to their extinction with different shading patterns used to demonstrate these groups. In this way five major evolutionary species groups can be identified in the surface mixed layer and also to a lesser extent at intermediate depths. However, only two species groups are present in the deep habitat. This implies that speciation and evolutionary diversification took place preferentially in the mixed surface layer and secondarily at intermediate depths below the mixed layer and above

the base of the thermocline. There appears to be little evolutionary activity at depths below the thermocline.

Also evident from Fig. 5 is that the transition from one faunal assemblage to another is generally a gradual process occurring over a period of several million years. The process is usually marked by a terminal decline in numerical abundance and the lingering of these numerically rare species during the rise to dominance of a new faunal group. Where abrupt faunal changes are observed, it is generally due to artifacts of the stratigraphic record such as short hiatuses and carbonate dissolution.

Major faunal turnovers can be recognized during the Late Eocene to Early Oligocene, the Early/Late Oligocene boundary, the earliest Miocene (Zone N.4–N.5), the Early/Middle Miocene boundary and Late Miocene (Zone N.15–N.16). The late Middle Eocene to Oligocene faunal turnover is characterized by the decline and eventual extinction of the warm water Middle and Late Eocene fauna (black pattern) and a correlative increase in the cooler water (intermediate) globigerine fauna

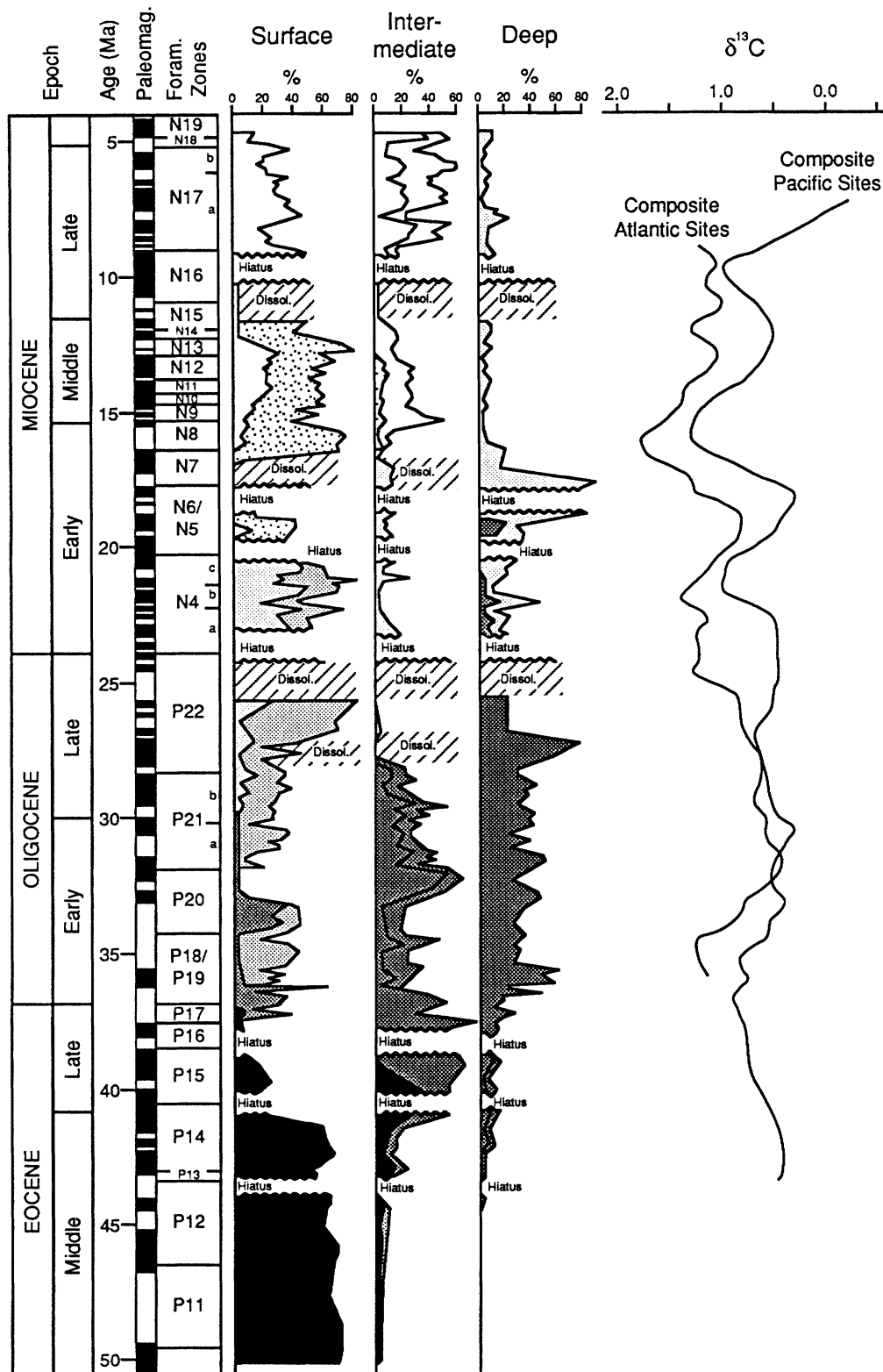


Fig. 5. Depth stratification of Middle Eocene to Miocene planktonic foraminifera. Relative abundance of species grouped into surface, intermediate and deep dwellers based on oxygen isotopic ranking of species. Faunal changes within each group are illustrated by changing patterns. Oligocene and Miocene faunal data from east equatorial Pacific DSDP Site 77B; Eocene faunal data from Indian Ocean DSDP Site 219. Composite benthic foraminiferal $\delta^{13}\text{C}$ curves for Atlantic and Pacific deep-sea sites modified from Miller and Fairbanks (1985). Note the coincidence of major positive excursions in $\delta^{13}\text{C}$, or high marine productivity, and major faunal turnovers: Late Eocene to earliest Oligocene, the Early Miocene (N4), Early/Middle Miocene (N8), Late Miocene (N16). See text for discussion.

(dark stipples, Fig. 5). A new, but short-lived cooler water surface fauna evolved in the latest Eocene (dark stipples). This faunal turnover is associated with a well documented global cooling as indicated in the composite Pacific and Atlantic oxygen isotope curves (Fig. 6; Miller *et al.*, 1987; Keigwin and Corliss, 1986) and heavier carbon isotope values implying increased marine productivity (Fig. 5). Temperatures remained cool through the Early Oligocene with maximum cooling in Zone P.21 (Keigwin and Keller, 1984) coincident with the extinction of all but one species (*Globigerina angustiumbilitata*) of the latest Eocene to Early Oligocene surface water group. *Globigerina angustiumbilitata* (marked by third stippling pattern) remained abundant into the Early Miocene (see also Keller, 1981, 1983a,b) while other Eocene globigerine morphotypes remained abundant in intermediate depths through Zone P.21 and *Catapsydrax* and *Globoquadrina* species were abundant at greater depths (Fig. 5).

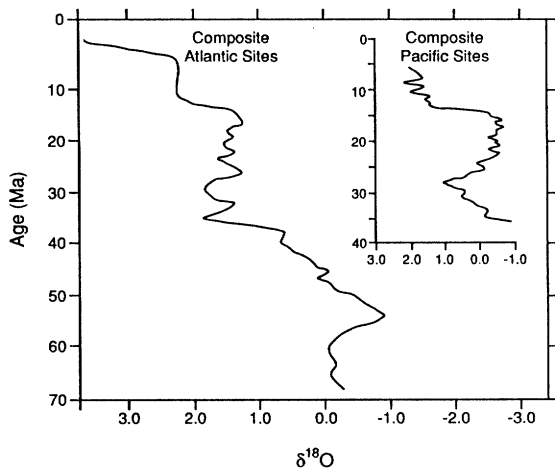


Fig. 6. Composite benthic foraminiferal oxygen isotope curves for Atlantic and Pacific deep-sea sites modified from Miller *et al.* (1987). Note the major global cooling trend beginning in the Early Eocene, the sharp drop in temperatures at the E/O boundary and permanent drops in bottom water temperatures during the Middle Miocene and Pliocene marking major changes in oceanic circulation.

During the latest Oligocene a new surface group evolved consisting of small globigerine and globorotaliid morphotypes (Keller, 1983b). Nearly all of these taxa became extinct in the earliest Miocene (Zone N.4–N.5) at a time of major evolutionary diversification that coincided with the rise of the Tertiary surface water fauna (white pattern) (Keller, 1981, 1983b). Once again, there is no significant change in the intermediate and deep water faunas (Fig. 5) despite the fact that this Early Miocene faunal turnover is also associated with a global cooling and increased marine productivity (Figs. 5, 6; Savin *et al.*, 1985).

The faunal turnover at the Early/Middle Miocene boundary is marked by continued evolutionary diversification in the surface (*Orbulina*, *Globigerinoides*, white pattern) and intermediate water assemblages (*Globo-*

rotalia fohsi group, stippled pattern and *Globorotalia continuosa-acostaensis* group, white pattern). *Globorotalia siakensis*, which evolved during the latest Oligocene, dominates the surface water during the Middle Miocene (stippled pattern) along with the genus *Globigerinoides* (white pattern). Contrary to other faunal turnovers, the Early/Middle Miocene faunal change is associated with generally warm temperatures (Woodruff *et al.*, 1981; Savin *et al.*, 1985) but high marine productivity (Fig. 5).

The Late Miocene faunal turnover (Zone N.15–N.16) is characterized by the extinction of *Globorotalia siakensis* (stippled pattern) in the surface layer, the extinction of the *Gl. fohsi* group (stippled pattern) in the intermediate layer and the evolution of the intermediate layer *Gl. menardii* group (white pattern). During the Late Miocene the *Gl. menardii* and *Gl. acostaensis* groups dominate the intermediate layer and *Globigerinoides* taxa and *Globoquadrina altispira* dominate the surface mixed layer (white pattern). Similar to earlier faunal turnover events the Late Miocene event correlates with global cooling (Woodruff *et al.*, 1981; Savin *et al.*, 1985; Vincent *et al.*, 1985; Miller *et al.*, 1987) and increased marine productivity.

Thus, the extinction of one faunal group and evolution of the succeeding fauna in all but one case is closely related to global climatic cooling and high marine productivity as is evident in the oxygen and carbon isotope curves (Figs. 5, 6). The one exception is the Early/Middle Miocene boundary faunal change that is associated with warm temperatures, but heavy $\delta^{13}\text{C}$ values indicating high marine productivity. Moreover, most of the faunal turnovers are associated with either short hiatuses or carbonate dissolution events implying intensified circulation and erosion during these times of global cooling (Keller and Barron, 1983, 1987; Keller *et al.*, 1987). Curiously, the Early/Late Oligocene boundary faunal change is not associated with any variations in the composite isotope curves, although climatic cooling and increased marine productivity are evident in individual site data (Keigwin and Keller, 1984). It is likely that insufficient high-resolution isotope data were available at the time the composite carbon and oxygen isotope curves were constructed by Miller and Fairbanks (1985) and Miller *et al.* (1987). Nevertheless, the trends evident in the composite isotope curves imply a possible cause-effect relationship between major faunal turnovers and major variations in paleoclimate and paleoproductivity. Apparently, high rates of planktonic foraminiferal speciation and evolutionary diversification occur during times of climatic change generally related to cooling, intensified current circulation and increased marine productivity while low rates of speciation coincide with relatively stable climatic intervals and reduced marine productivity. It is unclear, however, which of these abiotic parameters (*e.g.*, temperature-density or nutrient supply) is the driving force behind major faunal turnovers. The high rates of speciation during the high productivity but warm Early/Middle Miocene interval suggests that productivity may be a controlling factor in evolution.

FAUNAL TURNOVER EVENTS

In order to better understand the nature of faunal turnover events and their relationship to temperature, productivity and paleoceanographic events, four of the five faunal turnovers are examined based on the numerical abundance of taxa evolving and taxa becoming extinct in surface, intermediate and deep water depths.

Late Eocene—Early Oligocene

The Late Eocene-Early Oligocene faunal turnover event is commonly considered a mass extinction event although it has been shown that there is no major increase in the rate of species extinctions (Keller, 1983a, 1986; Corliss *et al.*, 1984). Nevertheless, when viewed in terms of the numerical abundance of taxa evolving and those becoming extinct, this faunal turnover clearly marks a major crisis for planktonic foraminifera. For instance, the relative number of individuals in all taxa becoming extinct at DSDP Site 219 constitutes over 80% of the Middle Eocene population (Fig. 7). Their decline in numerical abundance begins near the top of Zone P.14 and rapidly proceeds through Zone P.15 with few relatively rare taxa surviving up to the Eocene/Oligocene

boundary. This faunal decline is accompanied by the evolution and rise to dominance of a new fauna, but the evolving fauna is strikingly different from that which it is replacing. Extinction differentially affects warm surface dwellers and the dominant constituents decline through the Middle Eocene. The newly evolving fauna consists primarily of intermediate dwellers and few but increasing numbers of deep dwellers. Only near the Eocene/Oligocene boundary does a new surface water group evolve (Fig. 7).

This faunal turnover spans an estimated 4 million year time period between the onset of the terminal decline of the Eocene fauna and the establishment of a new fauna. What caused this faunal turnover? The gradual disappearance of warm water surface dwellers and evolution of cooler water intermediate and deep dwellers point towards climatic cooling. A global cooling trend is well documented during this time and has been discussed by many workers including Kennett *et al.* (1972), Kennett and Shackleton (1976), Corliss *et al.* (1984), Miller and Fairbanks (1985), Keigwin and Corliss (1986) and Miller *et al.* (1987). Extraterrestrial bolide impacts which occurred within Zone P.16 and upper part of Zone P.15 do not appear to have significantly contributed to this faunal decline (Keller, 1986; Keller *et al.*, 1987).

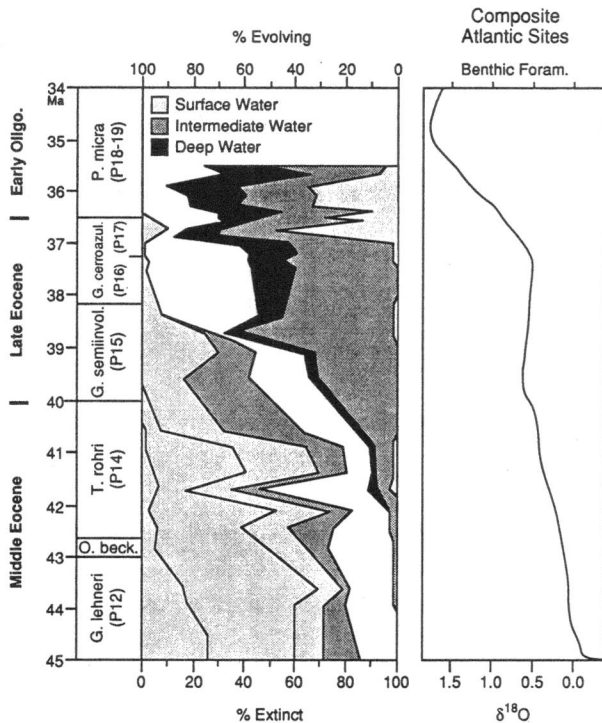


Fig. 7. Middle Eocene to Early Oligocene faunal turnover at Indian Ocean DSDP Site 219. The relative abundances of species going extinct and of species evolving are grouped into surface, intermediate and deep dwellers based on oxygen isotope ranking. Note, the gradual decline in numerical abundance of species going extinct beginning in Zone P.14; most of these species are warm surface water dwellers whereas species evolving are cooler water intermediate and deep dwellers. This faunal change is accompanied by global cooling as illustrated in the composite $\delta^{18}\text{O}$ curve modified from Miller *et al.* (1987).

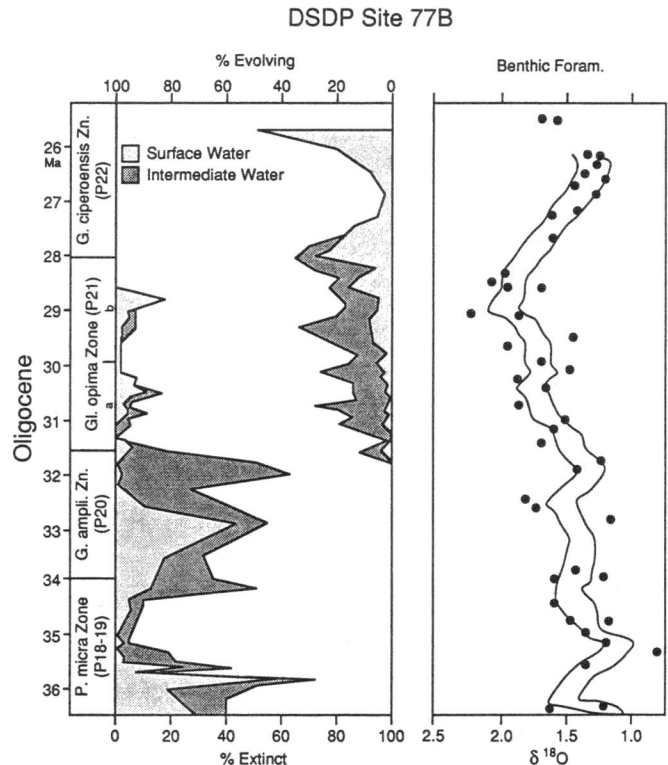


Fig. 8. Middle Oligocene faunal turnover and benthic foraminiferal $\delta^{18}\text{O}$ curve (Keigwin and Keller, 1984) at east equatorial Pacific DSDP Site 77B. Note, coincidence in maxima of global cooling and faunal turnover, but a relatively small percentage of the fauna is affected by this turnover event.

Early/Late Oligocene

The Oligocene faunal turnover event affects a relatively small proportion of the total planktonic foraminiferal population as illustrated in DSDP Site 77B (Fig. 8). The faunal group becoming extinct consists primarily of the surface dwellers which evolved during the latest Eocene (*Globigerina ampliapertura*, *Pseudohastigerina*) and the intermediate water Eocene survivors *Subbotina linaperta* and *S. angiporoides*. Among the evolving species is the relatively short-lived *Globorotalia opima* (Zone P.21) and small globigerine and globorotaliid surface dwellers which survive into the Early Miocene. *Globigerina angustiumbilitata* constitutes the relatively unaffected dominant faunal component of this faunal turnover in surface waters whereas *Catapsydrax* and *Globoquadrina* taxa dominate in deeper waters (Keller, 1983a).

The Oligocene faunal turnover indicates a faunal decline that parallels a gradual cooling and reaches a maximum coincident with the extinction of the Eocene survivors (Fig. 8). The maximum cooling has been interpreted as a major continental ice buildup (Keigwin and Keller, 1984; Miller and Thomas, 1985). The subsequent warming (Zone P.22) coincides with increased diversity and numerical abundance in the surface dwellers.

Early Miocene

The Early Miocene faunal turnover event is similar in magnitude to the Late Eocene-Early Oligocene event. An essentially modern fauna evolves at this time and nearly all Oligocene survivors become extinct (Keller, 1981, 1983b; Wei and Kennett, 1986). Figure 9 illustrates this faunal turnover in the western Pacific DSDP Site 292. Over 90% of the individuals in the population are affected by this extinction event and nearly all are surface dwellers. Less than 10% are deep and intermediate dwellers. The evolving taxa are primarily surface

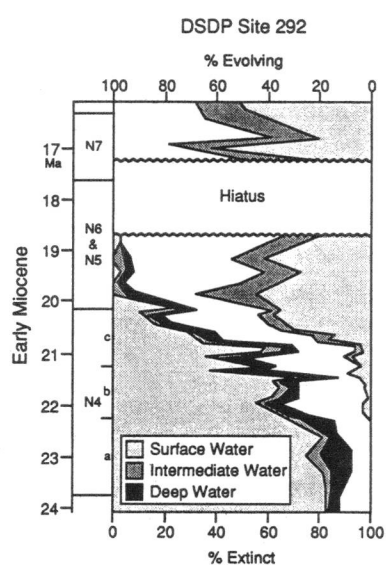


Fig. 9. Early Miocene faunal turnover at west Pacific DSDP Site 292. Note, over 85% of the fauna (in numerical abundance) is becoming extinct and most of these are surface dwellers. The evolving fauna also consists largely of surface dwellers.

dwellers (*Globigerinoides* taxa) and few are intermediate dwellers. This faunal turnover occurred over a 2 million year time period.

No high resolution Early Miocene isotope research is available to date. However, stable isotopic data indicate cooling in Zone N.4 reaching a maximum in Zone N.5 (Savin *et al.*, 1985; Miller *et al.*, 1987). This suggests that the Early Miocene faunal turnover also coincides with a temperature change and increased marine productivity as illustrated in Fig. 5. Global cooling and a change in the water mass stratification during the Early Miocene have been related to intensified oceanic circulation as a result of the opening of the Drake Passage (Kennett *et al.*, 1975; Keller, 1981, 1985; Wei and Kennett, 1986).

Late Miocene

The Late Miocene faunal turnover is shown for east equatorial Pacific DSDP Site 77B along with the oxygen isotope curve from west equatorial Pacific Site 289 (Woodruff *et al.*, 1981) (Fig. 10). One characteristic of this faunal turnover is the pronounced carbonate dissolution in Zones N.15–N.16 frequently associated with a hiatus in virtually all deep-sea sections (Keller and Barron, 1983, 1987). Consequently, the actual faunal decline cannot be documented, but it must have occurred over a period of less than 2 million years. Both surface (*Gl. siakensis*) and intermediate dwellers (*Gl. fohsi* group) disappear at this time. A predominantly globorotaliid intermediate fauna evolves (*Gl. menardii* group, *Gl. acostaensis*) and oxygen isotope data from Site 289 indicates global cooling at this time (Fig. 10).

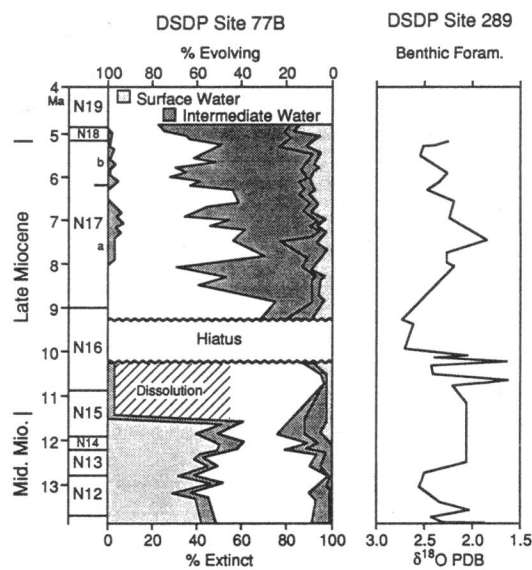


Fig. 10. Middle to Late Miocene faunal turnover at east equatorial Pacific DSDP Site 77B and benthic foraminiferal $\delta^{18}O$ curve from west equatorial Pacific DSDP Site 289 (Woodruff *et al.*, 1981). This faunal turnover coincides with global cooling and is characterized by increased dissolution and a short hiatus in all examined Pacific sites (Keller and Barron, 1983, 1987). Note, the fauna becoming extinct consists primarily of surface dwellers whereas the evolving fauna consists primarily of intermediate dwellers.

DISCUSSION

What drives major faunal turnovers or the decline and eventual extinction of a dominant faunal component and the evolution of a new faunal group? Figure 5 illustrates that each of the faunal turnovers during the Late Eocene to Late Miocene is associated with times of increased nutrient supply and productivity. In contrast, population stability is apparently enhanced during periods of relatively low nutrient supply and correspondingly low productivity. Moreover, the previous discussion and Figs. 7 to 10 point to the coincidence between faunal turnovers and climatic cooling for all but one faunal turnover event (Early/Middle Miocene). It is therefore tempting to conclude that changes in climate and productivity are the primary driving force in major faunal turnovers. Although we believe this conclusion is premature based on our study, there is no doubt that changes in temperature, density, nutrient supply and productivity are intimately linked to evolutionary faunal turnovers. Although our present data set does not allow linkage of specified parameters to specific faunal elements, some generalizations can be made.

The Middle Eocene to Late Miocene cooling trend is interrupted by times of accelerated temperature declines associated with increased productivity presumably as a result of increased mixing in the oceanic water column. To each of these periods of accelerated environmental change planktonic foraminifera respond with accelerated faunal change. If cooling is the primary driving force, one would expect a decrease in the warm surface dwellers and an increase in cooler water taxa. This is indeed the case during the Late Eocene to earliest Oligocene (Fig. 7) and Late Miocene (Fig. 10), but is contrary to the Early Miocene data where Oligocene surface dwellers are replaced by Miocene surface dwellers and Oligocene deep dwellers (*Catapsydrax*) become extinct (Fig. 9). Temperature change alone therefore does not seem to be a sufficient criterion for evolutionary turnover. Salinity and density changes may also play an important role, but present analytical techniques are insufficient to isolate these parameters.

All faunal turnovers examined are accompanied by increased nutrient supply and hence productivity (Fig. 5). The availability of nutrients therefore appears to be a necessary prerequisite for accelerated evolutionary activity. If abundant nutrient supply is a controlling factor, one would expect increased competition primarily in the photic zone (surface layer) and thermocline (intermediate) layer. One would also expect extinctions and originations through competition to be random. This does not appear to be the case because surface dwellers always seem to be affected first, intermediate dwellers second and deep dwellers last. Thus, there appears to be a complex relationship between temperature-density and productivity-nutrient supply that requires further study and in particular studies based on oxygen and carbon isotope analyses of individual planktonic foraminiferal taxa.

Despite the preliminary nature of many of our results, we believe that they offer a tantalizing overview of the

historical complexity of planktonic foraminiferal population dynamics as well as provide a sober realization that any attempt to analyze evolutionary patterns that fails to take temperature, productivity and differences in the spatial distributions of species in the pelagic environment into account is incomplete at best. Our study so far has neglected biotic factors known to influence modern faunas, but a few comparisons between the ecologies of modern faunas and Middle Eocene to Miocene fossil faunas seem relevant. For instance, our data appear to indicate that throughout the study interval, most evolutionary turnovers occur in the surface and intermediate water faunas. If the present really is the key to the past in terms of planktonic foraminiferal ecology, this may be a reflection of the importance of phytoplankton to the maintenance of planktonic foraminiferal diversity. In modern oceans the deep chlorophyll maximum layer typically coincides with the thermocline and exhibits a high density of phytoplankton, a primary food source of many modern adult species as well as the juveniles of both omnivorous and carnivorous taxa, too small to be effectively subdue zooplankton prey (Hemleben *et al.*, 1989). In addition, the thermocline layer represents a region of high physical water density that may offer a relaxation of selection pressures involved in maintaining the organisms' position in the water column, thereby allowing comparatively greater latitude in terms of test shape experimentation.

Moreover, the unanticipated stability of the deep water planktonic foraminiferal fauna may also be explained by analogy with modern fauna. Deep dwellers are exclusively nonspinose taxa (*Catapsydrax* and *Globoquadrina*) whose modern counterparts are omnivorous and depend to a large extent on herbivory to meet their nutrient requirements. However, since these particular fossil taxa are inferred to live well below the photic zone it is difficult to envision that their diet was rich in diatoms and algae or that they depended to any large extent on algal symbiosis. It seems more reasonable to regard these organisms as scavengers that subsisted on a steady rain of organic detritus from shallower, more productive depths. This deep water habitat would then be one of the most specialized that planktonic foraminifera have historically occupied, as well as exhibiting the simplest trophic relationships and being the least disturbed both in terms of changes in the physical environment and in the constancy of nutrient supply.

SUMMARY

In the study of major events in the history of life on earth it is misleading to ignore the fact that each species has its own pattern of distribution and relative abundance in favor of an approach in which all species are regarded as evolutionary and ecological equivalents. The sudden disappearance of a formerly widespread and abundant species is more noteworthy than the extinction of rare forms and the progressive replacement of a fauna adapted to a particular set of environmental conditions in the face of global climate change is more readily understandable than a catastrophic sweepstakes in which

the pattern of faunal turnover is more or less random. An analysis of patterns of variation within Late Eocene through Late Miocene planktonic foraminifera has demonstrated the necessity and practicality of incorporating paleoecological data directly into the analysis of faunal turnover dynamics and has revealed that these organisms display a complex history of faunal decline and replacement that appears to have been mediated by intrinsic changes in the thermal structure of oceanic surface waters over time. Based on these results, we are confident that the general approach to the analysis of planktonic foraminiferal faunas outlined here will provide micropaleontologists with a new and more detailed understanding of planktonic foraminiferal evolution and ecology.

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