A PALEOCEANOGRAPHIC MODEL FOR THE EARLY EVOLUTIONARY HISTORY OF PLANKTONIC FORAMINIFERA

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Abstract

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The first major radiations of planktonic foraminifera occurred during the mid-Cretaceous. However, this period of great diversification was interrupted by two intervals of pronounced paleoceanographic/paleoecologic change, one during the latest Aptian–early Albian and a second associated with the Cenomanian–Turonian boundary. Both of these times corresponded with widespread organic carbon burial during intervals commonly referred to as Oceanic Anoxic Events (OAE) 1 and 2, respectively. This synthesis focuses on the evolutionary history of Aptian–early Cenomanian planktonic foraminifera and the relationship with OAE 1.

Dynamic paleoceanographic changes controlled the course of planktonic foraminiferal evolution during the mid-Cretaceous. Heightened plate tectonic activity, a major long-term rise of global sea level and an overall increase of global temperatures characterized Aptian–Albian time. As proposed here, the evolutionary history of Aptian–early Cenomanian planktonic foraminifera was influenced most strongly by changes in the density structure and stability of the upper water column via changes in the sites and rates of water mass production through time, and perhaps by subtle changes in oceanic productivity (including trophic structure) and shifts in productivity centers with rising sea level. The creation and growth of epicontinental seas played a major role in regional climate change, water mass production and water column structure.

Epicontinental seas were also an important factor in creating vast new niche space and increased biotic diversity for many marine organisms. The amplified seasonality and instability of epicontinental seas resulted in habitation of the upper water column by morphologically simple, eurytopic planktonic foraminifera. Several new species of epicontinental sea dwelling planktonic foraminifera appeared during the mid-Cretaceous. However, much of the diversification of morphologic form took place *in oceanic areas* during times of oceanic stability and upper water column stratification during mid-to late Aptian and late Albian time. A decline in diversity and return to simple morphotypes occurred when oceanic stability was disrupted and the upper water column was poorly stratified during latest Aptian–early Albian time.

Introduction

Planktonic foraminifera have been described from rocks as old as Middle Jurassic (Bajocian Stage). However, this biostratigraphically important group of marine zooplankton did not experience a major diversification in numbers of taxa and in morphologic form until the late Early Cretaceous (Aptian Stage). During the mid-Cretaceous[1], the planktonic foraminifera experienced three episodes of major adaptive radiation (Wonders, 1980). Each of these episodes was characterized by the appearance (and reappearance) of new and varied test

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[1]The mid-Cretaceous is used here to describe the Aptian through Turonian Stages, 119–88.5 Ma based on Harland et al. (1982) and Kent and Gradstein (1985).
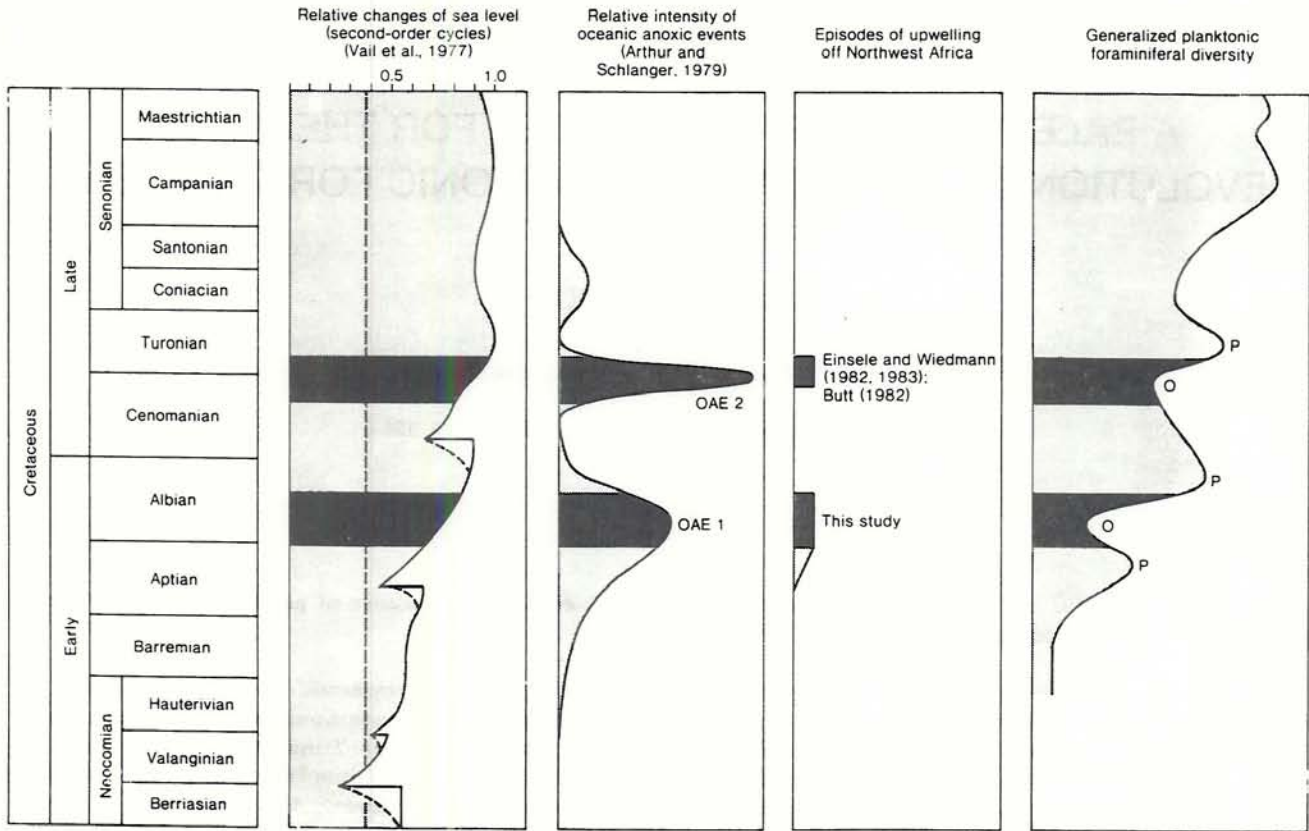
Fig.1. Correlation of global sea level changes, oceanic anoxic events, episodes of upwelling off northwest Africa, and generalized diversity trends in planktonic foraminifera. O = oligotaxic; P = polytaxic (from Leckie, 1984).

morphologies (polytaxic times of Fischer and Arthur, 1977). The intervening times were characterized by marked declines in diversity and a return to simpler test morphologies (oligotaxic times, Fig.1). The purpose of this paper is to examine the earliest of these episodes of adaptive radiation in the planktonic foraminifera from the Aptian through lower Cenomanian record. The focus is on diversity trends and morphologic development, and the possible paleoceanographic conditions that may have significantly influenced the evolutionary history of mid-Cretaceous plankton.

The mid-Cretaceous was an interval of about 30 million years, characterized by significant plate tectonic reorganization and climatic and oceanographic change. During the mid-Cretaceous, the continued breakup of Pangea resulted in the gradual opening of the South Atlantic (Fig.2). Its subsequent connection with the North Atlantic by the end of Cenomanian time (Tucholke and Vogt, 1979) caused a major reorganization of deep water circulation by interrupting the east–west Tethyan regime with a new north–south Atlantic component. Rates of sea floor spreading were also elevated during the mid-Cretaceous (Pitman, 1978; Kominz, 1984; Rich et al., 1986), which coupled with the continued continental dispersal and increase in length of spreading ridges, caused a major rise of global sea level beginning in the Aptian (Vail et al., 1977; Haq et al., 1987). Sea level remained high throughout much of the Cretaceous, although numerous transgressions and regressions of epicontinental seas are recognized (e.g., Kauffman, 1977; Hancock and Kauffman, 1979; Schlanger, 1986). Associated with the high Cretaceous sea level was a shoaling of the carbonate compensation depth (CCD) (Thierstein, 1979; Arthur et al., 1985).
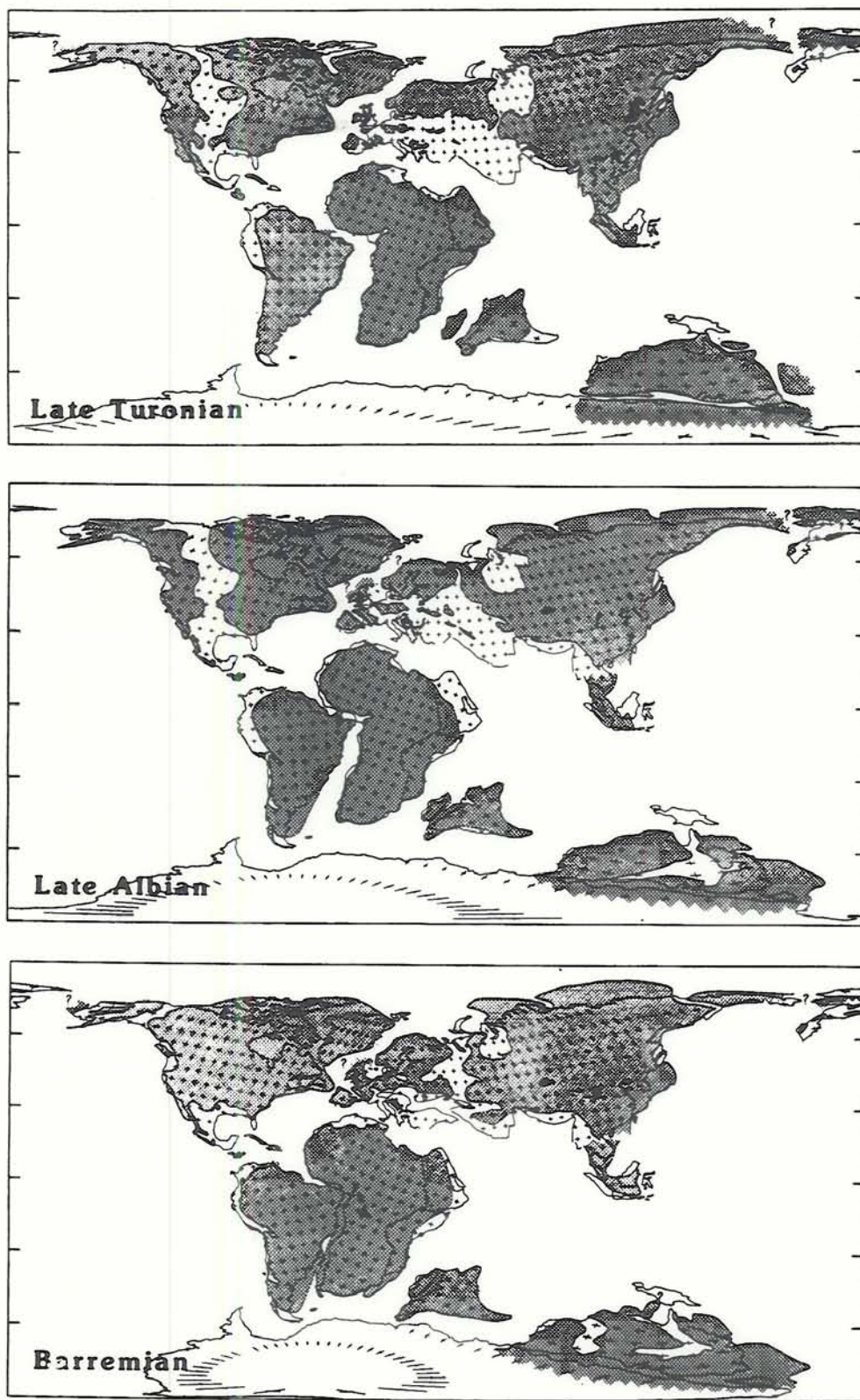
Fig.2. Paleogeography of the mid-Cretaceous. Maps are plotted on a cylindrical equidistant projection. The reconstruction of relative positions of continents is with respect to paleolatitude. Land area is shaded, heavy lines represent ancient shorelines. Top: late Turonian, Middle: late Albian, Bottom: Barremian (from Barron, 1987).

Global climate was considerably warmer during the mid-Cretaceous; equator-to-pole temperature gradients were reduced and the poles were probably ice-free (Barron and Washington, 1982). This had a significant effect on bottom water production and oxygenation. Vast amounts of organic carbon accumulated widely in both epicontinental sea and deep sea environments. Two episodes of intensive organic carbon burial are recognized in the mid-Cretaceous; the first was a protracted interval of cyclical "black shale" deposition during Aptian–Albian time, frequently referred to as Oceanic Anoxic Event 1 (OAE 1), and a second occurred during a brief interval across the Cenomanian–Turonian Stage boundary, referred to as OAE 2 (Schlanger and Jenkyns, 1976; Arthur and Schlanger, 1979).

The level of atmospheric CO_2 is believed to have been elevated during the mid-Cretaceous, due in part to the increased rates of sea floor spreading and concomitant increases in plate margin volcanism and plutonism, but also due to widespread and intense off-ridge volcanism, particularly in the Pacific (Schlanger et al., 1981; Arthur et al., 1985; Barron and Washington, 1985). Increased CO_2 levels may have had profound effects on terrestrial vegetation and the evolution of the flowering plants (angiosperms), on weathering rates and the delivery of nutrients to the marine realm, on phytoplankton productivity and the accumulation of organic matter and carbonate, on climate intensity and vertical mixing in the upper ocean, and on carbonate solubility in the deep sea.

It is within this interval of dynamic change that the planktonic foraminifera and other marine plankton experienced considerable evolution (e.g., Tappan and Loeblich, 1973). There is a striking correlation between the evolutionary history of planktonic foraminifera and oceanographic change during the mid-Cretaceous (Fig.1). The earliest major radiations of planktonic foraminifera correspond closely with the rise of global sea level and subsequent high stands of the middle and Late Cretaceous. Sea level rise and the creation of widespread epicontinental seas may have been a major impetus for their initial diversification and invasion of the open ocean, but changes in the density structure of the upper water column, and perhaps changes in trophic structure, changes in rates of primary productivity and shifts in productivity centers, are here proposed to have most strongly influenced the early evolutionary history of planktonic foraminifera.

An important component of this paper is in the form of a review, with an emphasis on two aspects: first is plankton ecology and the significance of planktonic foraminiferal diversity, and second is mid-Cretaceous paleoceanography. Together these will be used to address possible changes in physical and biological oceanographic conditions during the mid-Cretaceous and the extent to which such changes influenced the evolution of oceanic plankton. This synthesis differs from others (e.g., Tappan and Loeblich, 1973: Fischer and Arthur, 1977; Caron and Homewood, 1982/1983) in that it focuses on a relatively short interval of time, with much of the discussion devoted to the Albian stage. In addition, the model presented at the end of the paper contains alternative hypotheses concerning the nature of the mid-Cretaceous oceans, particularly with regard to the way in which oceanic productivity is interpreted.

Models of planktonic foraminiferal evolution

Numerous studies have examined the Mesozoic–Cenozoic evolutionary history and diversity trends of oceanic plankton. Two fundamentally important observations have emerged from these studies. First is the parallel evolution of the phytoplankton and zooplankton (Tappan and Loeblich, 1973). Second is the iterative evolution (repeated rise of similar morphologies) displayed in the planktonic foraminifera (see review by Vincent and Berger, 1981). Sea level and paleotemperature have frequently been cited as important controls on the observed changes in plankton

diversity through the late Mesozoic and Cenozoic (see review comments by Wei and Kennett, 1986). It is probably not temperature per se, but changes in latitudinal thermal gradients and upper water column thermocline structure that influence ecosystem stability and plankton evolution (Cifelli, 1969; Lipps, 1970; Tappan and Loeblich, 1973; Douglas and Savin, 1978). Likewise, it is probably not sea level per se, but the impact that changes in sea level and extent of epicontinental seas have on regional climate, water mass production, upper water column density structure, and sites of productivity that also influence plankton evolution.

For the planktonic foraminifera, despite different oceanographic regimes during Cretaceous and Cenozoic times, a similar succession of morphotypes has reappeared following a major faunal perturbation (i.e., an ancestral stock of "globigerine" morphotypes gave rise to a diverse assemblage that included "globorotalid-like" morphotypes). Douglas and Savin (1973) attributed the successive appearance of morphotypes during the major Late Cretaceous, Paleogene and Neogene radiations to the development of progressively deeper dwelling species as caused by changes in structure of the oceanic thermocline. According to this depth stratification model, the compressed or keeled morphotypes, in general, represent the deepest-dwelling planktonic foraminifers by analogy with modern species of "Globorotalia". Recent oxygen isotope data suggest that late Paleocene–early Eocene keeled taxa were surface-dwellers (Boersma et al., 1979; Shackleton et al., 1985; Corfield, 1987). However, these taxa also possess surface ornament/texture unlike keeled taxa of either the mid-Cretaceous or Neogene. The importance of depth stratification in the evolutionary history of Cretaceous planktonic has been addressed by numerous authors (e.g., Hart and Bailey, 1979; Hart, 1980; Wonders, 1980; Caron and Homewood, 1982). Wonders (1980) also considered the importance of oxygen-deficient water masses during the mid-Cretaceous Oceanic Anoxic Events on the biostratigraphic record of the presumed deeper-dwelling taxa.

Significance of planktonic foraminiferal diversity

Role of an upper water column thermocline

The functional morphology of the planktonic foraminiferal test is most likely related to maintenance of position in the upper water column (Lipps, 1979), and is controlled in part by the species-specific density of the foraminiferan in relation to the density and viscosity of seawater. The upper water column (0–300 m) of the low to mid-latitudes is characterized by pronounced year-round or seasonal vertical density gradients below the surface mixed layer. Seawater density is controlled primarily by temperature and salinity. Salinity in the open ocean varies much less than temperature, and despite important local salinity effects, the pycnocline over most of the ocean is controlled by the development of the thermocline (Gross, 1985). Seawater viscosity is controlled primarily by temperature in the open ocean (Defant, 1961). Viscosity decreases rapidly with increasing temperature and hence warm water provides less resistance to the sinking of planktonic organisms than does cold water (dynamic viscosity of seawater with salinity of 35‰ at 0°C and 20°C is 0.01877 and 0.01075 g cm^{-1} s^{-1}, respectively; Fofonoff, 1962).

Low latitude species of planktonic foraminifera adapted to the ecologic niche of the warmer, near-surface waters above the thermocline tend to have inflated chambers with little chamber overlap and overall spherical shape. Their flotation is aided by wind-driven mixing, but additional resistance to sinking is afforded by thin test walls, long spines, pronounced test porosity, large apertures, or various combinations thereof (especially Globigerinoides, Globigerina and Globigerinita). Species adapted to the ecologic niche of the cooler, deeper waters within or below the thermocline tend to have non-spinose, thicker, heavier adult tests with lesser porosity. Overall test shape in many of these taxa tends to be more compressed than near-surface dwellers (e.g., Neogloboquadrina and "Turborotalia"); some species have an

angular periphery and/or thickened peripheral keel (e.g., "*Globorotalia*"). This crude depth stratification is borne out by plankton tow and oxygen isotope data (e.g., Bé, 1977; Fairbanks et al., 1980, 1982). A similar depth stratification has been proposed for Cretaceous low to mid-latitude planktonic foraminiferal morphotypes (Douglas and Savin, 1978; Hart and Bailey, 1979; Hart, 1980; Wonders, 1980; Caron and Homewood, 1982; Leckie, 1987).

The diversity (species richness) and morphologic complexity of planktonic foraminifera are greatest in the tropics and subtropics (Fig.3). Time-averaged diversity (i.e., that recorded in well-preserved sediment assemblages) remains fairly high into the temperate mid-latitudes due to a seasonal succession of species which respond to seasonal changes in the structure of the upper water column and seasonal productivity (Bé, 1960; Tolderlund and Bé, 1971; Deuser et al., 1981; Thunell and Reynolds, 1984; Reynolds and Thunell, 1985). The maintenance of "high diversity", in part, reflects the development of strong density contrasts in the upper water column, either year-round (tropics) or seasonal (subtropics and mid-latitudes), which provides the ecologic niches for both "near-surface" and "deeper-dwelling" morphotypes. By contrast, the high latitude thermocline is seasonal and much weaker (Fig.4). Cold near-surface waters make it easier for passive flotation due to the higher
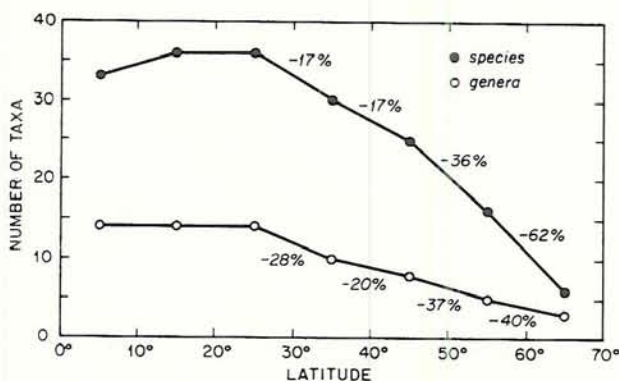

Fig.3. Number of modern species and genera ("morphotypes") of planktonic foraminifera as a function of latitude (expressed as number of taxa per 10° of latitude). Percentages reflect magnitude of change between points. Data from Vincent and Berger (1981).

viscosity. Planktonic foraminiferal diversity and morphologic variability are markedly reduced, depth stratification is much less pronounced and morphologies tend to be simpler. A similar relationship is observed in Cretaceous high latitude planktonic foraminiferal assemblages (e.g., Sliter, 1976; Huber, 1988).

The depth of the thermocline relative to the euphotic zone (e.g., Fairbanks and Wiebe, 1980), also affects diversity and the composition of sediment assemblages. Sediment trap data from two tropical Pacific locations, station P_1 (15°N, 151°W) in the central Pacific and station PB (5°N, 82°W) in the Panama Basin, illustrate the importance of thermocline depth (Thunell, in press). The thermocline is relatively deep and stable (about 100 m) at station P_1 during the time of deployment, while at station PB the thermocline fluctuates and is signficantly shallower (from about 25–50 m). Near-surface dwelling taxa dominate the assemblages at station P_1 to the near-exclusion of deep-dwelling forms, while deep-dwelling taxa make up a third of the assemblage at station PB (Fig.5). At station P_1, primary productivity is low (Honjo and Okada, 1974) due to the depressed thermocline which isolates nutrient-rich deeper waters from the euphotic zone. This also prohibits the deeper-dwelling species of planktonic foraminifera from fluorishing relative to the near-surface dwellers whom bask in the expanded oligotrophic niche space. At station PB, primary productivity is higher (Thunell et al., 1983) due to the relatively shallow thermocline. Both deeper-dwelling taxa and near-surface dwellers flourish in the eutrophic upper water column.

The importance of thermocline depth on the composition of planktonic foraminiferal assemblages is clearly demonstrated by the sediment trap results (Fig.5). Both of these low latitude sites have a strong thermocline within the euphotic zone (upper 100–200 m of the water column). The development of a thermocline *within* the euphotic zone may be an important factor in the maintenance of high species diversity among the planktonic foraminifera. If, however, the upper water column thermo-

	PB (5°N)	PAPA (50°N)
Diversity of Planktonic Foraminifera (total for year)	27	6
Foraminiferal Shell Flux (specimens/m²/day)	210 - 1944	200 - 6800
Depth to top of Thermocline (persistence)	5 - 50 m (year-round)	10 - 20 m (seasonal)
Yearly Range of Surface Temperature	25 - 28°C	5.5 - 14°C
Maximum Temperature Contrast in Upper 100 m	15 - 28°C	4 - 14°C
Maximum Density Gradient (σ_t) for Upper 100 m	19.8 - 25.9 $\triangle$ = 6.1	24.3 - 26.8 $\triangle$ = 2.5

Fig.4. Comparison of sediment trap data from the eastern equatorial Pacific (Panama Basin, Station PB; 5°N, 83°W) with the north Pacific (Station PAPA; 50°, 145°W). PB data from Thunell and Reynolds (1984), PAPA data from Reynolds and Thunell (1985).
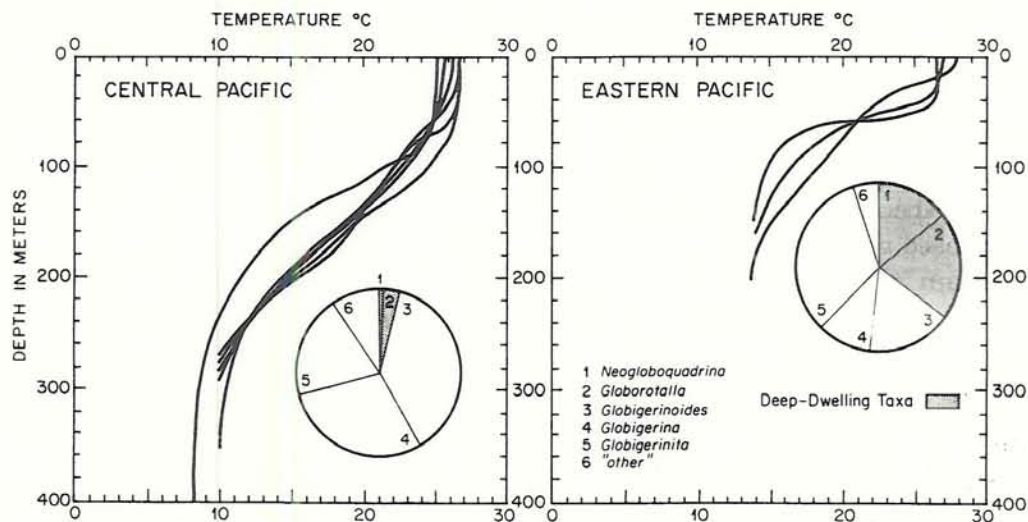

Fig.5. Comparison of sediment trap data from the central Pacific (Station P_1; 15°N, 151°W) and eastern Pacific (Station PB; 5°N, 83°W). The traps were deployed for 61 days (9/78–11/78) and 112 days (7/79–11/79), respectively. Central Pacific thermocline data from Wyrtki et al. (1977; 15°N, 157°W) for the months of September through December. Panama Basin thermocline data from Thunell and Reynolds (1984) for the months of June, August and November. Planktonic foraminiferal assemblage composition based on traps shallower than 2900 m. Diversity: P_1 = 25, PB = 23; Average Shell Flux (specimens m^{-2} day^{-1}): P_1 = 367.5, PB = 1361.7. Trap data from Thunell (in press).

cline was depressed below 200–300 m, the loss of density gradients within the euphotic zone may be expected to greatly reduce species diversity.

Role of ecologic succession and environmental stability

The degree of stability or predictability of an environment has been considered a primary causal factor in the origin and maintenance of species diversity (Lipps, 1979, p. 90). Tappan (1971) observed that the patterns of Phanerozoic microplankton radiations and extinctions resemble that of ecologic succession. On a vastly different time scale, Valiela (1984, p. 414) also notes that the seasonal succession of marine phytoplankton (diatoms, coccoliths) resembles the classical concept of succession developed for terrestrial ecosystems.

Ecologic succession is an orderly process of community development that results from the feedback of inter-organism and organism-environment interactions. The result is a stabilized ecosystem which is biologically accommodated and is characterized by its complexity, high diversity, and efficient utilization of resources. However, if changes occur in the biotic structure or in physical or chemical conditions, the normal developmental sequence is disrupted and succession is slowed, stopped or returned to an earlier, physically accommodated state. Ecologic succession, and hence increasing species diversity and specialization, will proceed only when environmental conditions remain sufficiently constant (Tappan, 1971).

Odum (1971, p. 251) states that "succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go." Following a perturbation, a community evolves towards increased complexity and increased efficiency.

Stability has been correlated with community complexity; the argument being that the greater the number of potential pathways for energy flow, the more stable that community should be (e.g. Odum, 1971). However, Hurd et al. (1971) showed that stability, defined as resistance to perturbations, declined with succession duration and with species diversity of both herbivores and carnivores (Golley, 1977). Might "later stages" of succession, therefore, be expected to show higher rates of evolutionary turnover in response to ever-changing biotic and environmental conditions, with only major perturbations causing community succession to be disrupted?

Tappan (1971) examined the relationship of productivity and ecologic succession to the evolutionary pathways of microplankton. It is important to distinguish between gross production (primary production: the total amount of energy fixed to organic carbon per unit time) and net community production (the rate of storage of organic matter not consumed by heterotrophs). Diversity is low and the ratio of primary productivity to biomass is high in an immature, physically-controlled ecosystem. Gross productivity is not necessarily high although net productivity is relatively high because much of the primary production is not utilized by consumers. Community structure is poorly organized and food chains are linear. Under the right depositional conditions the excess organic matter will accumulate in the sedimentary record. In contrast, diversity is high in a mature, biologically-accommodated ecosystem. Net productivity is low while gross productivity and biomass are high due to efficient resource utilization. Community structure is well-organized, food chains are complex and web-like, and nutrients are tied up in the large biomass (Odum, 1971; Tappan, 1971; Tappan and Loeblich, 1973). Near-surface ecosystem maturity results from factors that increase hydrographic stability of the upper water column and reduce mixing.

The relationship between productivity and diversity has yielded conflicting results (see review by Valiela, 1984). A low supply of an essential nutrient may be insufficient to maintain many species and therefore diversity may be low. Likewise, excess resources may also lower diversity due to exploitation by a fewer

number of opportunistic species (Margalef, 1958; Valiela, 1984). However, diversity is found to be inversely proportional to resource availability in many ecosystems (e.g. Sanders, 1968; Russell-Hunter, 1970; Valentine, 1971). In the northern Sargasso Sea and tropical Atlantic, zooplankton diversity decreases with increasing abundance of zooplankton, and because zooplankton standing crops are correlated to productivity, higher production is correlated to lower diversity (Sutcliffe, 1960; Valiela, 1984). A similar relationship between abundance and diversity is observed in North Pacific coccolithophorids (Honjo and Okada, 1974).

The "cores" of modern pelagic biogeographic provinces (e.g. Bé and Tolderlund, 1971) are thought to represent organized, highly evolved ecosystems made up of species which have all experienced a long period of evolutionary adaptation together (McGowan, 1974). These core ecosystems are large, few in number, relatively old and stable. The ecosystems are separated by ecotones where mixing of species and nutrients occurs. These features are ultimately related to major surface circulation patterns.

Bé (1977, p. 41) noted that, in general, species diversity of planktonic foraminifera decreases from the fertile to infertile areas within a water mass (e.g. from the outer fringe to the central part of the Sargasso Sea). However, the areas of greatest oceanic fertility (boundary currents, divergences, upwelling zones) also correspond to areas of faunal mixing (e.g., Cifelli and Benier, 1976). Foraminiferal abundances, diversity and assemblage composition fluctuate seasonally, especially in the ecotones and mid-latitudes (Bé, 1960; Tolderlund and Bé, 1971; Deuser et al., 1981; Thunell and Reynolds, 1984; Reynolds and Thunell, 1985). This is the result of seasonal succession in the planktonic foraminifera. As a consequence, total species diversity in sediment assemblages beneath the ecotones can be as high or higher than those of the adjacent core ecosystems.

The relationship between diversity and productivity in modern planktonic foraminifera is unclear. It is clear, however, that diversity and productivity are not necessarily correlated (Fig.5). Because sediment assemblages are time-averaged due to seasonality or faunal mixing, it is difficult to interpret the paleoecologic significance of "diversity" and morphologic variability in terms of paleofertility; diversity will be low in a homogeneous upper water column irrespective of fertility. A much stronger correlation exists between diversity and upper water column density structure. However, the long-term evolution of near-surface marine ecosystems (ecologic succession) including changes in resource utilization efficiency and trophic structure, following some form of major ecologic perturbation may have been an important factor in the evolutionary history of planktonic foraminifera.

Data base

The principal data base of this study is the stratigraphic occurrence of simple planktonic foraminiferal diversity (species richness) through the mid-Cretaceous as reported by a number of specialists from a variety of localities. The diversity curves recorded in Fig.6 represent the "raw" data; no attempt is made to standardize species concepts. The most important criterion in selection of data sources was a thorough documentation of the planktonic foraminiferal assemblages (i.e., all taxa, not simply the biostratigraphically useful forms). One of the sources represents a major collaborative review of taxon ranges by a European working group (Robaszynski, Caron et al., 1979), while another is a major taxonomic and biostratigraphic synthesis of Cretaceous planktonics (Caron, 1985). The majority of the other sources come from detailed local or regional studies. Additional criteria considered in their selection for use here included good stratigraphic resolution of the sections and good preservation of the assemblages. The primary data comes from Europe (Moullade, 1966; Longoria, 1974; Robaszynski, Caron et al., 1979; Premoli-Silva, 1980, unpublished data; Caron, 1985), the eastern North Atlantic

AGE		Planktonic Foraminiferal Zones	Planktonic Foraminiferal Diversity

Planktonic Foraminiferal Diversity

5 10 15 20

AGE			Planktonic Foraminiferal Zones
TURONIAN	Late		Marginotruncana sigali
	Mid		Helvetoglobotr. helvetica
	Early		Whiteinella archeocretacea
CENOMANIAN	Late		Rotalipora cushmani
	Middle		Rotalipora reicheli
	Early		Rotalipora gandolfii
ALBIAN	Late	Vrac.	Rotalipora appenninica / P. praebuxtorfi
			Rotalipora ticinensis / subticinensis
	Mid.		Ticinella praeticinensis
	Early		T. primula
			Globigerinelloides gyroidinaeformis
	Cl.		Planomalina cheniourensis
APTIAN	Late		H. trocoidea
			Gl. algerianus
			Gl. ferreolensis
			S. cabri
	Early		Gl. blowi
			H. sigali

(zonal side-labels: buxtorfi, breggiensis, T. roberti s.l., T. roberti s.l.)

SOURCES:

○ CARON, 1985 (Cretaceous Review)

✕ FRUSH & EICHER, 1975 (Cenom–Turon boundary)

● LECKIE, 1984 (mid-Aptian – late Cenomanian)
LECKIE, 1985 (Cenomanian–Turonian boundary)

■ LONGORIA, 1974 (Aptian)
LONGORIA & GAMPER, 1977 (Albian)

+ MOULLADE, 1966 (Aptian – Albian)

▼ PREMOLI SILVA, 1980, unpubl. (Aptian – Tur)

▲ ROBASZYNSKI, CARON, et al., 1979 (Cen – Tur)

◆ SIGAL, 1979 (Aptian – Albian)
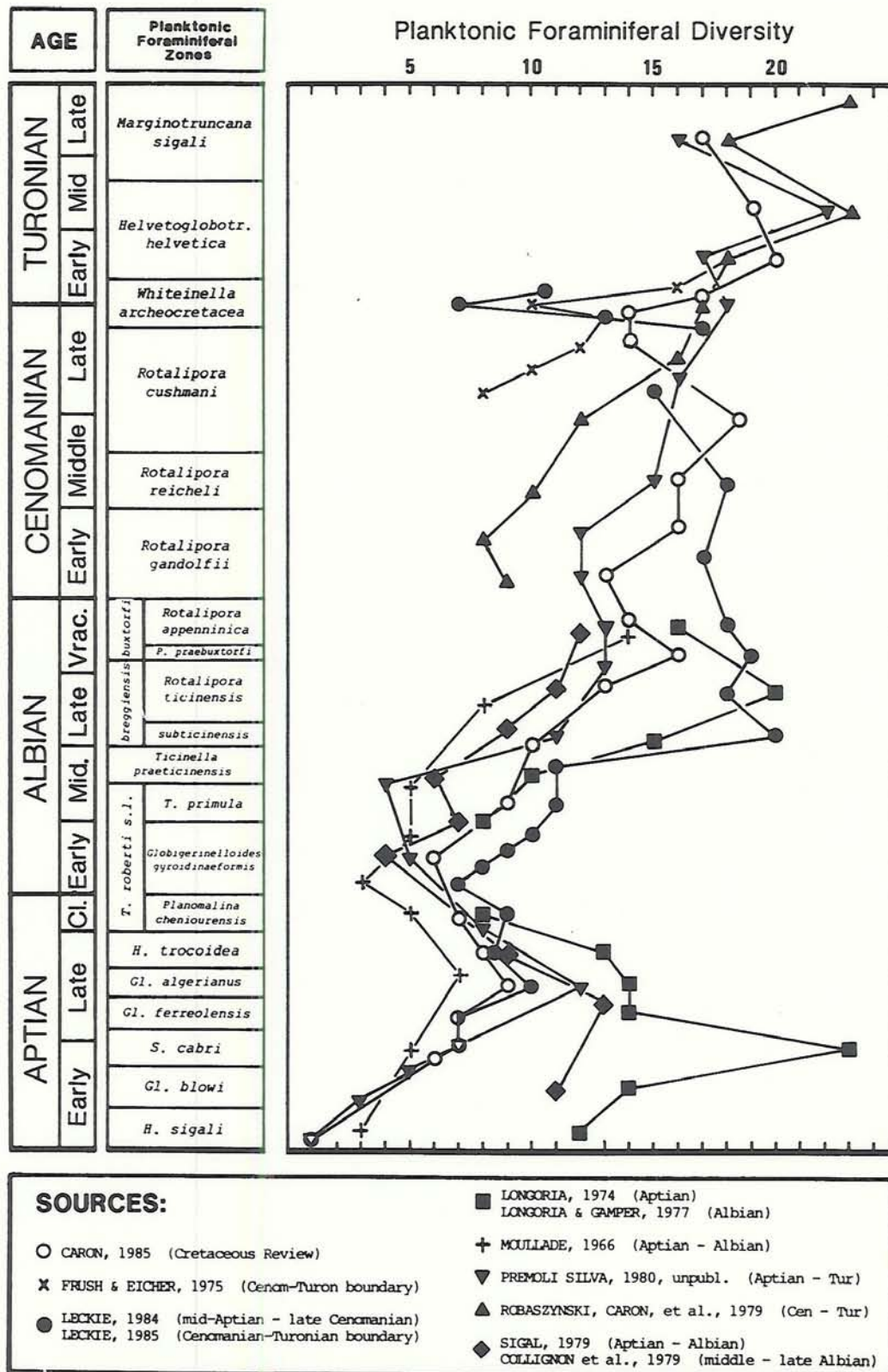COLLIGNON et al., 1979 (middle – late Albian)

Fig.6. Planktonic foraminiferal diversity through the mid-Cretaceous. Fluctuations in individual curves are not an artifact of preservation. Data from many of the sources are derived from composite detailed stratigraphic range information (see text). Differences between curves, especially the magnitude of changes, reflect the taxonomic approaches of the many specialists represented here and the extent to which the small taxa were fully documented. Frush and Eicher (1975) diversity data from Hot Springs, Texas section only. Leckie (1985) data from Rock Canyon, Colorado. Leckie (1984) data from DSDP Sites 545 and 547 off Morocco. Sigal (1979) data from DSDP Site 398 off Iberian peninsula. The other sources represent composite stratigraphic range data from numerous sections. Zonal scheme after Leckie (1984).

(Sigal, 1979; Leckie, 1984), northern Mexico (Longoria, 1974; Longoria and Gamper, 1977), U.S. Western Interior (Frush and Eicher, 1975; Leckie, 1985), and Madagascar (Collignon et al., 1979). Published results from the Pacific also support the diversity trends from this predominantly Tethyan margin/North Atlantic data set (Luterbacher, 1975; Boersma, 1981).

Differences in the individual diversity curves arise from several factors. Most importantly are differences in the taxonomic approaches of the workers represented (i.e., "lumpers" vs. "splitters"), as well as the extent to which the smaller taxa are fully documented. Despite the obvious discrepancies, examination of individual diversity curves shows clear, consistent trends: (1) increase in taxonomic diversity through the early Aptian, peaking in the mid to late Aptian; (2) decrease during the latest Aptian and early Albian; (3) marked increase during the late Albian; (4) slight decline during the early or mid-Cenomanian; (5) general increase through the late Cenomanian; (6) marked decrease across the Cenomanian–Turonian boundary (as documented at many localities); (7) increase during the early Turonian; (8) decrease in the mid-Turonian. These trends are summarized in a generalized diversity curve in Fig.7.

It is unlikely that the apparent decline in diversity during the latest Aptian-early Albian is an artifact of widespread poor preservation. Some of the taxa lost in this interval include heavily calcified forms (e.g., *Planomalina cheniourensis*), while other smaller, less heavily calcified forms range throughout (e.g., *Hedbergella planispira*, *Gubkinella graysonensis*). In addition, much of the data comes from relatively shallow, mid- to upper bathyal paleoenvironments, well above the CCD (e.g., Leckie, 1984).

Diversity trends and morphologic development in mid-Cretaceous planktonic foraminifera

Planktonic foraminifera of the Jurassic and early part of the Cretaceous were smallish
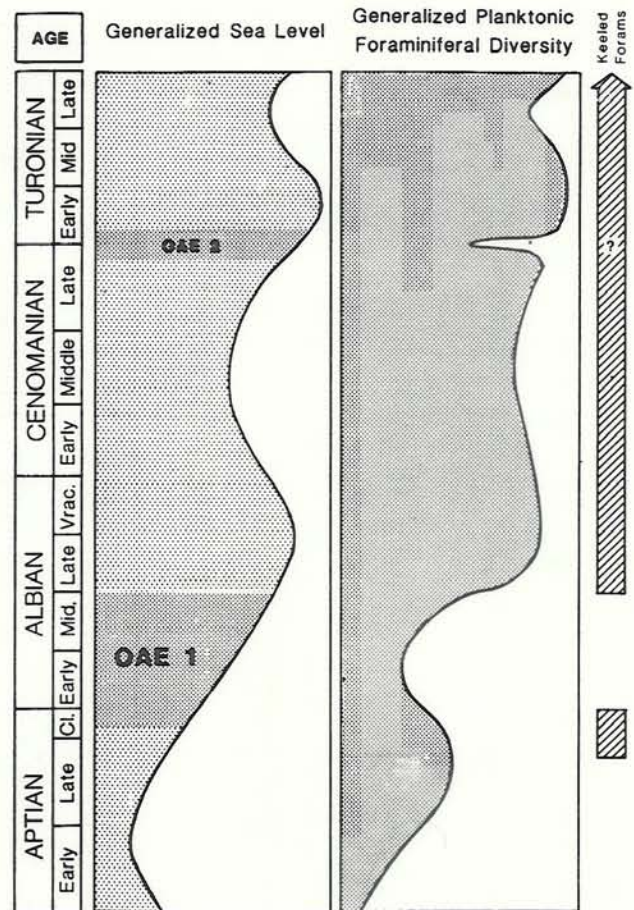

Fig.7. Generalized planktonic foraminiferal diversity curve compared with "long-term" eustatic cycles of Haq et al. (1987). Note close similarity of the curves except for diversity perturbations during latest Aptian–middle Albian time and near the Cenomanian–Turonian boundary. These intervals correspond to OAE 1 and OAE 2, respectively. The stratigraphic distribution of keeled planktonic foraminiferal morphotypes also reflects the marked declines in diversity.

trochospiral forms with simple "globigerine" morphologies (simple: referring to forms with inflated globular chambers and little chamber overlap, simple umbilical apertures, absence of thickened sutures or peripheral keels). Variability was primarily expressed as differences in spire height, and subtle differences in surface texture and/or apertural shape (e.g., Grigelis and Gorbatchik, 1980; Stam, 1986; Riegraf, 1987). These early taxa were very rare in oceanic settings and are believed to have been restricted to relatively shallow marginal seas (Masters, 1977; Caron and Homewood, 1982;
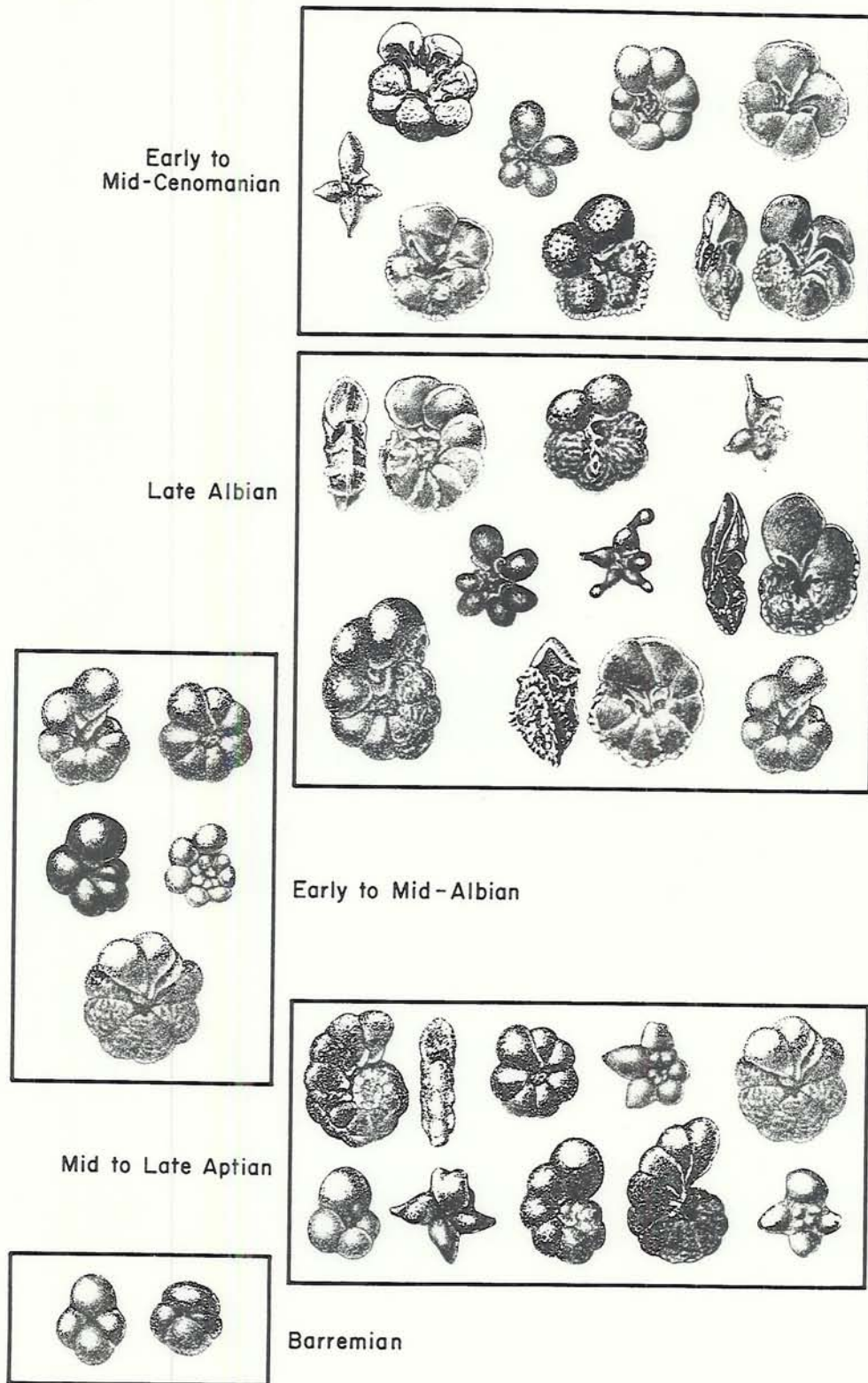
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Fig.8. Planktonic foraminiferal morphotype evolution during late Early Cretaceous. Note relatively simple inflated morphotypes in Barremian and early to mid-Albian versus diverse, complex, specialized morphotypes in mid to late Aptian, late Albian, and early to mid-Cenomanian.

Riegraf, 1987). Caron (1983) has suggested that they had a benthic stage in their life cycles. Invasion of the pelagic habitat may have been stimulated by oxygen-poor conditions associated with warm, stratified oceans (Tappan and Loeblich, 1973).

Planktonic foraminifera experienced their first major adaptive radiation in the Aptian (Fig.6). During this interval the planispiral morphotypes appeared (*Globigerinelloides*), as well as morphotypes with radially elongate chambers (*Leupoldina*) and a greater variety of trochospiral forms (especially species of *Hedbergella*) (Fig.8). By late Aptian time, specialized morphologic features such as primitive apertural plates and accessory apertures (*Tici-*

nella), and peripheral keels (*Planomalina*) had appeared (Fig.9; see also Longoria, 1974; Leckie, 1984; Sliter, 1989). Diversity reached a peak in the mid- to late Aptian and then declined markedly during the latest Aptian and early Albian (Fig.6). Lost were all radially elongate planispiral species and the keeled morphotype, among others.

Although several new taxa evolved during the early and middle Albian, diversity of planktonic foraminifera remained significantly lower than that of the late Aptian, and oceanic assemblages consisted of relatively simple morphotypes (mainly *Hedbergella*, *Globigerinelloides* and primitive *Ticinella*) (Fig.9). Cancellate ("honey-comb") taxa of the genus *Favusella* became abundant in warm neritic carbonate environments during the mid- to late Albian but are not known from oceanic settings (Michael, 1972; Longoria and Gamper, 1977; Grigelis and Gorbatchik, 1980).

An explosion of planktonic foraminiferal diversity occurred during late Albian time (Fig.6). Numerous keeled taxa appeared (*Rotalipora*, *Planomalina*, *Praeglobotruncana*) as well as new and different taxa with radially elongate chambers (*Clavihedbergella*, *Schackoina*). The biserial morphotype (*Heterohelix*) also appeared during the late Albian. Latest Albian time witnessed the demise of *Ticinella* and *Planomalina* and continued diversification of *Rotalipora* and *Praeglobotruncana* (Fig.8). Total diversity remained high into the Cenomanian and, like those of the late Albian, Cenomanian assemblages are characterized by a great variety of morphologies (Fig.9; see also Loeblich and Tappan. 1961; Robaszynski, Caron et al., 1979; Leckie, 1984; Caron, 1985). Double-keeled taxa of the genus *Dicarinella* first appeared in the late Cenomanian.

Another marked, though brief, decline in planktonic foraminiferal diversity occurred during latest Cenomanian–earliest Turonian time (Fig.6). The Cenomanian-Turonian boundary interval is characterized by the extinction of the genus *Rotalipora*, "brief absence" of other keeled morphotypes at many localities, and abundance of large, inflated, relatively
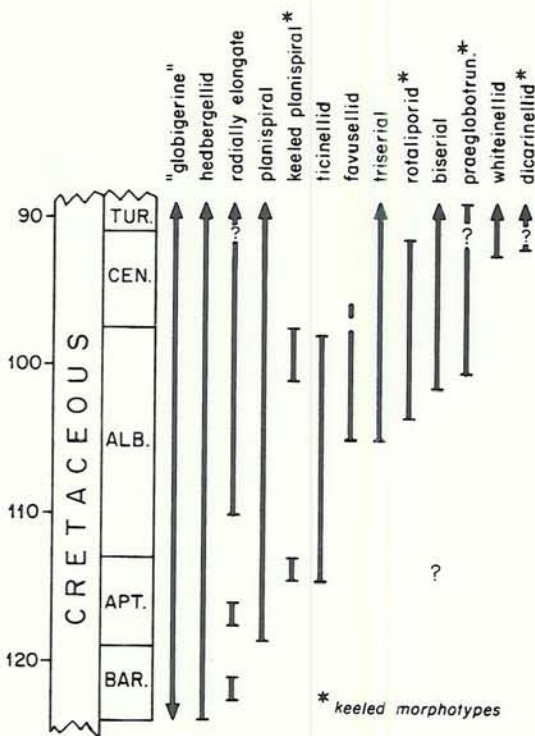

Fig.9. Planktonic foraminiferal morphotypes from the mid-Cretaceous "Globigerine" includes *Globuligerina* (last occurrence in Aptian) and *Gubkinella* (first appearance in Aptian), radially elongate forms include *Clavihedbergella* (first appearance in Barremian), *Leupoldina* (restricted to Aptian) and *Schackoina* (first appearance in latest Albian), planispiral refers to *Globigerinelloides*, keeled planispiral refers to *Planomalina*, triserial refers to *Guembelitria*, and biserial refers to *Heterohelix*. Data from Caron (1985), Leckie (1984), Longoria (1974) and Moullade (1966). Time scale from Harland et al. (1982) and Kent and Gradstein (1985).

simple taxa of the genus *Whiteinella* (see also Pessagno, 1967; Eicher and Worstell, 1970; Robaszynski, Caron et al., 1979; Leckie, 1985; Premoli-Silva and Sliter, 1985). During the early and middle Turonian, keeled taxa of the genera *Dicarinella* and *Marginotruncana* diversified rapidly while *Praeglobotruncana* declined.

A comparison of long-term eustatic sea level changes (Haq et al., 1987) with the generalized diversity trends of planktonic foraminifera through the mid-Cretaceous shows a striking positive correlation (Fig.7). Note, the correspondence between highest diversities and peak transgressions in the late Albian and early Turonian. There are, however, two notable exceptions to the correlation between sea level and planktonic foraminiferal diversity: latest Aptian–middle Albian time and the Cenomanian–Turonian boundary interval. Both of these intervals corresponded with times of vast accumulation of organic carbon in the marine realm during OAE 1 and OAE 2. This coincidence suggests that there may have been a close causal relationship between the tectonic, climatic and oceanographic factors responsible for the deposition and preservation of organic carbon, and the evolutionary history of the planktonic foraminifera. It does not, however, imply that OAE 1 and OAE 2 were repetitions of the same physical, chemical and biological phenomena (Arthur et al., 1985).

The lack of a refined and accurate absolute time scale for the mid-Cretaceous, particularly at the substage and biostratigraphic zonal level, precludes all but qualitative assessment of evolutionary rates. The number of first and last appearances of taxa based on several studies is shown in Fig.10. Times of heightened evolutionary turnover (speciation plus extinction) alternate with intervals of reduced turnover. The greatest "rates" of evolutionary turnover are associated with times of peak transgression (late Albian, late Cenomanian–early Turonian), while reduced "rates" are associated with minor regressions (early to mid-Cenomanian, mid to late Turonian) and the OAEs (early Albian, Cenomanian–Turo-

nian boundary interval). A similar trend is also documented in the calcareous nannoplankton (Roth, 1987). Although this study focuses on the Aptian–lower Cenomanian record, there are enough gross similarities between OAE 1 and OAE 2 to warrant a brief appraisal of the younger and better known Cenomanian-Turonian event.

The Cenomanian–Turonian boundary event (OAE 2)

The Cenomanian–Turonian boundary has received considerable attention due to its paleoceanographic and paleobiologic significance (see reviews by Arthur et al., 1987; Schlanger et al., 1987). The changes that occurred in the planktonic foraminiferal assemblages across the boundary have been addressed by numerous studies (e.g., Hart, 1980; Wonders, 1980; Caron and Homewood, 1982; Leckie, 1985; Hart and Ball, 1986). Marine strata of the upper Cenomanian and lower Turonian record the periodic deposition of organic carbon-rich sediment believed to have accumulated in oxygen-deficient environments (e.g., Barron et al., 1985). Such conditions were particularly characteristic of upper continental slope and epicontinental sea environments (e.g. Pratt et al., 1985; Schlanger et al., 1987). Extreme oxygen deficiency occurred during a brief period of less than 1 million years embracing the Cenomanian–Turonian boundary (Schlanger et al., 1987). This boundary interval is coincident with the widespread accumulation of organic carbon-rich black shale or marlstone in which the carbonate fraction is characterized by a positive excursion in $\delta^{13}C$ values and corresponds to Oceanic Anoxic Event 2 (OAE 2) of Arthur and Schlanger (1979).

The predominantly marine character of the organic matter and the enriched $\delta^{13}C$ values of the carbonate are convincing evidence for enhanced rates of primary productivity during this event, which in turn is considered responsible for the creation of widespread oxygen-deficient water masses in the form of expanded
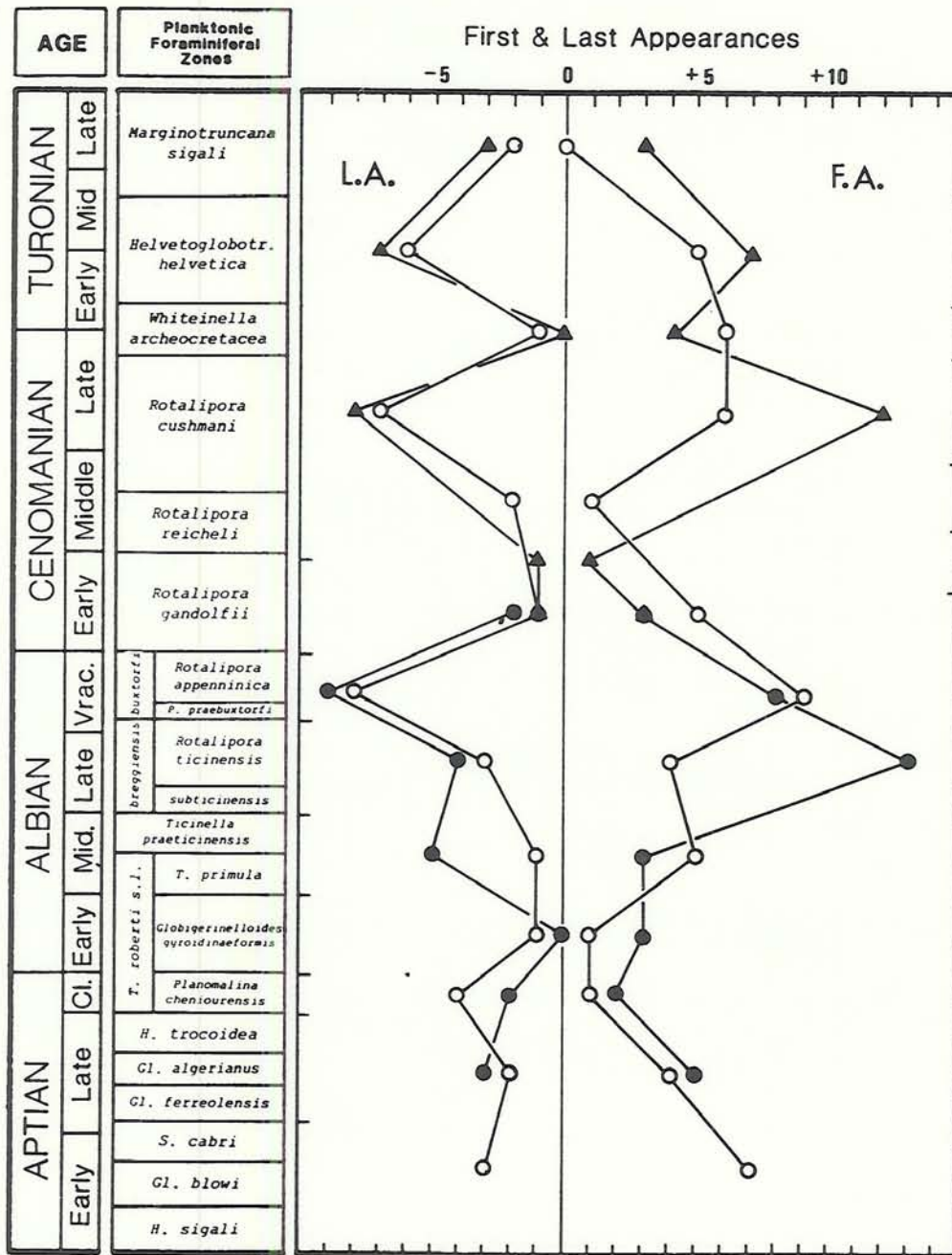
Fig.10. Number of first and last appearances of planktonic foraminifera through the mid-Cretaceous. Data from Leckie (1984) (solid circles), Caron (1985) (open circles) and Robaszynski et al. (1979) (solid triangles). Curves were constructed following the methodology of Bujak and Williams (1975). Tick marks on left represent the intervals used for the Aptian–Albian, tick marks on right for Cenomanian–Turonian.

and intensified oxygen-minimum zones (Schlanger and Jenkyns, 1976; Schlanger et al., 1987; Arthur et al., 1987; Jarvis et al., 1988). Increased sea-surface fertility and productivity are thought to have been stimulated by increased rates of warm, saline deep water formation associated with approach of maximum transgression (see models by Eicher and Diner, 1985; Arthur et al., 1987). Another model (Arthur and Natland, 1979; Tucholke and Vogt, 1979) relates the increased productivity to gradual breaching of a critical sill depth which

then allowed the exchange of deep waters between the North and South Atlantic towards the close of Cenomanian time. This exchange may have flushed out nutrient-laden deep waters thereby enhancing surface-water fertility.

Perhaps, too, the role of multiple deep water sources became increasingly important as epicontinental seas reached into the higher latitudes with rising sea level. Boreal water masses, in particular (e.g., Hilbrecht and Hoefs, 1986), may have contributed to the enhanced productivity by enhancing circulation intensity. The vast extent of latest Cenomanian–earliest Turonian epicontinental seas themselves may have provided an enormous reservoir of nutrients via swamping of the land masses. Even if these epeiric seas were stratified, horizontal advection may have been more than adequate to stimulate high primary productivity and resultant expansion of oxygen minimum zones well beyond the continental margins.

The planktonic foraminiferal assemblages of the Cenomanian–Turonian boundary interval are characterized by an abundance of relatively simple inflated morphotypes and an absence of keeled species, and hence show a marked decline in diversity (Fig.6). It is, however, noted that species of *Praeglobotruncana* and the earliest representatives of *Dicarinella* must have "survived" the boundary interval somewhere (Fig.6). The keeled species of planktonic foraminifera are believed to have had narrow environmental tolerances (i.e., stenotopic) and to have been the deepest-dwelling (e.g., Douglas and Savin, 1978; Hart, 1980; Wonders, 1980; Caron and Homewood, 1982; Leckie, 1987). The brief absence of keeled species may have resulted from several factors:

(1) Expansion of oxygen-minimum zones to within tens of meters of the surface thereby impinging on the niche of the deepest-dwelling planktonic foraminifera (Hart, 1980; Wonders, 1980; Leckie, 1985). Leckie (1985) noted that the last two species of *Rotalipora* became more inflated compared to their earlier morphologies during the later part of their ranges. This trend was taken to an extreme in the U.S.

Western Interior Seaway where Eicher (1972) documented the evolution of *Anaticinella multiloculata* from *Rotalipora greenhornensis* by the loss of the peripheral keel and increased chamber inflation. A similar morphologic transformation may also occur in *R. cushmani* (Leckie, 1985). Wonders (1980) suggested that the *Rotalipora–Anaticinella* transformation represented an evolutionary response to occupy shallower habitats in the face of expanding oxygen minimum zones. The earliest representatives of the twin-keeled genus *Dicarinella* first appeared in the latest Cenomanian at a time when *Rotalipora* was on its way out. Like the last species of *Rotalipora*, the first *Dicarinella* had generally inflated tests. Perhaps the cores of oligotrophic central oceanic gyres provided the refugia for *Praeglobotruncana* and *Dicarinella* (i.e., the keeled "survivors") as the areas of the ocean farthest removed from the expanded oxygen minimum zones of the epicontinental seas and continental margins.

(2) Homogenization of the upper water column and breakdown of stable density stratification by cooling of upper water masses, warming of deep or intermediate water masses, or enhanced rates of vertical mixing. Accordingly, the loss of pronounced density stratification might disrupt the niche of the deepest-dwelling (i.e., keeled) taxa. Contrasting models have been invoked: increased production of warm, saline deep waters (Eicher and Diner, 1985; Arthur et al., 1987) and cooling of water masses (Hilbrecht and Hoefs, 1986). Bralower (1988) has stressed the importance of local tectonic, climatic and oceanographic perturbations and their ability to mask global phenomena. In this case, the global phenomenon was an apparent increase in productivity. The widespread expansion of oxygen minimum zones, as evidenced by the biotic and rock records (Arthur et al., 1987; Schlanger et al., 1987), may have been coupled with local changes in upper water column density stratification.

(3) Ecologic stress related to high surface water fertility thereby eliminating the stenotopic taxa. The influence of high productivity on diversity and community structure is difficult

to prove. As currently understood, the Cenomanian–Turonian boundary interval records a far-reaching, synchronous or nearly synchronous oceanographic event. The apparent increase in oceanic fertility was dramatic. Not only did gross productivity increase, but inefficient(?) utilization by consumers may have increased net productivity thereby supplying "excess" organic matter to the sedimentary record. Increased marine productivity was responsible for the expansion of oxygen minimum zones, which may themselves have been solely responsible for the demise of some planktonic foraminifera as outlined above. The record of decreased planktonic foraminiferal diversity across the Cenomanian–Turonian boundary might also be a partial result of widespread perturbation of trophic resources or trophic structure and resultant disruption of ecologic succession. This hypothesis needs to be tested further.

The Aptian–early Cenomanian record and OAE 1

Like late Cenomanian–earliest Turonian time, the Aptian–Albian was a time of rising global sea level. There are, however, important distinctions related to sea level and paleogeography that bear on paleoceanographic differences between these two time intervals. Firstly, there were marked differences in the areal extent of continental flooding during Aptian–Albian and Cenomanian–Turonian times. The first major transgression, with its widespread drowning of vegetated continental margins and coastal plains, began during the mid-Aptian and reached peak transgression during the late Albian by most accounts (Sliter, 1976; Kauffman, 1977; Matsumoto, 1980; Schlanger, 1986; Haq et al., 1987). Despite a minor regression in the early to mid-Cenomanian, epeiric seas remained fairly extensive and did not withdraw from many continental areas. The subsequent earliest Turonian peak transgression yielded the greatest flooding of continental areas during Cretaceous time. Secondly, Aptian–Albian time was dominated by

east–west circulation and water mass exchange while Cenomanian–Turonian time saw the introduction of new north–south exchange routes. The North and South Atlantic were separated for much of Aptian–Albian time, especially to exchange of deep water masses (Fig.2). This situation changed markedly by the end of the Cenomanian (Tucholke and Vogt, 1979; Arthur and Dean, 1986). Because of these differences, one would expect different paleoceanographic regimes related to circulation and sites of water mass production, for example, and perhaps in the delivery of nutrients to the oceans and sites of highest primary productivity.

Other important differences with the latest Cenomanian–earliest Turonian interval are related to the duration of widespread organic carbon burial and the type of organic matter. OAE 1 was a protracted interval of cyclic, organic carbon-rich sediment deposition, but like OAE 2, was characterized by a positive excursion in $\delta^{13}C$ carbonate values. This excursion peaked during latest Aptian and early Albian time, and may represent the time of maximum organic carbon burial during OAE 1 (Scholle and Arthur, 1980). A decline in planktonic foraminiferal diversity as well as minor declines in dinoflagellate and calcareous nannofossil diversity are coincident with the $\delta^{13}C$ peak (Fig.11). The $\delta^{13}C$ enrichment near the Cenomanian–Turonian boundary (OAE 2) has been attributed to the burial of organic carbon, due in part to a brief interval of enhanced primary productivity (Arthur et al., 1987). Planktonic foraminiferal populations were clearly affected by the dynamic oceanographic changes responsible for that increased fertility, either through expanded oxygen-minimum zones and/or trophic perturbation (see previous section). Does a similar scenario apply to OAE 1?

The organic matter deposited during OAE 2 is dominantly marine. The organic matter deposited during OAE 1 varies from basin to basin as did the specific oceanographic, climatic and tectonic conditions that controlled its deposition, but the Aptian–Albian black shale
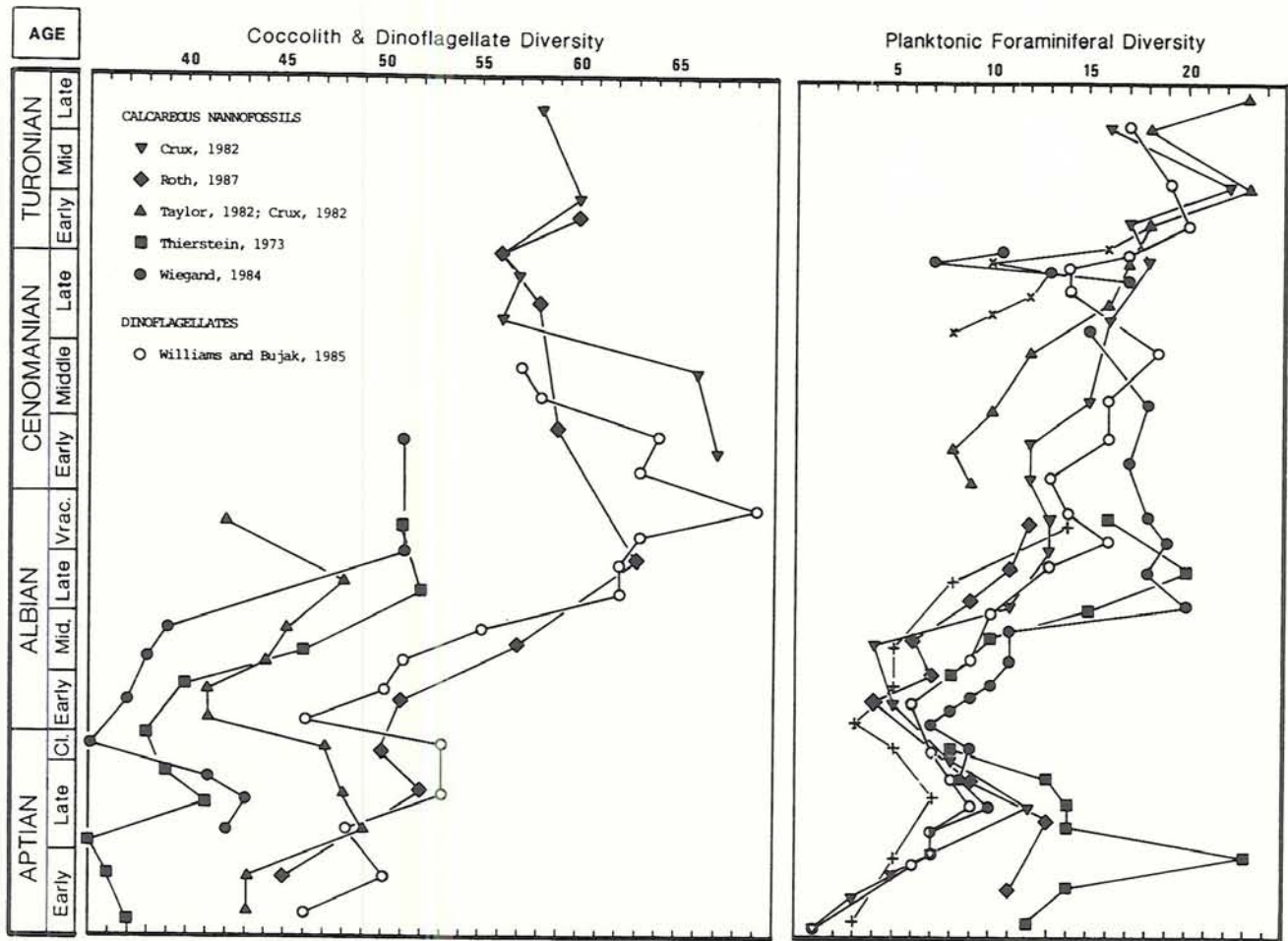
Fig.11. Comparison of planktonic foraminiferal diversity curves with those of phytoplankton. Note decline in plankton diversity during latest Aptian–early Albian time and marked increase during late Albian time. Wiegand (1984) data from DSDP sites 545 and 547 in the eastern North Atlantic (same sites as Leckie, 1984). Data of Crux (1982) and Taylor (1982) represents composite stratigraphic distribution of calcareous nannoplankton from Great Britain. Thierstein (1973) data from southeastern France sections only (La Charce, La Bédoule Station de Cassis, Lesches-en-Diois, Col de Pallvel). Roth (1987) represents composite stratigraphic range data. Dinoflagellate diversity of Williams and Bujak (1985) represents a composite tabulation of their Boreal and Tethyan range data.

facies is characterized by an abundance of terrigenous organic matter (e.g. Tissot et al., 1980). However, significant quantities of marine organic matter are also reported in the southern and southeastern North Atlantic, the South Atlantic, and the equatorial Pacific (Tissot et al., 1980; Dean and Gardner, 1982; Thiede et al., 1982).

Both the Aptian–Albian and the Cenomanian–Turonian records contain an interval of significant decline in planktonic foraminiferal diversity during a time of overall diversification of marine plankton (Fig.1). Changes in the density gradient of the upper water column, and perhaps ecologic perturbations related in part

to productivity and ecosystem succession, are believed to be important controls on planktonic foraminiferal diversity. In the sections that follow, models of mid-Cretaceous water mass production and productivity will be reviewed and further developed, as well as salinity and temperature trends, in an attempt to relate these oceanographic dynamics to the evolution of planktonic foraminifera during Aptian–early Cenomanian time.

Water mass production and circulation

The possibility for a reversal in thermohaline circulation was first suggested by Cham-

berlin (1906). Under warm climatic conditions and in the absence of significant high latitude sea-ice formation, deep water production may have occurred in arid low latitude areas by the sinking of warm, oxygen-poor saline waters ("buoyant plumes" of Brass et al., 1982). It has been proposed that this process was a major source of deep water masses during the mid-Cretaceous and the principal reason for the widespread preservation of organic carbon in the deep sea (see reviews by Arthur, 1979; Roth and Bowdler, 1981; Weissert, 1981; Hay, 1983; Arthur and Dean, 1986; Barron, 1986). Recent models of "Warm Saline Bottom Water" (WSBW) production support a hypothesis of active thermohaline circulation, as opposed to the more widely modeled conditions of sluggish circulation (Barron and Washington, 1982; Brass et al., 1982; Saltzman and Barron, 1982; Southam et al., 1981; Hay, 1983; Barron, 1986). The vigor of bottom water circulation has a significant effect on nutrient recycling and hence fertility in the surface waters.

According to a model by Brass et al. (1982), WSBW originated from marginal seas in zones of net evaporation. This model infers that the buoyancy flux of WSBW (product of the density difference between the buoyant plume and its surrounding environment, and the rate of production) is essentially dependent upon the area of the basin and the evaporation rate. Hay (1983) suggests that WSBW plumes probably had lower buoyancy fluxes than the present polar plumes. It is likely that there were numerous sources. The plumes were probably delicately balanced with local differentiation of bottom, deep and intermediate (or shallow) water masses between ocean basins (Hay, 1983). The production of WSBW from the various sources may have been episodic (or periodic), much the same way as other climatically-influenced processes were controlled. Climatic cyclicity may have been controlled by Milankovitch orbital perturbations (e.g. Arthur et al., 1984; Barron et al., 1985).

Alternate models are presented by Wilde and Berry (1982). According to their Case A model, 18°C "Salinity Maximum Water" (SMW) formed in oceanic areas where evaporation exceeded precipitation and mixed with >5°C "High Latitude Water" to form "Salinity Maximum Bottom Water." They also suggest that denser water may have formed in marginal evaporative basins ("Shelf Sea Water," SSW) but probably did not have the necessary buoyancy flux to become bottom water. Therefore, SSW would have mixed with other water masses and spread out at intermediate (or shallow?) depths similar to the outflow of Mediterranean and Red Sea waters into the North Atlantic and Indian Oceans today. According to the Case A model, the base of the oceanic pycnocline would be at about 2900 m compared with 1000 m in today's oceans. This model suggests a weakened density gradient within the upper water column. Their Case B model corresponds to times when bottom waters were produced in the high latitudes but not by sea ice-formation as in the modern ocean. The pycnocline shoals to 1500 m in this model. Wilde and Berry (1982) suggest that climatic regimes transitional between Case A and Case B may create conditions of neutral density stratification with the potential for oceanic overturn.

The creation of "Meddie"-like plumes (McDowell and Rossby, 1978; Armi et al., 1988; Marshall, 1988) is perhaps one mechanism by which discrete coherent lenses of warm saline water could spread from numerous sources and reduce density gradients within the upper water column. Such plumes form sporadically, spread laterally for great distances, and, as suggested here, may have mixed with other similarly formed water masses during their decay. An upper water column dominated by this type of episodic mixing process might be expected to be dynamic and ecologically unstable.

The dynamics of water mass production may have changed dramatically during Aptian–Albian time. As global sea level rose, continental margins were flooded and marginal seas formed; evaporative basins grew and buoyant plumes of SSW were supplied to the ocean. Rising sea level greatly affected the geometries

and degree of isolation of the marginal seas. Continued growth and expansion of epicontinental seas may have altered regional climatic regimes, created new deep water sources, drowned others, and opened new avenues to the higher latitudes (e.g., the late Albian Mowry Sea of the Western Interior Basin). Perhaps warm, saline deep water mass production from numerous evaporative basins and subtropical oceanic areas characterized the early part of the mid-Aptian–late Albian transgression (similar to the Case A model of Wilde and Berry, 1982) but as inundation of continental areas continued and climates changed, new and varied sources emerged to dominate deep water mass production (similar to the Case B model). The net effect on deep water circulation intensity is unclear, but changes in the rates and sites of water mass production may have greatly affected the density structure of the water column, including the thermal gradient between surface and deep water masses, and/or the upper water column thermocline. A general decline in SSW production during the latter part of this transgression (late Albian), and concomitant increase in high latitude deep water production, may have contributed to a strengthening of the vertical density structure of the upper water column by increasing the temperature gradient between surface and deep water masses.

Primary productivity

Bralower and Thierstein (1984) estimated that average mid-Cretaceous primary production rates were as much as an order of magnitude lower than today's rates. Their estimates are based on organic carbon accumulation rates from three mid-Cretaceous deep sea sites and preservation factors determined for modern anoxic environments. Possible uncertainties in their estimates of marine productivity center on the ability to accurately define bulk accumulation rates which exert the dominant control on the preservation of organic matter that accumulates on the sea floor. The problem lies principally with the lack of a well-constrained absolute time scale for the mid-Cretaceous, particularly at the sub-stage and biostratigraphic zone level. Other uncertainties with the calculations and assumptions have been addressed by Arthur and Dean (1986).

The carbon isotopic composition of marine organic carbon in most mid-Cretaceous sediments is anomalously lighter than modern marine organic carbon (Arthur et al., 1985; Arthur, 1986; Dean et al., 1986). It is thought that the lighter $\delta^{13}C$ values are related to low productivity and higher concentrations of CO_2 during the mid-Cretaceous. While the $\delta^{13}C$ values of latest Aptian–early Albian (OAE 1) pelagic carbonates indicate intensive burial of organic carbon, the $\delta^{13}C$ values of the organic matter suggest that organic carbon burial was not primarily a function of increased marine productivity (Arthur, 1986), a conclusion that agrees in principle with the findings of Bralower and Thierstein (1984).

The latest Aptian–early Albian was the time of most intense organic carbon burial during OAE 1 (Scholle and Arthur, 1980). It may also have been the time of greatest production of warm, saline, oxygen-poor water masses due in part to the gradual growth of shallow, relatively isolated marginal seas (see previous section). Concomitant with the growth of marginal seas was the flooding of vegetated continental margins. A tremendous volume of terrestrial organic matter was shed to the deep basins, particularly the western North Atlantic, during this time (Hochuli and Kelts, 1980; Tissot et al., 1980; Summerhayes, 1981; Habib, 1982; Arthur and Dean, 1986). Much of this organic matter and its bound nutrients was ultimately buried due in part to the generally low dissolved oxygen concentrations of the relatively warm deep waters. Such conditions may be the principal reason for the observed carbon shift (Arthur et al., 1985; Dean et al., 1986). However, the initial widespread flooding of continental margins, and the mixing and transport of terrestrial organic matter in the oxidized upper water column no doubt liberated abundant nutrients. As sea level continued to rise during later Albian time nutri-

ents may have been increasingly sequestered into the expanding areas of coastal wetlands thereby decreasing nutrient delivery to the oceans. The question of the relative importance of enhanced marine productivity versus enhanced organic carbon burial and preservation during OAE 1 is still unclear.

The marked decline in planktonic foraminiferal diversity associated with OAE 2 may have been due in part to a brief geologic interval of enhanced primary productivity. What, if any, role did resource availability play on the decline in diversity during latest Aptian–early Albian time (height of OAE 1)? Perhaps there were no major changes in nutrient availability or trophic structure during Aptian–Albian time to account for the observed diversity trends. Yet, the presumed changes in water mass sources (and circulation?), paleogeography, sea level, carbonate productivity, and diversity fluctuations in phytoplankton (Fig.11) argue against a static trophic structure during this time interval.

The flow of energy from phytoplankton is transferred along food chains or webs of varying complexity. In nutrient-limited open ocean environments today, the food chain is based on nanno-phytoplankton, e.g., coccolithophorids, μ-flagellates, and naked dinoflagellates (Russell-Hunter, 1970; Tappan and Loeblich, 1973; Valiela, 1984). These cells are too small to be utilized directly by most macrozooplankton and larger carnivores. Therefore, many links may exist between the primary producers and top carnivores (Lipps, 1979). In fertile coastal waters or in areas of upwelling food chains are shorter due to the predominance of larger phytoplankton cells, e.g., diatoms and larger dinoflagellates (Valiela, 1984). Although diatoms were rare during the mid-Cretaceous, dinoflagellates were abundant and diverse (Williams and Bujak, 1985). However, many oceanic species of dinoflagellates do not produce resistant resting cysts and therefore leave only a fragmentary record (Tappan and Loeblich, 1973; Williams and Bujak, 1985).

Diatoms are dependent on renewal of inor-

ganic nutrients through upwelling, while dinoflagellates become dominant in stratified waters associated with oceanic fronts where the major source of utilizable phosphorous and nitrogen is generated *in situ* from the degradation of dissolved organic compounds by bacteria (Wangersky, 1977; Pingree et al., 1978). The relative size (e.g., nanno- vs. micro-) of the phytoplankton and proportions of the various phytoplankton groups in the sediment assemblage may serve as a rough gauge of oceanic paleofertility or an indicator of changes in the processes of nutrient recycling. Changes in productivity are related to both *nutrient recycling* in the oceans and nutrient delivery to the oceans. Bacteria are important in nutrient recycling and cyanobacteria may also prove to be important primary producers in oligotrophic waters (e.g., Valiela, 1984; Glover et al., 1988).

Rates of productivity during latest Aptian–early Albian time varied significantly across the oceans with highest rates along the continental margins and in areas of upwelling, for example, off northwest Africa (Tissot et al., 1980; Leckie, 1984), west Africa (Dean et al., 1984), equatorial Pacific (Thiede et al., 1982), and occasionally along the Tethyan margin (Arthur and Premoli-Silva, 1982; Pratt and King, 1986). Episodes of higher productivity have also been recorded in the mid-Cretaceous central North Atlantic. For example, the frequency of radiolarian sands is greatest in lower and middle Albian strata of DSDP Site 386 and wane through the upper Albian and Cenomanian (McCave, 1979). In addition, fluctuations in the composition of palynomorph assemblages (dinoflagellates, acritarchs), including occasional monospecific dinoflagellate "blooms," in lower and middle Albian strata of DSDP Sites 417 and 418 also indicate episodic high productivity (Hochuli and Kelts, 1980) in what may have been the core of a subtropical surface water gyre.

Because the CCD was high during the early Albian (2 km; Arthur et al., 1985) and much of the organic matter that accumulated in the deep sea was of terrestrial origin, dissolution of carbonate and dilution by terrigenous mate-

rial may both have played a role in distorting the true rates of marine productivity. Possible changes in trophic structure, specifically the relative importance of calcareous phytoplankton versus other non-mineralized primary producers, must also be considered in our assessments of mid-Cretaceous productivity.

Salinity

As the Brazil–Angola basin of the northern South Atlantic opened during the late Early Cretaceous, thick sequences of evaporites accumulated (e.g., Arthur and Natland, 1979). Salt deposition ceased by the end of Aptian time when normal marine conditions became widespread. Arthur and Kelts (1979) suggested that evaporite deposition may have signficantly depleted the world ocean of Ca^{2+}, SO_4^{2-} and nutrients. They attribute the abrupt rise in the CCD and widespread extinctions of the heavily calcified nannoconid phytoplankton to this episode. A possible decrease in oceanic salinity associated with evaporite deposition apparently did not have a deleterious effect on the plankton, as the mid-to late Aptian was a time of relatively high diversity amongst both zooplankton and phytoplankton (Fig.11). A decrease of oceanic salinity by as much as 6% during the Messinian salinity crisis (Cita, 1979) also did not have a significant impact on latest Miocene low latitude planktonic foraminiferal diversity (Wei and Kennett, 1986). The latest Miocene did, however, have high evolutionary turnover rates (Wei and Kennett, 1986) as did the mid- to late Aptian (Fig.10).

Temperature

Temperature trends through the mid-Cretaceous, based on oxygen isotope compositions of benthic and planktonic foraminifera (Douglas and Savin, 1975; Savin, 1977), and inoceramids and belemnites (summarized by Arthur et al., 1985) indicate that oceanic paleotemperatures rose during Aptian–Albian time, perhaps reaching a peak in the late Albian. Several

factors may have contributed to the rise of global temperature through the mid-Cretaceous, including plate configuration, rising global sea level, and perhaps increases in atmospheric CO_2 concentration (Barron and Washington, 1984, 1985). A rise in global temperatures through this interval and its influence on climate and heat transport by the oceans and atmosphere probably had a significant effect on the marine biota that lived in the upper water column.

According to Scott (1984), coral–algal reefs were on the demise in the Gulf of Mexico during the early Aptian and were largely replaced by coral–algal–rudist reefs. The latter characterized Gulf of Mexico reefal communities through the middle Albian. By the late Albian, rudists dominated the reefs (Scott, 1988). As pointed out by Scott (1984, 1988), the demise of coral reefs was probably not a result of widespread extinction of colonial corals; rather he suggests that the cause was related to a combination of enivronmental factors such as increased surface water temperatures, fluctuations in productivity or incursion of the oxygen-minimum zone onto the shelf associated with rising sea level.

Climate models suggest that a rise in tropical temperatures of only a few degrees may have increased atmospheric circulation, zonal wind speeds, and storm intensity (Barron, 1986; Emanuel, 1987). Perhaps the late Albian stenotopic corals of the Gulf of Mexico were perturbed by nutrient excess (see model by Hallock and Schlager, 1986) due to enchanced vertical mixing associated with storm tracks across the reef. Similarly, it is also suggested that environmental disruption by intensified seasonal storms or hurricanes may have been responsible for the drowning of part of the Bahamian carbonate platform during the late Albian (see Austin, Schlager et al., 1986). Elevated temperatures probably had a significant effect on the stability and thermal structure of the upper water column, and perhaps played a key role in the evolutionary radiation of marine plankton during late Albian time.

A paleoceanographic model for the evolution of Aptian–Early Cenomanian planktonic foraminifera

The earliest planktonic foraminifera were probably generalists and perhaps had a benthic stage in their life cycles. They lived in relatively shallow mariginal seas or along continental margins and were tolerant of the amplified seasonal changes in environmental conditions such as temperature, salinity, and primary productivity (i.e., they were eurytopic). During the mid-Cretaceous, planktonic foraminifera invaded the open ocean and diversified greatly. Perhaps this was partly in response to the development of oxygen-poor benthic conditions along continental margins associated with the onset of the protracted Aptian–Albian OAE 1. This adaptive radiation basically parallels the mid-Cretaceous global rise in sea level. As sea level rose and marginal seas expanded or epicontinental seas were created, vast new niches opened up. Planktonic foraminiferal evolution was probably stimulated both by the abundance of nutrients and by the wide range of environments in these relatively shallow seas. Planktonic foraminifera diversified into more stable oceanic environments at this time as well. Such upper water column environments were basically nutrient-poor (oligotrophic) and well stratified. Upper water column stability during mid- to late Aptian time may have been responsible for supporting the high diversity of morphologic forms, which included presumed stenotopic forms with short geologic ranges (e.g., *Leupoldina cabri*, *Globigerinelloides algerianus*, *G. saundersi*, *Planomalina cheniourensis*).

The latest Aptian–early Albian was a time of marked decline in planktonic foraminiferal diversity and minor declines in the calcareous nannoplankton and dinoflagellates (Fig.11). Salt deposition ceased in the northern South Atlantic by the end of the Aptian. Productivity increased dramatically off parts of northwest Africa at this time. This interval also corresponds with the greatest intensity of organic carbon burial (OAE 1) based on the widespread distribution of organic carbon-rich strata and $\delta^{13}C$ enrichment of pelagic carbonates. Warm, saline, oxygen-poor deep and/or intermediate waters may have been produced from relatively isolated low latitude marginal seas as continued rise of global sea level gradually flooded continental margins. It is possible that warm saline water masses were produced from numerous sources. Perhaps this mode of deep water formation dominated thermohaline circulation during early Albian time (Fig.12).

The rather sudden, widespread reduction of planktonic foraminiferal diversity and return to relatively simple morphologies was undoubtedly caused by a combination of paleoceanographic factors. Perhaps the most important was a change in the density structure of the upper water column. The suspected importance of warm, saline deep and/or intermediate water mass production from numerous low to mid-latitude sources, such as Salinity Maximum Water (Wilde and Berry, 1982), may have been responsible for a marked decline in the thermal gradient between surface and deeper waters. Alternatively, a weakly stratified uppermost water column or deepening of the thermocline could have resulted from the production of Shelf Sea Water (terminology of Wilde and Berry, 1982). Meddie-like production, mixing and decay processes may have contributed to unstable upper water column density gradients (Fig.12).

In addition to creating new water mass sources, the continued rise of sea level during latest Aptian–early Albian time also caused the drowning of broad vegetated coastal plains and the delivery of vast amounts of terrestrial organic matter to the deep sea. While abundant nutrients were undoubtedly buried along with the terrestrial organic matter, oxidation of some of this material during erosion and transport must have supplied ample nutrients to sustain moderate levels of oceanic productivity, especially along continental margins and in areas of upwelling. Nutrient delivery, nutrient recycling and oceanic productivity were not catastrophically low; had they been, mass extinctions in the phytoplankton might

be expected, but only minor declines are observed. Productivity by naked phytoplankton (e.g., non-cyst producing dinoflagellates, weakly silicified diatoms or cyanobacteria?) may have prevailed over productivity by calcareous nannoplankton. Such a change in trophic structure may be partially responsible for the apparent decline in pelagic carbonate accumulation rates during the early Albian. A shallow CCD and dilution by terrestrial organic matter also obfuscate the early Albian record of marine productivity.

In areas not affected by wind-driven upwelling, oceanic productivity would also have been influenced by the strength (and depth?) of the oceanic pycnocline and the circulation vigor of deep water masses. Had there been a weak pycnocline, nutrient recycling between nutrient-depleted surface waters and nutrient-enriched deeper waters may have been more efficient, albeit dependent on vertical advection. Moderate oceanic fertility would be possible under such conditions. On the other hand, a depressed upper water column thermocline could have prohibited nutrient renewal to the upper water masses thereby resulting in low oceanic fertility. This latter scenario best fits the preponderance of data which indicate that oceanic productivity was in general very low. Superimposed on either situation was the possibility of basin-specific changes in water column stability and structure controlled by climatically forced changes in water mass production. Brief episodes of high productivity affected some oceanic areas during latest Aptian–early Albian time.

Perhaps the loss of morphologic variability and reduction of species diversity during the latest Aptian–early Albian was related in part to ecologically unstable surface water conditions. Arguments can be made for decreased rates of productivity (nutrient burial in organic matter, sluggish oceans) or increased rates or productivity (nutrient liberation and delivery to oceans via sea level rise, active thermohaline circulation) during this interval of most intense organic carbon burial and preservation. In either case, widespread ecologic perturbation, coupled with unstable upper water column density gradients, may have altered the trophic structure of the plankton. The apparent decrease in pelagic carbonate accumulation rates may reflect a decrease in the contribution of calcareous nannoplankton to primary productivity. Other non-mineralized phytoplankton may have dominated under such conditions. While gross productivity rates may have either increased or decreased during OAE 1, net community productivity may have increased due to inefficient utilization by consumers thereby contributing to the accumulation of organic matter (Fig.12). The accumulation of organic matter, the decline in plankton diveristy and the suspected changes in trophic structure suggest a perturbation to ecologic succession during latest Aptian–early Albian time.

As sea level continued to rise during the middle and late Albian, the area of epicontinental seas and coastal wetlands expanded. A greater proportion of land-derived nutrients was trapped in the growing epeiric seas. The major focus of marine productivity shifted from oceanic and continental margin areas into the epicontinental seas. Continued continental flooding probably also created enhanced regional maritime climates with more rainfall and lessened areas of net evaporation. The rise of sea level may have flooded some of the relatively isolated evaporative marginal basins and thereby shut down some of the production of SSW. New cooler water mass sources may have been created as epicontinental seas reached into the high latitudes during the late Albian (Fig.12). Perhaps deep water mass temperatures declined somewhat while surface water temperatures continued to rise due to overall global warming. This also enhanced the overall stability of water column. Atmospheric warming may have intensified wind-driven circulation thereby increasing rates of primary pioductivity in areas of coastal upwelling and oceanic divergence, despite an overall decrease in primary productivity in other oceanic areas (e.g. gyre centers).
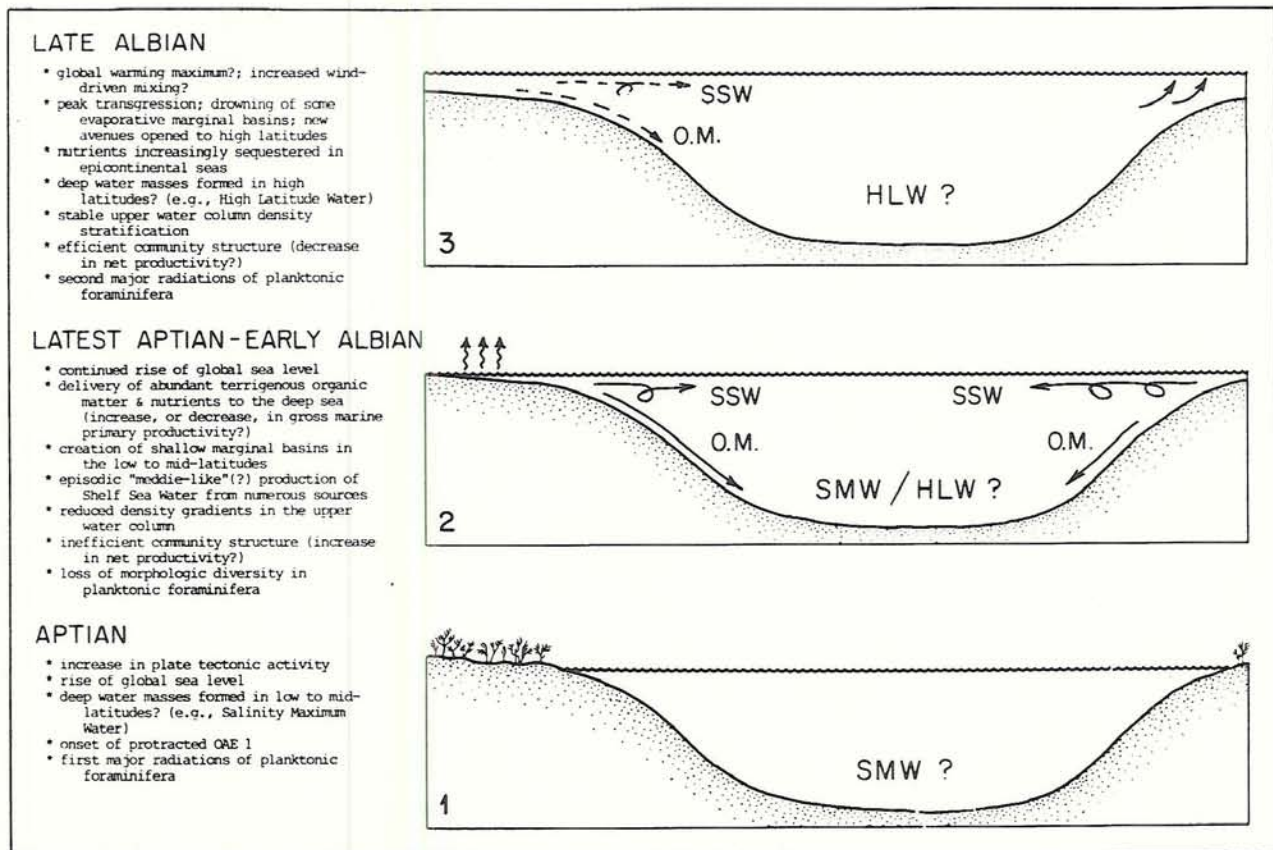
LATE ALBIAN

- global warming maximum?; increased wind-driven mixing?
- peak transgression; drowning of some evaporative marginal basins; new avenues opened to high latitudes
- nutrients increasingly sequestered in epicontinental seas
- deep water masses formed in high latitudes? (e.g., High Latitude Water)
- stable upper water column density stratification
- efficient community structure (decrease in net productivity?)
- second major radiations of planktonic foraminifera

SSW
O.M.
HLW ?
3

LATEST APTIAN-EARLY ALBIAN

- continued rise of global sea level
- delivery of abundant terrigenous organic matter & nutrients to the deep sea (increase, or decrease, in gross marine primary productivity?)
- creation of shallow marginal basins in the low to mid-latitudes
- episodic "meddie-like"(?) production of Shelf Sea Water from numerous sources
- reduced density gradients in the upper water column
- inefficient community structure (increase in net productivity?)
- loss of morphologic diversity in planktonic foraminifera

SSW   SSW
O.M.   O.M.
SMW / HLW ?
2

APTIAN

- increase in plate tectonic activity
- rise of global sea level
- deep water masses formed in low to mid-latitudes? (e.g., Salinity Maximum Water)
- onset of protracted OAE 1
- first major radiations of planktonic foraminifera

SMW ?
1

Fig.12. Hypothetical changes in water mass sources, upper water column density structure, nutrient delivery to the oceans, and oceanic productivity, with rising sea level during Aptian and Albian time. Water mass terminology (SSW, SMW, HLW) from Wilde and Berry (1982). *O.M.* = organic matter.
The following points are emphasized: (1) nutrient delivery to the oceans and sites of water mass production changed with eustatic sea level rise, (2) warm, saline water mass production was important during latest Aptian–early Albian time and contributed to a breakdown in upper water column density gradients and resultant decline in planktonic foraminiferal diversity, and (3) warm, saline water mass production declined with approach of peak transgression during late Albian time, high latitude (?) water mass sources and an overall increase of global temperatures contributed to an intensification of upper water column density gradients and resultant marked increase in planktonic foraminiferal diversity at that time.

The net result was the development of a strong thermocline in oceanic areas by late Albian time, as well as better defined current-bound surface water masses. The enhanced upper water column stratification coupled with the inferred landward shift of productivity centers created hydrographic stability in many oceanic areas. Carbonate productivity by coccolithophorids once again became widespread. The combination of paleoceanographic conditions triggered the explosion in evolutionary diversification of planktonic foraminifera and other plankton during the late Albian. Many of the newly evolved planktonic foraminiferal taxa were probably stenotopic and many were probably deep-dwelling forms. A great variety of morphologic forms reappeared during the late Albian including taxa with clavate or radially elongate chambers, both trochospiral (species of *Clavihedbergella*) and planispiral (species of *Schackoina*), and numerous forms with keeled peripheries and/or specialized apertural systems (species of *Praeglobotruncana*, *Rotalipora*, *Planomalina*, *Ticinella* and *Biticinella*). Newly evolved eurytopic taxa flourished in and along the margins of the epicontinental seas (e.g., *Heterohelix* and *Guembelitria*), while others adapted to the warm, shallow carbonate platforms (e.g., *Favusella*). Stable conditions persisted in oceanic areas for

much of the Cenomanian, although the slight decline in planktonic foraminifera during the mid-Cenomanian may be related to the minor regression which brought the Aptian–Albian eustatic cycle to an end.

Conclusions

(1) High diversity (simple diversity, species richness) in sediment assemblages of open ocean planktonic foraminifers is primarily the function of well-developed density gradients within the euphotic zone; either year-round (tropics) or seasonal (temperate). Species composition, dominance, and equitability are a function of uppermost water column structure (including depth of the thermocline), productivity, seasonality, predation and postmortem processes.

(2) Changes in water mass production and upper water column structure are believed to have strongly influenced the evolutionary history and morphologic development of Aptian–Albian planktonic foraminifera. Beginning in the Barremian, but particularly during the Aptian, foraminifera exploited the pelagic habitat with the onset of OAE 1. During latest Aptian–early Albian time, the widespread, episodic production of warm, saline water masses in numerous, relatively isolated, net evaporative, marginal basins, and/or in subtropical oceanic areas, are believed to have weakened upper water column density gradients and be the primary cause for the marked decline in planktonic foraminiferal diversity. Epicontinental seas expanded and regional climates changed as global sea level continued to rise through late Albian time. As a consequence, the modes and rates of water mass production changed, stable uppermost water column stratification was restored, and low to mid-latitude planktonic foraminifera diversified greatly. This hypothesis is based primarily on the diversity fluctuations and iterative patterns of morphologic change observed in Aptian–Albian planktonic foraminifera, and published models of mid-Cretaceous water mass production.

(3) Rates of Aptian–Albian primary productivity are difficult to assess. Parallel trends in phytoplankton and zooplankton diversity through this interval and changes in the pelagic carbonate content of sedimentary sequences suggest that the oceanic trophic regime was not static. Changes in nutrient delivery to oceanic areas with rising sea level, shifts in productivity centers, and changes in water column structure and circulation vigor may have influenced ecosystem structure and stability. In our paleoceanographic models we must carefully consider possible changes in the relative contributions of various primary producers (coccolithophorids, dinoflagellates, early naked? diatoms, other flagellates, cyanobacteria) and the impact of such changes on rates of primary productivity (gross productivity), net community productivity, and overall trophic structure of the plankton. Changes in resource availability or long-term ecosystem stability may indeed have had a significant effect on the early evolutionary history of planktonic foraminifera. The relationship between ecosystem succession and patterns of evolution in the marine plankton needs to be examined further and on time scales from hundreds of years to millions of years.

(4) While several new taxa of epicontinental sea-dwelling planktonic foraminifera appeared during the mid-Cretaceous, much of the diversification of morphologic form occurred in stratified oceanic waters (i.e., deeper epicontinental seas, continental margins and open ocean) away from the amplified seasonal fluctations of epicontinental sea margins or shallow epicontinental seas.

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