

## Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous

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[1] Mid-Cretaceous (Barremian-Turonian) plankton preserved in deep-sea marl, organic-rich shale, and pelagic carbonate hold an important record of how the marine biosphere responded to short- and long-term changes in the ocean-climate system. Oceanic anoxic events (OAEs) were short-lived episodes of organic carbon burial that are distinguished by their widespread distribution as discrete beds of black shale and/or pronounced carbon isotopic excursions. OAE1a in the early Aptian (~120.5 Ma) and OAE2 at the Cenomanian/Turonian boundary (~93.5 Ma) were global in their distribution and associated with heightened marine productivity. OAE1b spans the Aptian/Albian boundary (~113–109 Ma) and represents a protracted interval of dysoxia with multiple discrete black shales across parts of Tethys (including Mexico), while OAE1d developed across eastern and western Tethys and in other locales during the latest Albian (~99.5 Ma). Mineralized plankton experienced accelerated rates of speciation and extinction at or near the major Cretaceous OAEs, and strontium isotopic evidence suggests a possible link to times of rapid oceanic plateau formation and/or increased rates of ridge crest volcanism. Elevated levels of trace metals in OAE1a and OAE2 strata suggest that marine productivity may have been facilitated by increased availability of dissolved iron. The association of plankton turnover and carbon isotopic excursions with each of the major OAEs, despite the variable geographic distribution of black shale accumulation, points to widespread changes in the ocean-climate system. Ocean crust production and hydrothermal activity increased in the late Aptian. Faster spreading rates [and/or increased ridge length] drove a long-term (Albian–early Turonian) rise in sea level and CO<sub>2</sub>-induced global warming. Changes in ocean circulation, water column stratification, and nutrient partitioning lead to a reorganization of plankton community structure and widespread carbonate (chalk) deposition during the Late Cretaceous. We conclude that there were important linkages between submarine volcanism, plankton evolution, and the cycling of carbon through the marine biosphere. *INDEX TERMS*: 3030 Marine Geology and Geophysics: Micropaleontology; 4267 Oceanography: General: Paleooceanography; 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4855 Oceanography: Biological and Chemical: Plankton; 9609 Information Related to Geologic Time: Mesozoic; *KEYWORDS*: mid-Cretaceous, oceanic anoxic events, planktic foraminifera, calcareous nannofossils, radiolarians, submarine volcanism

### 1. Introduction

[2] The mid-Cretaceous (~124–90 Ma) was a time of transition in the nature of the ocean-climate system. Changes were brought about by increased rates of tectonic activity and shifting paleogeography [e.g., *Larson and Pitman*, 1972; *Barron*, 1987; *Larson*, 1991a, 1991b; *Jones et al.*, 1994; *Ingram et al.*, 1994; *Hay*, 1995; *Poulsen et al.*, 1999a, 2001; *Jones and Jenkyns*, 2001]. Intervals of the Early Cretaceous were characterized by relatively cool high latitudes including evidence for ice rafting [*Frakes and Francis*, 1988; *Weissert and Lini*, 1991; *Frakes et al.*, 1992; *Stoll and Schrag*, 1996; *Weissert et al.*, 1998; *Clarke and Jenkyns*,

1999; *Ferguson et al.*, 1999; *Frakes*, 1999]. However, beginning in the Aptian, increased ocean crust production (greater rates of seafloor spreading and/or increased ridge length), coupled with active midplate and plate margin volcanism contributed to a greenhouse world of rising sea level and warming global climate that peaked in the early Turonian but persisted through early Campanian time [*Hays and Pitman*, 1973; *Kominz*, 1984; *Arthur et al.*, 1985; *Rich et al.*, 1986; *Larson*, 1991a, 1991b; *Huber et al.*, 1995, 2002; *Clarke and Jenkyns*, 1999]. Elevated levels of volcanically derived CO<sub>2</sub> in the atmosphere resulted in ice-free poles and contributed to a weak meridional temperature gradient and an increasingly active hydrologic cycle [*Barron and Washington*, 1985; *Barron et al.*, 1989, 1995; *Huber et al.*, 1995, 2002; *Schmidt and Mysak*, 1996; *Hay and DeConto*, 1999; *Poulsen et al.*, 1999b]. The accompanying widespread burial

of organic carbon punctuated this long-term global warmth a number of times with episodes of reverse greenhouse climate marked by cooling and perhaps glaciation [e.g., *Arthur et al.*, 1988; *Weissert and Lini*, 1991; *Weissert et al.*, 1998; *Hochuli et al.*, 1999; *Kuypers et al.*, 1999; *Stoll and Schrag*, 2000]. Many researchers have suggested that ocean circulation was driven in part by the sinking of warm, saline waters in subtropical regions of excessive evaporation [*Chamberlin*, 1906; *Brass et al.*, 1982; *Southam et al.*, 1982; *Wilde and Berry*, 1982; *Barron*, 1983; *Arthur et al.*, 1985, 1987; *Barron and Peterson*, 1990; *Woo et al.*, 1992; *Barron et al.*, 1993, 1995; *Hay*, 1995; *Johnson et al.*, 1996; *Schmidt and Mysak*, 1996]. However, ocean general circulation model experiments show that the southern high latitudes were likely the dominant sites of deep water formation during the mid-Cretaceous with subtropical convection restricted to isolated basins [*Poulsen et al.*, 2001].

[3] At times during the mid-Cretaceous, dysoxic and anoxic conditions developed in oxygen minimum zones along continental margins of the tropical Tethys Sea, in restricted epicontinental seas, and in basins of the widening North and South Atlantic Ocean basins. These conditions led to the regional deposition of rhythmically bedded sedimentary sequences including organic-rich black shale [e.g., *Dean et al.*, 1978; *McCave*, 1979; *Arthur and Premoli Silva*, 1982; *de Boer*, 1982; *Cotillon and Rio*, 1984]. The observed cyclicity has been interpreted as orbitally forced changes in climate, which controlled biogenic carbonate flux, productivity, and/or redox conditions at the seafloor [e.g., *Arthur et al.*, 1984; *de Boer and Wonders*, 1984; *Fischer*, 1986; *Herbert and Fischer*, 1986; *Herbert et al.*, 1986; *Pratt and King*, 1986; *Gale et al.*, 1993; *Arthur and Sageman*, 1994; *Sageman et al.*, 1998]. Oceanic anoxic events (OAEs), on the other hand, were generally short-lived (<1 Myr) episodes of organic carbon burial characterized by the widespread distribution of discrete beds of black shale and/or pronounced positive carbon isotopic excursions (typically >1.5–2‰) (Figure 1) [*Schlanger and Jenkyns*, 1976; *Arthur and Schlanger*, 1979; *Jenkyns*, 1980; *Arthur et al.*, 1987, 1990; *Bralower et al.*, 1993]. The major mid-Cretaceous OAEs are associated with the accumulation of marine organic matter [*Erbacher et al.*, 1996].

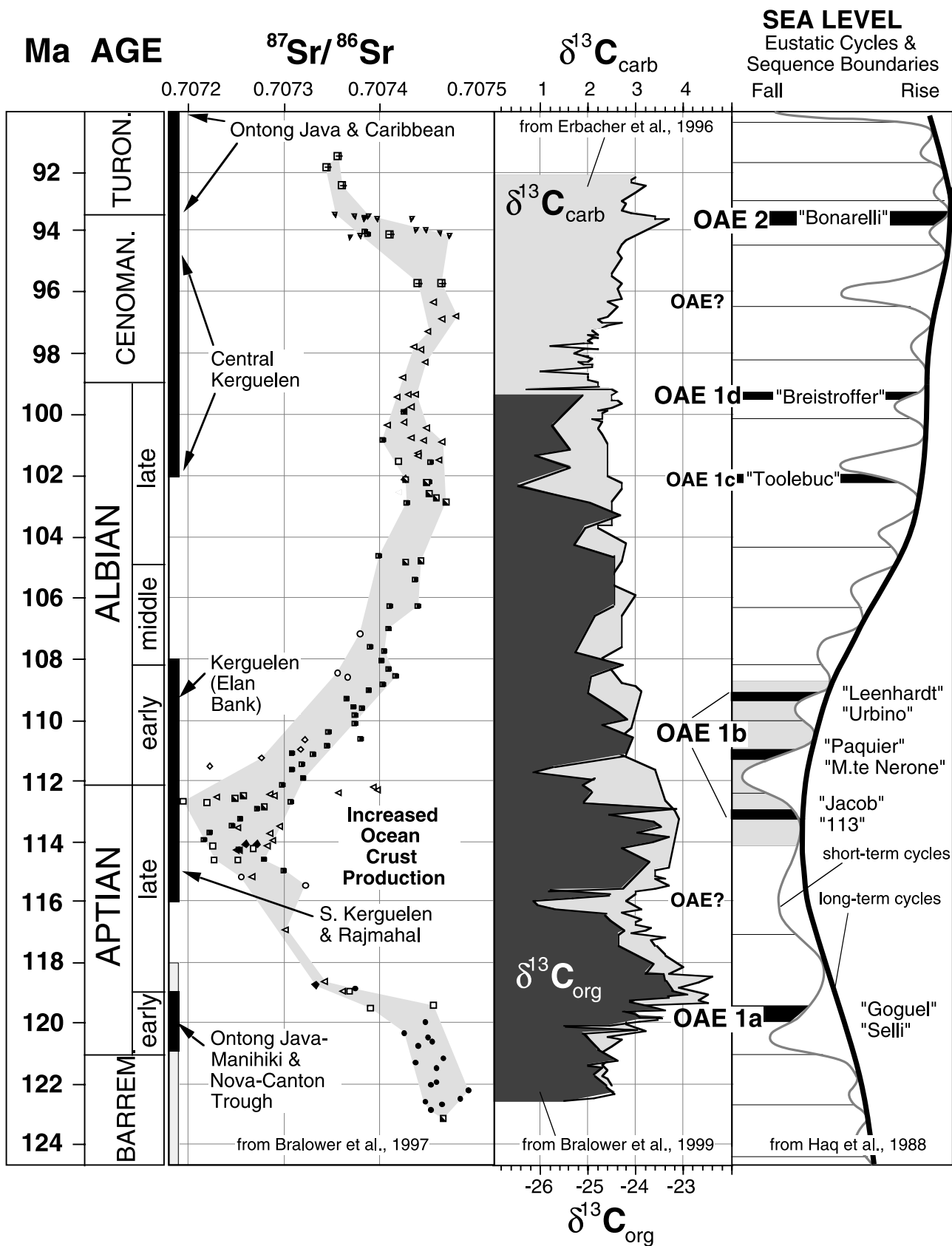
[4] As sea level rose and global climate warmed during the Albian-Turonian, there was a marked shift from organic carbon-rich black shale deposition in the basins of western (Atlantic-Caribbean) and eastern (Mediterranean) Tethys to

carbonate (chalk) deposition along flooded continental margins and in newly created or expanding epicontinental seas [e.g., *Arthur and Premoli Silva*, 1982; *Br  h  ret et al.*, 1986; *Premoli Silva et al.*, 1989; *Tornaghi et al.*, 1989]. By late Cenomanian-early Turonian time the deepening gateway between the basins of the North and South Atlantic altered ocean circulation and improved deep water ventilation through much of Tethys [*Arthur and Natland*, 1979; *Tucholke and Vogt*, 1979; *Summerhayes*, 1981; *Arthur and Premoli Silva*, 1982; *de Graciansky et al.*, 1982; *Cool*, 1982; *Zimmerman et al.*, 1987; *Leckie*, 1989; *Arthur et al.*, 1990; *Poulsen et al.*, 1999a, 2001].

[5] The mid-Cretaceous was also a time of rapid radiation and turnover in the marine plankton [*Lipps*, 1970; *Haq*, 1973; *Tappan and Loeblich*, 1973; *Bujak and Williams*, 1979; *Caron and Homewood*, 1983; *Roth*, 1987; *Leckie*, 1989], benthic foraminifera [*Sliter*, 1977, 1980; *Sikora and Olsson*, 1991; *Kaiho*, 1999; *Holbourn and Kuhnt*, 2001], molluscs [*Vermeij*, 1977; *Theyer*, 1983; *Signor and Vermeij*, 1994], and terrestrial plants [*Hickey and Doyle*, 1977; *Retallack and Dilcher*, 1986; *Lidgard and Crane*, 1988; *Crane et al.*, 1995]. This evolutionary activity, part of the so-called ‘‘Mesozoic revolution’’ of *Vermeij* [1977], transformed many of these groups on an ocean-wide basis. Diversity increased dramatically as organisms invaded new habitats and partitioned the changing ecospace. The reorganization of the global biosphere during the mid-Cretaceous paralleled the marked changes in the ocean-climate system, suggesting a causal relationship between biotic evolution and environmental stimuli [*Fischer and Arthur*, 1977; *Rich et al.*, 1986; *Leckie*, 1989; *Thurrow et al.*, 1992; *Vermeij*, 1995].

[6] Planktic protists with mineralized skeletons of calcium carbonate and silica, namely, the autotrophic calcareous nannoplankton and heterotrophic planktic foraminifera and radiolarians, are generally abundant and well preserved in mid-Cretaceous marine sediments. Radiolarians show high rates of evolutionary turnover (extinction plus radiation) at or near the OAEs [*Erbacher et al.*, 1996; *Erbacher and Thurrow*, 1997], and detailed studies of individual events have demonstrated that the calcareous nannoplankton and planktic foraminifera were likewise influenced to varying degrees by the OAEs [*Hart*, 1980; *Leckie*, 1985; *Hart and Ball*, 1986; *Bralower*, 1988; *Bralower et al.*, 1993, 1994; *Erba*, 1994; *Leckie et al.*, 1998; *Huber et al.*, 1999; *Premoli Silva et al.*, 1999]. These data suggest that the OAEs were

**Figure 1.** (opposite) The mid-Cretaceous record of major black shales and oceanic anoxic events (OAEs) in the context of the carbon isotopic record [*Erbacher et al.*, 1996; *Bralower et al.*, 1999], changing global sea level [*Haq et al.*, 1988], and seawater chemistry [*Bralower et al.*, 1997]. See text for discussion of emplacement history of submarine large igneous provinces (LIPs: Ontong-Java, Manihiki, and Kerguelen Plateaus and the Caribbean Plate). Short-term sea level changes are shown as the dark shaded line, and the long-term record of sea level is shown with the thick solid line (adapted from *Haq et al.* [1988]). OAE1a in the early Aptian (‘‘Selli event’’), OAE1b spanning the Aptian/Albian boundary (including the ‘‘Jacob,’’ ‘‘Paquier,’’ and ‘‘Urbino’’ events), and OAE2 at the Cenomanian/Turonian boundary (‘‘Bonarelli event’’) each correspond to negative  $^{87}\text{Sr}/^{86}\text{Sr}$  excursions indicative of elevated submarine volcanism [*Bralower et al.*, 1997; *Larson and Erba*, 1999; *Jones and Jenkyns*, 2001]. Note that the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio in marine carbonate declines to its most negative values in the latest Aptian, roughly coincident with increased rates of ocean crust production [*Kominz*, 1984; *Larson*, 1991a, 1991b]. Initiation of increased spreading rates drove the long-term (Albian-Turonian) rise of global sea level. After rising to a plateau by the late Albian, perhaps due to increased rates of continental weathering with global warming, the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio once again dropped sharply at or near the time of OAE2.



foci of evolutionary change for the plankton during the mid-Cretaceous.

[7] Beginning in middle to late Aptian time (~116–113 Ma), ocean crust production increased significantly [Kominz, 1984; Larson, 1991a, 1991b]; the timing is constrained by biostratigraphic and strontium isotopic data [Bralower et al., 1997; Jones and Jenkyns, 2001]. In addition to increased rates of ocean crust production during the mid-Cretaceous, plumes of hot, buoyant rock rose through the mantle forming anomalously thick and extensive oceanic plateaus, termed large igneous provinces (LIPs). These include (1) the Ontong-Java and Manihiki Plateaus and the intervening Nova Canton Trough (~125–118 Ma with renewed activity ~96–84 Ma [Mahoney et al., 1993; Tejada et al., 1996; Larson and Kincaid, 1996; Larson, 1997; Larson and Erba, 1999; Mahoney et al., 2002]), (2) the Kerguelen Plateau (KP) (~116–110 Ma for the southern KP and Rajmahal, 110–108 Ma for Elan Bank, and ~95–85 Ma for the central KP and Broken Ridge [Whitechurch et al., 1992; Coffin and Eldholm, 1994; Frey et al., 1999; Pringle and Duncan, 2000; Shipboard Scientific Party, 2000]), and (3) the Caribbean Plate (~94–87 Ma [Sinton et al., 1998]). An important consequence of this submarine volcanism was increased hydrothermal activity, particularly at the spreading centers, which caused secular changes in ocean chemistry [Vogt, 1989; Hardie, 1996; Bralower et al., 1997; Stanley and Hardie, 1998; Jones and Jenkyns, 2001].

[8] A succession of environmental changes links intraplate, mantle plume volcanism with biotic turnover, enhanced productivity, and widespread burial of marine organic matter during the early Aptian OAE (~120.5 Ma [Bralower et al., 1994; Erba, 1994; Larson and Erba, 1999]). Others have further suggested that the OAE at the Cenomanian/Turonian boundary (~93.5 Ma) was likewise related to submarine volcanism, including the formation of the Caribbean Plateau [Schlanger et al., 1987; Orth et al., 1993; Ingram et al., 1994; Sinton and Duncan, 1997; Kerr, 1998; Snow and Duncan, 2001]. The temporal association of increased submarine volcanism with the early Aptian and Cenomanian/Turonian boundary OAEs as well as additional activity at the end of the Aptian is strongly supported by strontium isotopic data [Bralower et al., 1997; Jones and Jenkyns, 2001] (Figure 1).

[9] The purpose of this paper is to review a 33 million year record of mid-Cretaceous plankton evolution in the context of the short-lived OAEs and the longer-term trend of rising sea level, changing paleogeography, and warming global climate. Here we present new data on the evolutionary rates of calcareous plankton based on an integrated calcareous plankton biostratigraphy and geochronology [Bralower et al., 1995, 1997; Erba et al., 1996]. Our plankton-based analysis supports the hypothesis that submarine volcanism, namely, oceanic plateau formation, coupled with increased ocean crust production and hydrothermal activity was an important catalyst of marine productivity and black shale deposition during the major mid-Cretaceous OAEs. However, the early Aptian world was very different from that of Cenomanian/Turonian boundary time, and therefore the individual OAEs share

some similarities as well as important differences. In particular, the Albian stage (112.2–98.9 Ma) records changes in the foci of organic carbon burial and pelagic carbonate deposition as well as major changes in planktic foraminiferal diversity, size, and wall structure [e.g., Bréhéret et al., 1986; Leckie, 1989; Premoli Silva and Sliter, 1999]. The degree to which these patterns were controlled by tectonically driven changes in ocean circulation, water column structure, productivity, and plankton community dynamics and to what extent such changes may or may not be related to the spatial and temporal distribution of the OAEs are central to the paleoceanographic research questions considered here.

## 2. Oceanic Anoxic Events

[10] There were arguably between two and seven OAEs during the mid-Cretaceous [Schlanger and Jenkyns, 1976; Arthur and Schlanger, 1979; Jenkyns, 1980; Arthur et al., 1987; Sliter, 1989a; Arthur et al., 1990; Bralower et al., 1993, 1999; Erbacher et al., 1996; Erbacher and Thurow, 1997]. Erbacher et al. [1996] distinguished between OAEs associated with rising sea level, heightened marine productivity (type II kerogen), and positive  $\delta^{13}\text{C}$  excursions, so-called POAEs (P for productivity), and DOAEs (D for detrital) characterized by falling sea level and terrestrial organic matter (type III kerogen). The two most widespread OAEs are the early Aptian OAE1a (Livello Selli; ~120.5 Ma) and the Cenomanian-Turonian boundary OAE2 (Livello Bonarelli; ~93.5 Ma) (Figure 1); these are both POAEs according to Erbacher et al. [1996]. The concentration of organic matter in distinct, widely distributed beds of black shale was facilitated by reduced terrigenous sedimentation during transgression and/or the incursion of upwelling-induced oxygen minima across the upper slope and shelf with rising sea level [Hallam and Bradshaw, 1979; Arthur et al., 1987; Schlanger et al., 1987; Loutit et al., 1988; Arthur et al., 1990; Bralower et al., 1993; Arthur and Sageman, 1994]. However, major unresolved questions remain: what could sustain widespread and elevated marine productivity, and were the individual OAEs triggered by similar forcing mechanisms?

### 2.1. OAE1a (Early Aptian)

[11] The characteristics of the individual OAEs illustrate their complex nature. The onset of OAE1a (Selli event), for example, is preceded by a sharp negative  $\delta^{13}\text{C}$  excursion (0.5–3.0‰), an abrupt decrease in  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope values (Figure 1), increased trace metal concentrations, and a major demise in the nannoconids (the “nannoconid crisis” [Erba, 1994]), followed by an abrupt and prolonged positive  $\delta^{13}\text{C}$  excursion (>2‰) and short-lived (0.5–1.0 Myr.) black shale deposition [Sliter, 1989a; Bralower et al., 1994, 1997, 1999; Föllmi et al., 1994; Jenkyns, 1995; Menegatti et al., 1998; Jones and Jenkyns, 2001]. The series of events across the *Globigerinelloides blowi-Leupoldina cabri* biozone boundary has been linked to the Ontong-Java Pacific “superplume” eruption [Larson, 1991a, 1991b; Tarduno et al., 1991; Erba, 1994; Larson and Erba, 1999]. The initial



negative  $\delta^{13}\text{C}$  excursion is recorded in marine carbonates at Resolution Guyot in the Pacific [Jenkyns, 1995], in Alpine sections of northern Tethys [Menegatti et al., 1998], and in Mexico [Bralower et al., 1999] as well as in fossil wood from the Isle of Wight [Gröcke et al., 1999]. Hypotheses to account for the negative excursion include (1) increased upwelling rates of nutrient- and  $^{12}\text{C}$ -rich intermediate waters [Menegatti et al., 1998], (2) accelerated hydrologic cycle and higher weathering rates induced by  $\text{CO}_2$ -driven global warming [Menegatti et al., 1998], (3) isotopically light, mantle-derived  $\text{CO}_2$  associated with the eruption of Ontong Java-Manihiki prior to an interval of enhanced productivity and organic carbon burial [Bralower et al., 1994; Larson and Erba, 1999], and (4) dissociation of isotopically light methane hydrates in continental margin sediments [Jahren and Arens, 1998; Opdyke et al., 1999; Jahren et al., 2001]. Larson and Erba [1999] hypothesized that iron fertilization associated with the superplume eruption triggered increased productivity during OAE1a.

## 2.2. OAE2 (Cenomanian/Turonian Boundary Interval)

[12] The OAE2 (Bonarelli event) also displays a marked positive  $\delta^{13}\text{C}$  excursion ( $>2\text{‰}$ ) related to the widespread burial of marine organic matter [Scholle and Arthur, 1980; Summerhayes, 1981, 1987; Pratt and Threlkeld, 1984; Arthur et al., 1987, 1990; Schlanger et al., 1987; Jarvis et al., 1988; Hilbrecht et al., 1992; Thurow et al., 1992; Gale et al., 1993; Pratt et al., 1993; Jenkyns et al., 1994; Sugarman et al., 1999], and a marked drop in  $^{87}\text{Sr}/^{86}\text{Sr}$  isotopic values has been attributed to submarine volcanism [Ingram et al., 1994; Bralower et al., 1997; Jones and Jenkyns, 2001] (Figure 1). Elevated rates of seafloor spreading and subduction are implicated by the volume, thickness, and extent of ashfall deposits (bentonites) through the Cenomanian/Turonian boundary interval in the Western Interior Sea of North America [e.g., Kauffman, 1984; Kauffman and Caldwell, 1993]. Additional supporting evidence for increased hydrothermal activity comes from elevated levels of trace metals in marls and organic-rich mudrocks of the southern part of the Western Interior Sea as tropical water masses invaded the seaway with rising sea level [Orth et al., 1993; Leckie et al., 1998; Snow and Duncan, 2001].

[13] A number of researchers have suggested that OAE2 was likewise triggered by iron fertilization associated with mantle plume volcanism [Sinton and Duncan, 1997; Kerr, 1998]. However, most of the dated lava flows from the younger volcanic sequence on Ontong-Java Plateau as well as flows from the Caribbean Plate are too young (92–88 Ma), and volcanism on the Kerguelen Plateau was subaerial by late Cenomanian-early Turonian time [Shipboard Scientific Party, 2000]. Alternatively, OAE2 may have been triggered by the injection of warm saline intermediate or deep waters that created favorable conditions for the vertical advection of nutrients, widespread productivity, expansion of oxygen minima, and the accumulation of organic matter. For example, Huber et al. [1999, 2002] showed that middle bathyal waters (~500–1000 m) in the western North Atlantic abruptly warmed from  $15^\circ$  to  $20^\circ\text{C}$  in the latest Cenomanian. These paleotemperature estimates are the

warmest known Cretaceous or Cenozoic intermediate waters. The loss of water column density gradients at the end of the Cenomanian may account for the extinction of deeper-dwelling foraminifera (*Rotalipora* spp., *Globigerinelloides bentonensis*), a condition that would have also facilitated the vertical advection of nutrients to fuel primary productivity [Leckie et al., 1998; Huber et al., 1999].

[14] Arthur et al. [1987] suggested that the creation of warm saline deep waters in the expanding epicontinental seas drove upwelling during OAE2. In addition, an abrupt change in Atlantic deep water circulation created by the breaching of the deep water sill separating the North and South Atlantic Ocean basins [Arthur and Natland, 1979; Tucholke and Vogt, 1979; Summerhayes, 1981, 1987; Cool, 1982; Zimmerman et al., 1987; Poulsen et al., 1999a, 2001] may have also facilitated nutrient delivery to the euphotic zone by ventilating the deep North Atlantic and adjacent Tethyan margins. Thus the high productivity of OAE2 may have been triggered by changes in deep and intermediate water circulation and/or source(s) of water mass production, which was sustained by a volcanically spiked, nutrient-rich water column. The accumulation and preservation of organic matter was further enhanced by the widespread latest Cenomanian-early Turonian transgression and by the warm, oxygen-poor intermediate and deep waters. Burial of organic carbon during OAE2 was modulated by orbitally forced climate cyclicity [Gale et al., 1993; Sageman et al., 1998]. For example, data from central Tunisia indicates that the accumulation of organic matter during OAE2 was driven by the precessional cycle (~20 kyr) for the duration of a single 400 kyr eccentricity cycle [Caron et al., 1999].

## 2.3. Other OAEs and Possible OAEs

[15] Additional intervals of black shale accumulation include the late Aptian (~116 Ma), latest Aptian-early Albian (OAE1b; ~113–109 Ma), late Albian (OAE1c and OAE1d; ~102 and ~99.2 Ma, respectively), and mid-Cenomanian (~96 Ma [Arthur et al., 1990; Bralower et al., 1993, 1999; Bréhéret, 1994; Erbacher et al., 1996, 2001; Wilson and Norris, 2001]). A black shale event in the late Aptian, between OAE1a and OAE1b in the *Globigerinelloides algerianus* biozone [Bralower et al., 1999; Sliter, 1999], may prove to be an OAE. It is represented by a discrete black shale bed in the Calera Limestone of northern California (paleolatitude of  $\sim 15^\circ$ – $17^\circ\text{N}$  in the eastern Pacific [Sliter, 1999; Premoli Silva and Sliter, 1999]) and in northeastern Mexico where an accompanying large negative-to-positive excursion in  $\delta^{13}\text{C}$ , similar to OAE1a, implies a widespread distribution (Figure 1) [Bralower et al., 1999]. This interval of the late Aptian has been linked to cooling and an eustatic sea level fall [Weissert and Lini, 1991; Weissert et al., 1998].

[16] The multiple black shales of OAE1b (upper *Ticinella bejaouaensis* and *Hedbergella planispira* biozones) are mostly restricted to Mexico and the North Atlantic basin (western Tethys) and the Mediterranean (eastern Tethys) region [e.g., Arthur and Premoli Silva, 1982; Bréhéret et al., 1986; Premoli Silva et al., 1989; Bralower et al., 1993, 1999]. This interval is associated with cooling and sea level fall in the latest Aptian and subsequent sea level rise during

the early Albian [Weissert and Lini, 1991; Weissert et al., 1998]. OAE1c in the lower upper Albian *Biticinella breggiensis* biozone has been identified in central Italy, the U.S. western interior, and Australia (“Toolebuc”) and is associated with the accumulation of terrigenous organic matter [Pratt and King, 1986; Bralower et al., 1993; Coccioni and Galeotti, 1993; Haig and Lynch, 1993; Erbacher et al., 1996].

[17] OAE1d (*Rotalipora appenninica* biozone), on the other hand, is widely preserved as a black shale across Tethys (“Breistroffer”) with sporadic occurrences in the South Atlantic, southern Indian, and eastern Pacific Ocean basins; it is associated with marine organic matter [Br  h  ret and Delamette, 1989; Br  h  ret, 1994; Erbacher et al., 1996; Wilson and Norris, 2001]. Cyclic black shales in the uppermost Albian of Ocean Drilling Program (ODP) Site 1052 on Blake Nose are correlative to OAE1d and correspond to an interval marked by collapse of upper water column stratification caused by intensified winter mixing and reduced summer stratification [Wilson and Norris, 2001]. Alternatively, the isotopic data of the thermocline-dwelling genus *Rotalipora* suggest that warming of intermediate waters may have also contributed to the collapse of upper water column density gradients. Another possible OAE occurs in the mid-Cenomanian of Tethys where it is associated with a positive carbon excursion ( $\sim 1\%$ ), marine organic matter, and an extinction event in the radiolaria [Erbacher et al., 1996; Stoll and Schrag, 2000]. Noteworthy are the large ( $\sim 1\text{--}2\%$ ) carbon isotopic excursions [e.g., Weissert and Lini, 1991; Weissert et al., 1998; Bralower et al., 1999; Stoll and Schrag, 2000; Wilson and Norris, 2001] and radiolarian turnover events [e.g., Erbacher et al., 1996] that are concentrated at or near the times of both OAE1b and OAE1d, suggesting widespread environmental changes.

#### 2.4. Significance of OAE1b (Latest Aptian–Early Albian)

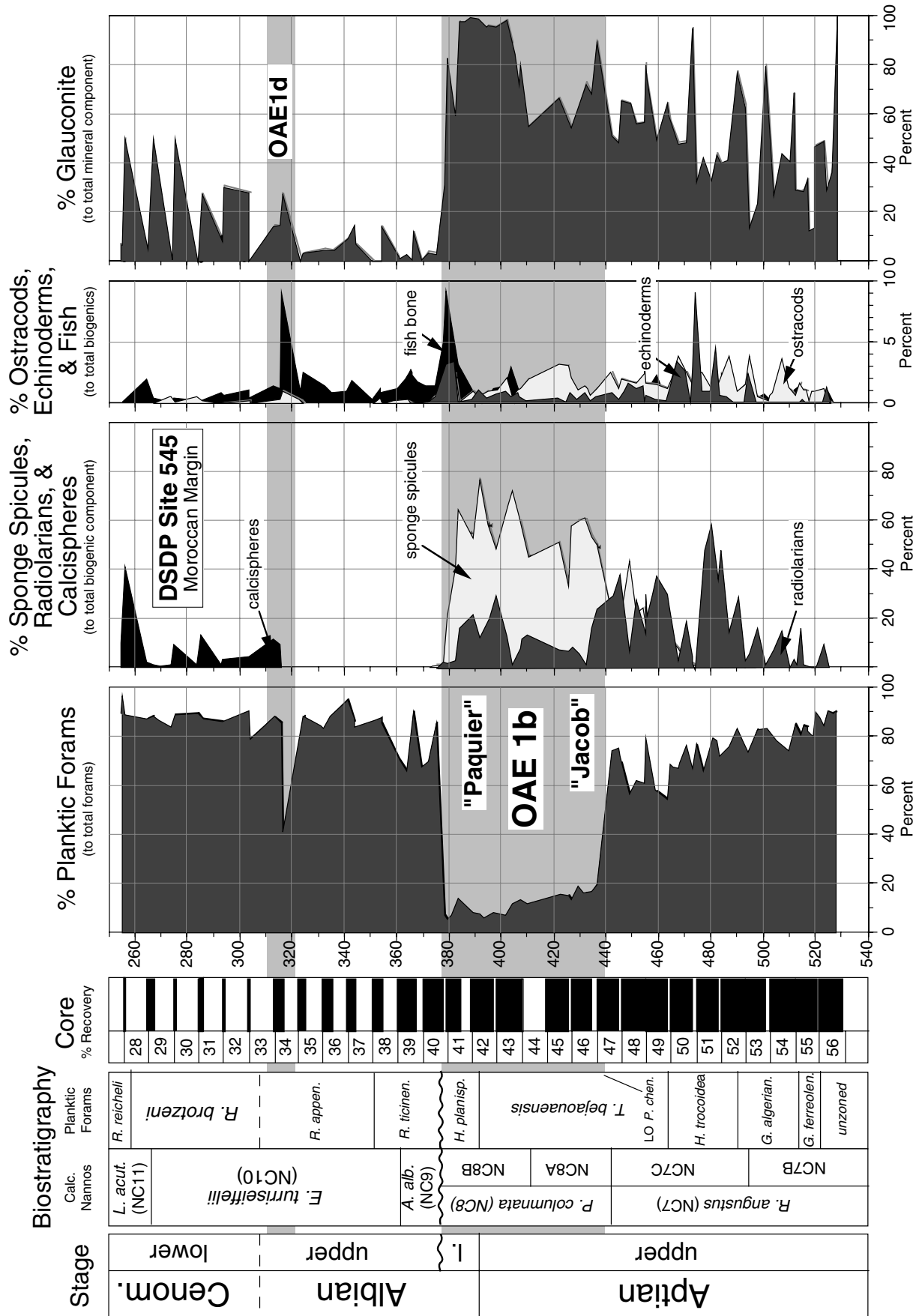
[18] OAE1b is particularly important in the analysis that follows because it represents a major transition in the nature of mid-Cretaceous tectonics, sea level, climate, lithofacies, and marine plankton communities. This is an interval that contains several prominent black shales spanning the time of the Aptian/Albian boundary [Arthur and Premoli Silva, 1982; Br  h  ret et al., 1986; Br  h  ret and Delamette, 1989; Premoli Silva et al., 1989; Tornaghi et al., 1989; Br  h  ret, 1991, 1994; Erbacher et al., 1996, 1998, 1999; Erbacher and Thurn, 1997]. A sea level fall near the Aptian/Albian boundary [Weissert and Lini, 1991; Br  h  ret, 1994; Weissert

et al., 1998] separates uppermost Aptian black shales (“Jacob” in the Vocontian Basin, and “113” in central Italy) from lower Albian black shales (“Paquier” and “Leenhardt” events in the Vocontian Basin, and the “Monte Nerone” and “Urbino” events in the Apennines of central Italy; Figure 1). Erbacher et al. [1998] interpreted the uppermost Aptian Jacob event of the Vocontian Basin as a DOAE (formed by detrital input; “fed black shale”) and the lower Albian Paquier and Leenhardt events as POAEs (driven by productivity and rising sea level; “condensed black shale”).

[19] The middle to late Aptian interval leading up to OAE1b is characterized by heavy  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$  values, punctuated by two episodes of sharply lighter isotopic ratios (Figure 1). Specifically,  $\delta^{13}\text{C}$  values continue to rise after the early Aptian OAE1a, suggesting the continued widespread burial of organic carbon through the mid-Aptian (*Leupoldina cabri* and *Globigerinelloides ferreolensis* biozones), in parallel with rising sea level [Menegatti et al., 1998]. This is followed by depleted values in the middle-late Aptian (*Globigerinelloides algerianus* biozone), enriched values again in the late Aptian (*Hedbergella trocoidea* and lower *Ticinella bejaouaensis* biozones), and depleted values in the latest Aptian (upper *T. bejaouaensis* biozone) before rising again in the early Albian (*H. planispira* zone [Weissert and Lini, 1991; Erbacher et al., 1996; Weissert et al., 1998; Bralower et al., 1999]). Weissert and Lini [1991] attribute the negative carbon excursions to global cooling, ice sheet growth, and sea level fall in the late Aptian and near the Aptian-Albian boundary as a positive feedback to the prolonged episodes of  $\text{C}_{\text{org}}$  burial in the *L. cabri*-*G. ferreolensis* biozones and again in the *H. trocoidea*-*T. bejaouaensis* biozones. The occurrence of ice-rafted debris and cool temperatures during the Aptian and Aptian/Albian transition in Australia support an interpretation of high-latitude glaciation(s) [Frakes and Francis, 1988; Ferguson et al., 1999; Frakes, 1999].

[20] Biogenic data from Deep Sea Drilling Program (DSDP) Site 545 [Leckie, 1984, 1987] suggest that the upper Aptian–basal Albian interval off northwest Africa was characterized by high productivity based on the abundance of radiolarians and benthic organisms (siliceous sponges, benthic foraminifera, echinoids, and ostracodes); the latter responded favorably to the enhanced export production [Leckie, 1987; Berger and Diester-Haas, 1988; Herguera and Berger, 1991] (Figure 2). The sharp drop in percent planktic foraminifera corresponds with the extinc-

**Figure 2.** (opposite) High biological productivity, represented in this expanded record of OAE1b at DSDP Site 545 off Morocco as suggested by the abundance of radiolarians and benthic organisms [Leckie, 1984, unpublished data]. Increased export production supported the rich benthic ecosystems [Leckie, 1987; Berger and Diester-Haas, 1988; Herguera and Berger, 1991]. Black shale lithofacies are weakly developed at this site, although elevated levels of organic carbon are preserved in cores 545-42 and 545-43 [Hinze et al., 1984]. The lithofacies and biofacies of Site 545 bear strong resemblance to those of the European margin of Tethys, particularly the Piobbico core from the Umbria-Marche Basin of central Italy [Premoli Silva et al., 1989; Tornaghi et al., 1989] (cores 545-55 to 47 are equivalent to unit 17 to the lower part of unit 14 in the Piobbico core; cores 545-46 to 545-41 are equivalent to the upper part of unit 14 to unit 11; strata above the disconformity in Site 545 are equivalent to midunit 2 in the Piobbico core). The larger planktic foraminifera were wiped out in the OAE1b interval, and tiny species dominate the assemblages. This was a watershed event in the evolutionary history of planktic foraminifera (see text).





tion of *Planomalina cheniourensis*, the earliest planktic foraminifer with a peripheral keel, and the pseudoextinction of *Nannoconus truittii* [Leckie, 1984; this study]. The low planktic:benthic ratio (percent planktics) across the Aptian/Albian boundary at Site 545 may be partially related to increased carbonate dissolution, although preservation of the tiny planktic and benthic species is moderately good to good with minimal test fragmentation and etching of the calcareous tests. However, correlative strata from the Apennines of central Italy show pronounced dissolution in the basal Albian [Premoli Silva *et al.*, 1989; Tornaghi *et al.*, 1989; Erba, 1992]. Despite the presumed high productivity off Morocco, black shale development is weak at this locality. High sedimentation rates (>35 m/Myr) diluted the lithologic expression of the correlative Jacob event at Site 545. In contrast, the basal Albian strata accumulated at significantly reduced rates (<15 m/Myr (Leckie, unpublished data)) and the presence of a thin dark-colored layer with elevated total organic carbon in core 545-42 [Hinze *et al.*, 1984; Bralower *et al.*, 1993] likely correlates with the Paquier black shale event (Figure 2). Like the Vocontian Basin of southeast France and the Umbria-Marche Basin of central Italy, the onset of OAE1b off northwest Africa is marked by an abrupt change in lithology and biota in the uppermost Aptian, just below the level of the Jacob and 113 black shale events.

[21] *Erbacher et al.* [2001] provide planktic and benthic foraminiferal stable isotopic data across the basal Albian part of OAE1b (correlative to the Paquier level) at ODP Site 1049 in the western tropical North Atlantic (Blake Nose) that show a sharp increase in planktic-benthic  $\delta^{18}\text{O}$  gradients across the black shale event. These authors attribute the findings to increased stratification of the water column by surface water warming and/or increased runoff and suggest that this black shale formed as a megasapropel by analogy to Plio-Pleistocene sapropel accumulation in the Mediterranean. *Kuypers et al.* [2001] concluded that severe oxygen depletion affected the water column during this event on the basis of the dominant fraction of organic matter derived from chemoautotrophic Crenarchaeota bacteria in this black shale. However, the basal Albian Paquier and lower Albian Leenhardt events in the Vocontian Basin of southeast France have been attributed to elevated primary productivity [Br  h  ret, 1994; *Erbacher et al.*, 1998, 1999], rather than increased thermohaline stratification. *Erbacher et al.* [1996] show three rock eval analyses for the interval around OAE1b; two have type II (marine) kerogen, and one has type III (terrestrial). These findings suggest that multiple triggers, including productivity, sea level, or climatically driven organic carbon burial events, characterize the broad interval of OAE1b.

[22] A marked lithologic change from poorly oxidized sediments with discrete black shale(s) to highly oxidized sediments is observed in lower Albian strata of ODP Site 1049 in the western North Atlantic (Blake Nose [Norris *et al.*, 1998]) and at DSDP Site 511 in the southern South Atlantic (Falkland Plateau [Ludwig *et al.*, 1983]), suggesting the possibility of an intermediate water (<1000 m) connection between the North and South Atlantic Ocean basins by early Albian time. In addition, the unconformity

separating the basal Albian and upper Albian strata at Site 545 (Figure 2) may be related to the inferred increase in intermediate water ventilation and circulation, thereby terminating OAE1b at middle (to lower?) bathyal depths. Poor ventilation at greater depths in the eastern North Atlantic persisted through much of the Albian [e.g., *Summerhayes*, 1981, 1987].

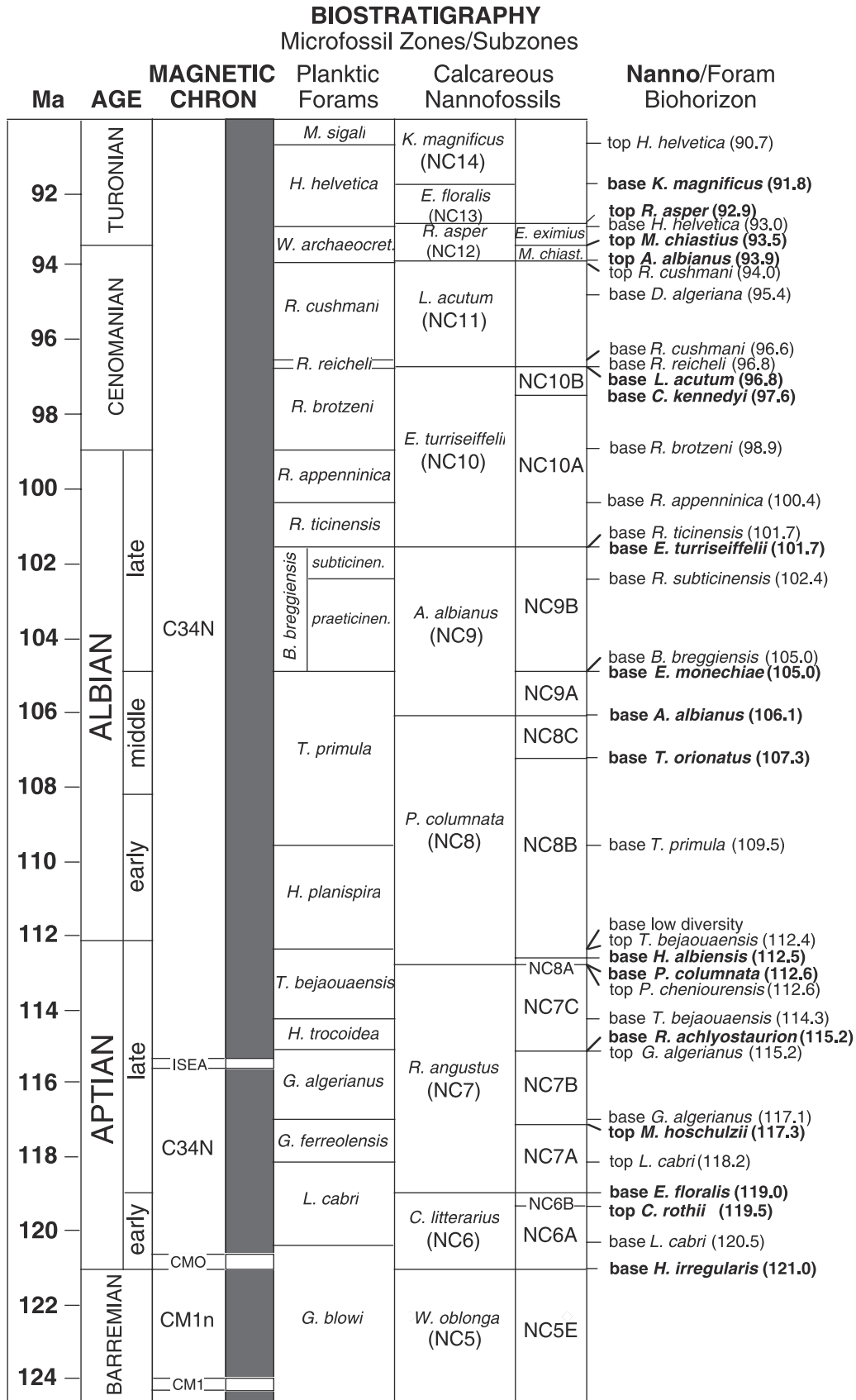
### 3. Methods

[23] One of the biggest challenges in studying the evolutionary history of ancient organisms is building the chronology required to calculate rates of change. Recent studies of mid-Cretaceous calcareous nannofossils and planktic foraminifera from deep-sea sections have established an integrated calcareous plankton biostratigraphy and improved geochronology [Bralower *et al.*, 1993, 1994, 1995, 1997; Erba *et al.*, 1996] (Figure 3). In this study, a 33 Myr interval encompassing the late Barremian to late Turonian (123–90 Ma) was divided into 1 million year increments using the timescale of *Gradstein et al.* [1994] and biostratigraphic age model of *Bralower et al.* [1997]. The stratigraphic ranges of 91 planktic foraminifera and 78 calcareous nannofossil taxa were compiled from numerous sources, including land sections and deep-sea sites (Figures 4 and 5). New and/or revised planktic foraminiferal range data from DSDP Sites 545 and 547 on the Moroccan continental margin [Leckie, 1984], DSDP Sites 364 and 511 in the South Atlantic, and ODP Site 763 on the Exmouth Plateau off northwest Australia (R. Cashman, M.S. thesis in progress, University of Massachusetts, 2002) are integrated with published data. The resulting compilations are based on a conservative taxonomic framework and best estimates of biostratigraphic range. Evolutionary rates were calculated following the method of *Wei and Kennett* [1986] (Tables 1 and 2).

[24] Here we compare the nature of biotic change as expressed by evolutionary rates in the planktic foraminifera and calcareous nannofossils (this study) and radiolarians [Erbacher *et al.*, 1996; *Erbacher and Thurow*, 1997] with the temporal and spatial distribution of the OAEs and other proxies of global change, including strontium isotopic ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) [Bralower *et al.*, 1997], carbon isotopes ( $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$ ) [Erbacher *et al.*, 1996; Bralower *et al.*, 1999], and oxygen isotopic analyses ( $\delta^{18}\text{O}$ ) of individual species of planktic foraminifera and monogeneric benthic foraminifera [Norris and Wilson, 1998; this study]. We also examined trends in planktic foraminiferal size and morphology as proxies of plankton trophic structure and upper water column structure, respectively.

[25] Isotope paleoecology ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) of individual species of planktic foraminifera is a useful tool to assess depth habitat or presence of photosymbionts in ancient species [e.g., *Berger et al.*, 1978; *Fairbanks and Wiebe*, 1980; *Fairbanks et al.*, 1982; *Deuser et al.*, 1981; *Gasperi and Kennett*, 1992; *Ravelo and Fairbanks*, 1992, 1995; *D'Hondt and Arthur*, 1995; *Norris*, 1996, 1998; *Pearson*, 1998; *Pearson et al.*, 2001]. Interplanktic species isotopic gradients reveal the nature of the upper water column (mixed layer and upper thermocline where most planktic





**Figure 3.** Integrated calcareous plankton biostratigraphy used in this study (modified from *Bralower et al.* [1997]) following revised range of *Leupoldina cabri* from *Erba et al.* [1999] and *Premoli Silva et al.* [1999].

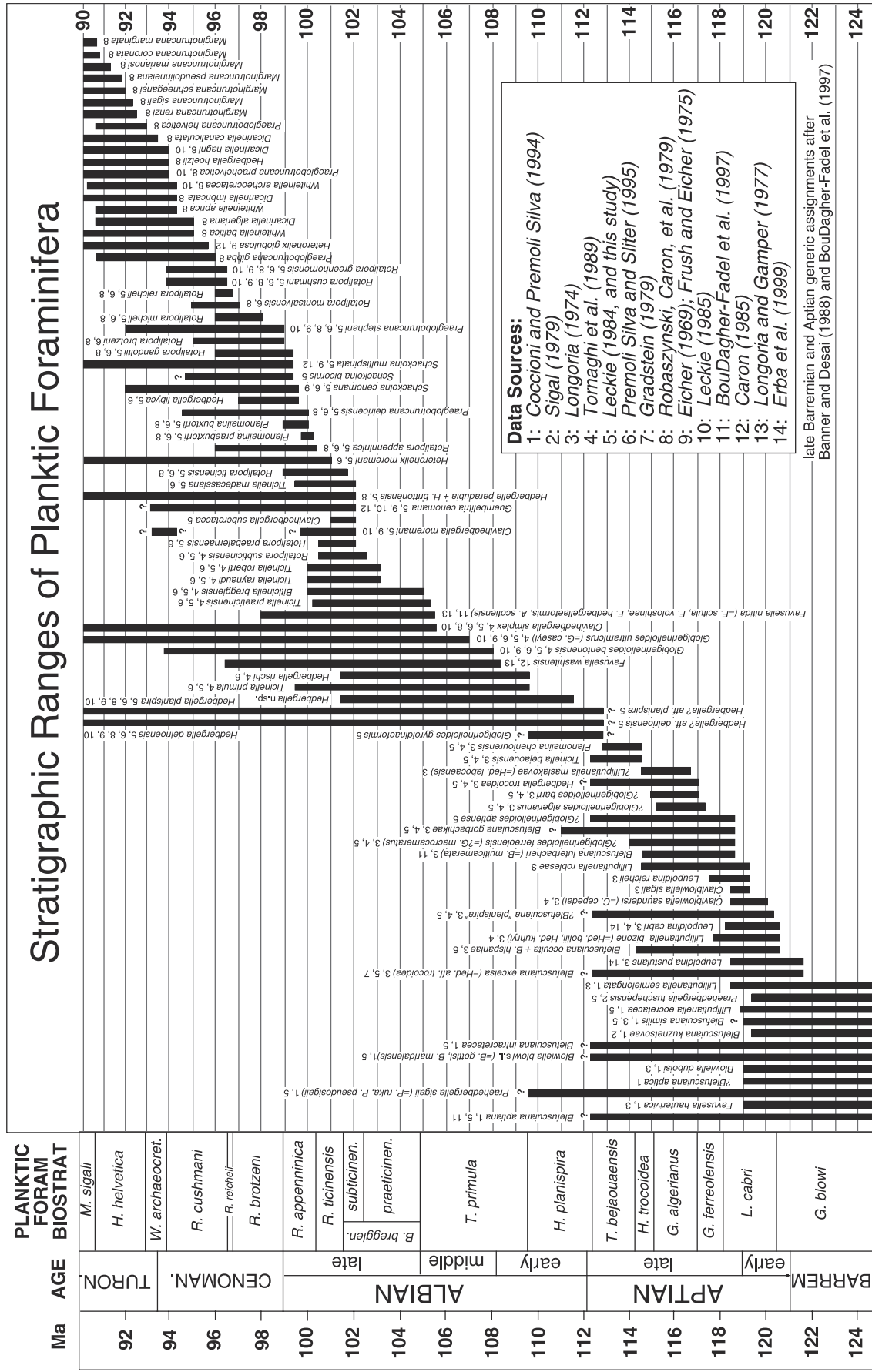
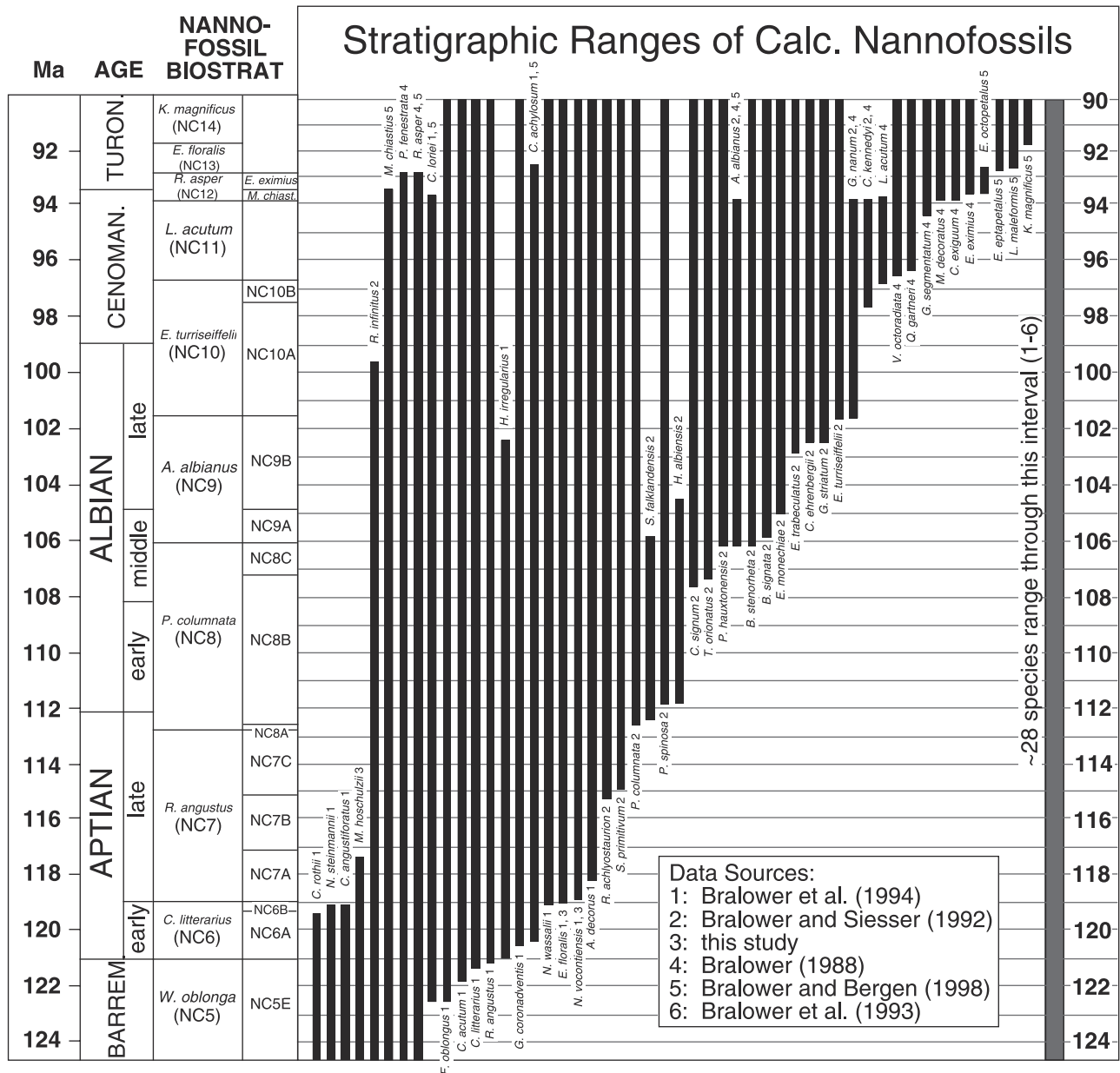


Figure 4. Interpreted stratigraphic ranges of 91 species of planktic foraminifera used to calculate the evolutionary rates presented in this study (Table 1).



**Figure 5.** Interpreted stratigraphic ranges of 78 species of calcareous nannofossils used to calculate the evolutionary rates presented in this study (Table 2). There are ~28 species that range through the entire mid-Cretaceous interval as represented by the wide shaded bar.

foraminifera live), including aspects of density structure and productivity, while planktic-benthic isotopic gradients serve as proxies of water column structure, productivity, and bottom water age. Changing patterns in mid-Cretaceous planktic foraminiferal morphological and trophic diversity have been linked with upper water column stratification and productivity [Sliter, 1972; Hart, 1980; Caron and Home-wood, 1983; Leckie, 1987, 1989; Premoli Silva and Sliter, 1999].

[26] Here we present new data on the isotope paleoecology of latest Aptian and middle Albian species of planktic foraminifera. We measured the carbon and oxygen isotopes

of multiple species of well-preserved planktic foraminifera and a single epifaunal benthic taxon (*Gavelinella*) from four uppermost Aptian and middle Albian samples of DSDP Site 392A on the Blake Nose, western subtropical North Atlantic (Table 3) [see Gradstein, 1978, plates]. The samples are from the type of clay-rich hemipelagic sediments shown to yield reliable paleotemperature estimates from foraminiferal calcite [e.g., Norris and Wilson, 1998; Pearson et al., 2001; Wilson and Norris, 2001]. Analyses were conducted at Woods Hole Oceanographic Institution on a Finnigan MAT 252 with a precision of better than 0.03‰ for  $\delta^{13}\text{C}$  and 0.08‰ for  $\delta^{18}\text{O}$ . Our results are integrated with other

**Table 1.** Planktic Foraminiferal Evolutionary Data Based on the Stratigraphic Ranges Presented in Figure 4<sup>a</sup>

Interval, Ma	Age	S	FO	LO	rs	re	rd	rt
90–91	90.5	26	2	5	0.08	0.19	-0.12	0.27
91–92	91.5	24	3	0	0.13	0.00	0.13	0.13
92–93	92.5	23	3	2	0.13	0.09	0.04	0.22
93–94	93.5	25	4	5	0.16	0.20	-0.04	0.36
94–95	94.5	23	5	2	0.22	0.09	0.13	0.30
95–96	95.5	19	2	2	0.11	0.11	0.00	0.21
96–97	96.5	22	4	5	0.18	0.23	-0.05	0.41
97–98	97.5	19	1	1	0.05	0.05	0.00	0.11
98–99	98.5	19	2	1	0.11	0.05	0.05	0.16
99–100	99.5	23	7	6	0.30	0.26	0.04	0.57
100–101	100.5	22	3	6	0.14	0.27	-0.14	0.41
101–102	101.5	22	7	3	0.32	0.14	0.18	0.45
102–103	102.5	15	3	0	0.20	0.00	0.20	0.20
103–104	103.5	12	0	0	0.00	0.00	0.00	0.00
104–105	104.5	12	1	0	0.08	0.00	0.08	0.08
105–106	105.5	11	3	0	0.27	0.00	0.27	0.27
106–107	106.5	8	1	0	0.13	0.00	0.13	0.13
107–108	107.5	7	1	0	0.14	0.00	0.14	0.14
108–109	108.5	6	1	0	0.17	0.00	0.17	0.17
109–110	109.5	7	2	2	0.29	0.29	0.00	0.57
110–111	110.5	5	0	0	0.00	0.00	0.00	0.00
111–112	111.5	6	1	1	0.17	0.17	0.00	0.33
112–113	112.5	13	3	9	0.23	0.69	-0.46	0.92
113–114	113.5	11	0	0	0.00	0.00	0.00	0.00
114–115	114.5	16	2	5	0.13	0.31	-0.19	0.44
115–116	115.5	16	0	2	0.00	0.13	-0.13	0.13
116–117	116.5	16	3	0	0.19	0.00	0.19	0.19
117–118	117.5	15	1	2	0.07	0.13	-0.07	0.20
118–119	118.5	20	4	6	0.20	0.30	-0.10	0.50
119–120	119.5	22	4	6	0.18	0.27	-0.09	0.45
120–121	120.5	18	4	0	0.22	0.00	0.22	0.22
121–122	121.5	14	2	0	0.14	0.00	0.14	0.14
122–123	122.5	12	0	0	0.00	0.00	0.00	0.00

<sup>a</sup>The data are plotted in Figure 6 and summarized in Figures 7 and 11. S, species richness (or simple diversity); FO, number of first occurrences per million year interval; LO, number of last occurrences per million year interval; rs, rate of speciation ((1/S)FO); re, rate of extinction ((1/S)LO); rd, rate of diversification (rs - re); rt, rate of turnover (rs + re). Rate of speciation (rs) = 1/species richness (S) × number of first occurrences (FO). Rate of extinction (re) = 1/species richness (S) × number of last occurrences (LO); rs and re are per species rates of speciation and extinction (1/S). Rate of diversification (rd) = rate of speciation (rs) - rate of extinction (re). Rate of turnover (rt) = rate of speciation (rs) + rate of extinction (re).

published data from Blake Nose DSDP and ODP sites [Norris and Wilson, 1998; Fassell and Bralower, 1999; Huber et al., 1999].

[27] Planktic foraminiferal size data are based on the largest dimension of all species known from a single tropical-subtropical planktic foraminiferal biozone or composite of two biozones. These data are derived from scanning electron photomicrograph images from various sources: late Barremian and early Aptian data are from ODP Site 641 on the Iberian margin (Leckie, unpublished) and outcrop localities in Mexico [Longoria, 1974] and Spain [Coccioni and Premoli Silva, 1994] and late Aptian, early Albian and late Albian data are from DSDP Sites 545 and 547 on the Moroccan margin [Leckie, 1984] with supplementary data from Longoria [1974]. Mid-Cretaceous planktic foraminiferal size data are compared with extant species [Hemleben et al., 1989] to illustrate the significant differences in size and trophic specialization between the

**Table 2.** Calcareous Nannofossil Evolutionary Data Based on the Stratigraphic Ranges Presented in Figure 5<sup>a</sup>

Interval, Ma	Age	S	FO	LO	rs	re	rd	rt
90–91	90.5	60	0	0	0.00	0.00	0.00	0.00
91–92	91.5	60	1	0	0.02	0.00	0.02	0.02
92–93	92.5	63	2	4	0.03	0.06	-0.03	0.10
93–94	93.5	67	4	6	0.06	0.09	-0.03	0.15
94–95	94.5	63	0	0	0.00	0.00	0.00	0.00
95–96	95.5	62	0	0	0.00	0.00	0.00	0.00
96–97	96.5	62	3	0	0.05	0.00	0.05	0.05
97–98	97.5	59	1	0	0.02	0.00	0.02	0.02
98–99	98.5	58	0	0	0.00	0.00	0.00	0.00
99–100	99.5	59	0	1	0.00	0.02	-0.02	0.02
100–101	100.5	59	0	0	0.00	0.00	0.00	0.00
101–102	101.5	59	2	0	0.03	0.00	0.03	0.03
102–103	102.5	58	3	1	0.05	0.02	0.03	0.07
103–104	103.5	55	0	0	0.00	0.00	0.00	0.00
104–105	104.5	56	1	1	0.02	0.02	0.00	0.04
105–106	105.5	56	1	1	0.02	0.02	0.00	0.04
106–107	106.5	55	3	0	0.05	0.00	0.05	0.05
107–108	107.5	52	2	0	0.04	0.00	0.04	0.04
108–109	108.5	50	0	0	0.00	0.00	0.00	0.00
109–110	109.5	50	0	0	0.00	0.00	0.00	0.00
110–111	110.5	50	0	0	0.00	0.00	0.00	0.00
111–112	111.5	49	2	0	0.04	0.00	0.04	0.04
112–113	112.5	48	2	0	0.04	0.00	0.04	0.04
113–114	113.5	46	0	0	0.00	0.00	0.00	0.00
114–115	114.5	46	1	0	0.02	0.00	0.02	0.02
115–116	115.5	45	1	0	0.02	0.00	0.02	0.02
116–117	116.5	44	0	0	0.00	0.00	0.00	0.00
117–118	117.5	45	0	1	0.00	0.02	-0.02	0.02
118–119	118.5	45	3	0	0.07	0.00	0.07	0.07
119–120	119.5	44	1	3	0.02	0.07	-0.05	0.09
120–121	120.5	44	3	0	0.07	0.00	0.07	0.07
121–122	121.5	41	3	0	0.07	0.00	0.07	0.07
122–123	122.5	38	2	0	0.05	0.00	0.05	0.05

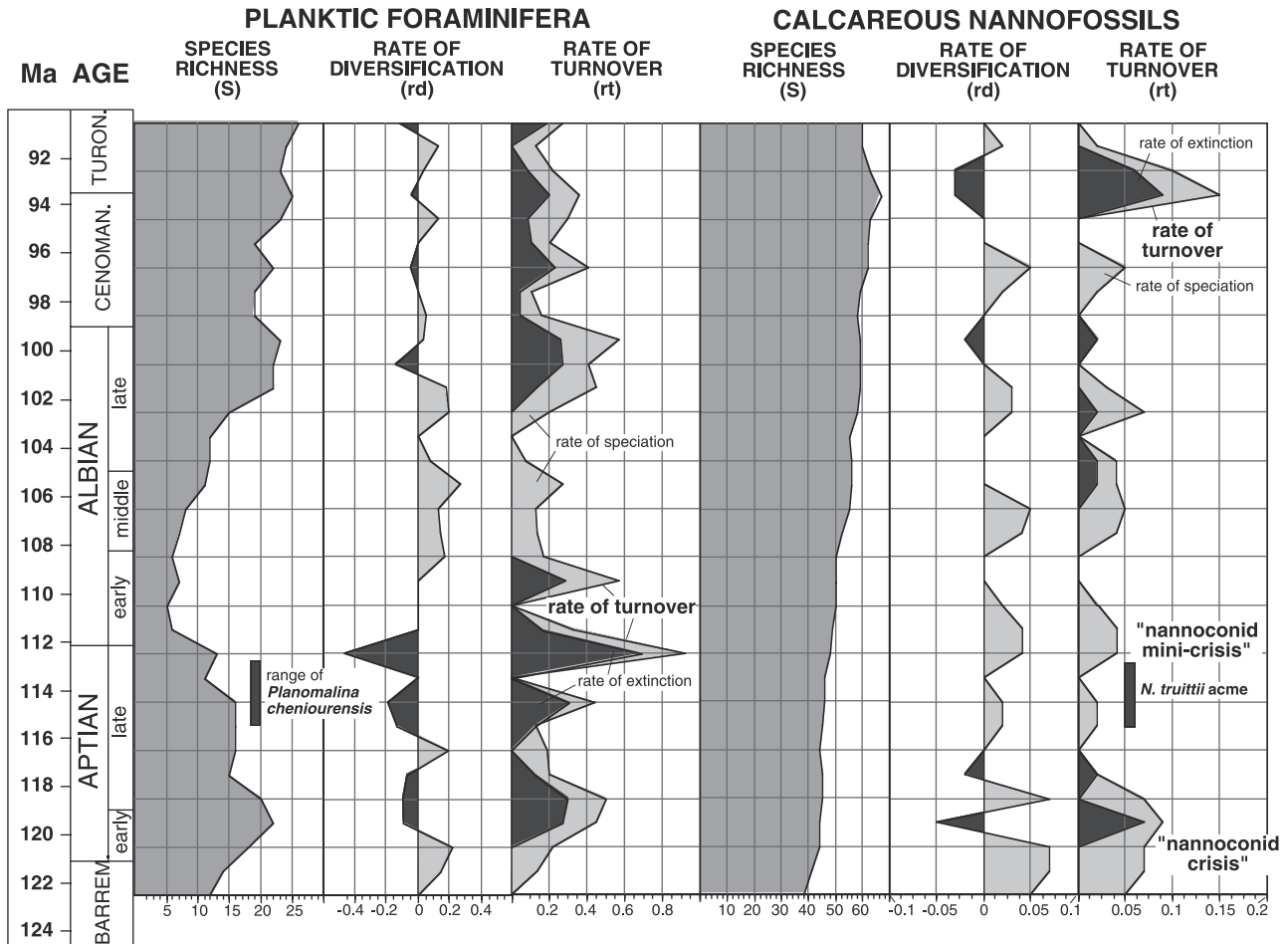
<sup>a</sup>See Table 1 for explanation. The data are plotted in Figure 6 and summarized in Figures 7 and 11. Rate of speciation (rs) = 1/species richness (S) × number of first occurrences (FO). Rate of extinction (re) = 1/species richness (S) × number of last occurrences (LO); rs and re are per species rates of speciation and extinction (1/S). Rate of diversification (rd) = rate of speciation (rs) - rate of extinction (re). Rate of turnover (rt) = rate of speciation (rs) + rate of extinction (re).

**Table 3.** Stable Isotopic Data for Individual Species of Planktic Foraminifera and the Benthic Foraminiferal Genus *Gavelinella* From Four Samples from DSDP Hole 392A (Blake Nose)<sup>a</sup>

Sample Number	Taxon	Age	δ <sup>13</sup> C	δ <sup>18</sup> O
392A-2-1, 73 cm	<i>T. primula</i>	105.2	2.202	-2.455
392A-2-1, 73 cm	<i>H. planispira</i>	105.2	2.202	-2.059
392A-2-1, 73 cm	<i>Hedbergella</i> n.sp.	105.2	2.052	-2.007
392A-2-1, 73 cm	<i>Gavelinella</i> sp.	105.2	1.338	-0.371
392A-3-1, 94 cm	<i>T. primula</i>	106.2	2.341	-2.150
392A-3-1, 94 cm	<i>Hedbergella</i> n.sp.	106.2	2.048	-1.847
392A-3-1, 94 cm	<i>Gavelinella</i> sp.	106.2	1.286	-0.374
392A-3-2, 102 cm	<i>T. bejaouaensis</i>	112.5	4.016	0.255
392A-3-2, 102 m	<i>H. trocoidea</i>	112.5	4.058	0.257
392A-3-2, 102 cm	<i>Blefuscuiana</i> sp.	112.5	4.155	0.415
392A-3-2, 102 cm	<i>Gavelinella</i> sp.	112.5	3.511	0.779
392A-3-2, 102 cm	<i>G. aptiense</i>	112.5	4.068	0.835
392A-3-3, 73 cm	<i>T. bejaouaensis</i>	112.8	3.783	0.096
392A-3-3, 73 cm	<i>Blefuscuiana</i> sp.	112.8	3.897	0.247
392A-3-3, 73 cm	<i>P. cheniourensis</i>	112.8	3.684	0.525
392A-3-3, 73 cm	<i>Gavelinella</i> sp.	112.8	3.193	0.566
392A-3-3, 73 cm	<i>G. aptiense</i>	112.8	3.757	0.721

<sup>a</sup>The data are presented in Figures 9 and 10. Here n.sp. is new species.





**Figure 6.** Evolutionary history of planktic foraminifera and calcareous nannofossils through the mid-Cretaceous (Tables 1 and 2). Evolutionary rates calculated following the method of *Wei and Kennett* [1986]: (1) rate of speciation ( $r_s$ ) =  $1/\text{species richness (S)} \times \text{number of first occurrences (FO) per million year interval}$ , (2) rate of extinction ( $r_e$ ) =  $1/\text{species richness (S)} \times \text{number of last occurrences (LO) per million year interval}$ , (3) rate of diversification ( $r_d$ ) =  $r_s - r_e$ , and (4) rate of turnover ( $r_t$ ) =  $r_s + r_e$ . The “nannoconid crisis” represents a global perturbation in calcareous nannoplankton communities that produced a dramatic reduction in nannoconid carbonate production immediately preceding OAE 1a [Erba, 1994; Larson and Erba, 1999]. Nannoconids make a resurgence of abundance in the late Aptian called the “*Nannoconus truittii* acme,” named for the dominant taxon [Mutterlose, 1989; Erba, 1994]. The *N. truittii* acme corresponds with the range of the earliest planktic foraminiferal taxon with a peripheral keel, *Planomalina cheniourensis*. Nannoconids abruptly drop in abundance at the extinction level of *P. cheniourensis* in the latest Aptian [Erba, 1994; Bralower et al., 1994; this study]. We refer to this second nannoconid crash in abundance as the “nannoconid minicrisis.” These two events mark the onset of OAE1b just prior to the “Jacob” black shale.

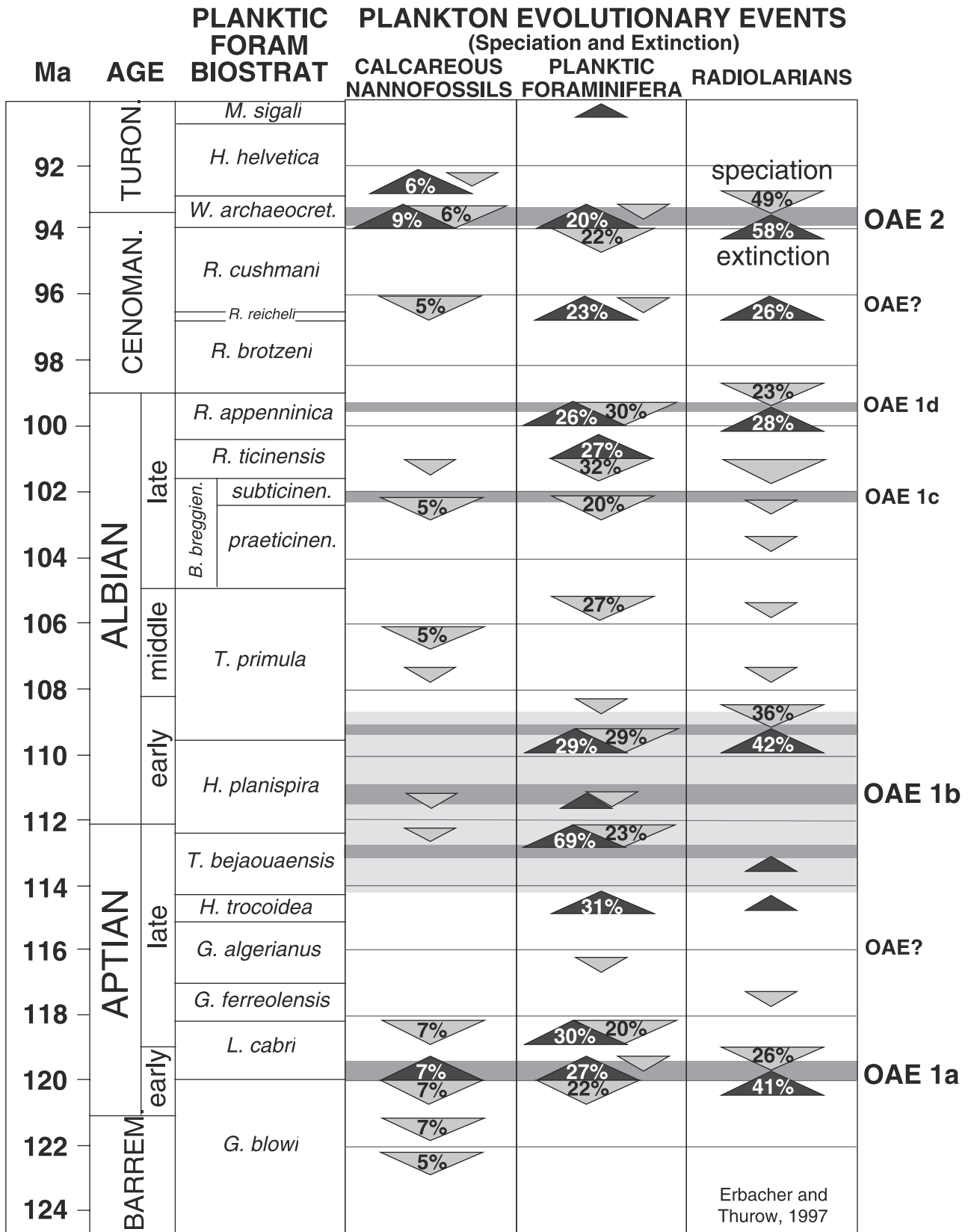
ancient and modern taxa. Plankton size in part reflects trophic position within the microbial loop and/or grazing food chain (see section 4).

## 4. Results

### 4.1. Evolutionary Rates of Mid-Cretaceous Calcareous Plankton

[28] The pattern of evolutionary activity in the calcareous nannoplankton reveal the greatest rates of turnover (speciation plus extinction) in the early Aptian and at the

Cenomanian/Turonian boundary (Figure 6). These two intervals also correspond with the highest rates of extinction. There were typically 2–3 times more species of calcareous nannoplankton than planktic foraminifera through much of the mid-Cretaceous, with the early to middle Albian showing the greatest disparity between the two groups. Calcareous nannofossil diversity gradually rises from ~40 species in the late Barremian to a high of nearly 70 species in the early Turonian. The rate of diversification (speciation minus extinction) is greatest in the late Barremian and in the early late Aptian; other times of significant



diversification include the Aptian/Albian boundary interval, middle Albian, late Albian, and mid-Cenomanian.

[29] Planktic foraminiferal evolution during the mid-Cretaceous was characterized by episodes of elevated rates of turnover alternating with times of relatively diminished rates (note the difference in scale between the planktic foraminifera and the calcareous nannofossils). The highest rates of turnover occurred in the early to middle Aptian, across the Aptian/Albian boundary, in the latest Albian, the mid-Cenomanian, and at the Cenomanian/Turonian boundary (Figure 6). Particularly noteworthy are the three peaks in turnover through the latest Aptian-early Albian interval, with the greatest turnover of planktic foraminifera of the entire mid-Cretaceous occurring near the Aptian/Albian boundary (e.g., 69% of the late Aptian species became extinct during the 112–113 Ma interval, while there was a 23% speciation rate for a total of 92% species turnover). This turnover resulted in the net loss of species and the lowest simple diversity of the study interval.

[30] In general, the Aptian was dominated by negative rates of planktic foraminiferal diversification, with exceptions at the beginning of the stage and in the early late Aptian. Positive rates characterize nearly all of the Albian with the exception of the end of the Albian. The resulting pattern of simple diversity through time shows a pattern of increasing species richness during the late Barremian that peaked in the early Aptian, decreased somewhat in the middle Aptian, and remained relatively stable through much of the late Aptian (Figure 6). There was a fourfold increase in diversity between the early and late Albian with total species richness remaining relatively stable through the mid-Turonian despite episodes of elevated turnover.

[31] An important result of this analysis is the strikingly similar patterns of evolutionary turnover in the planktic foraminifera and the radiolarians. *Erbacher et al.* [1996] showed that the highest rates of turnover in the radiolaria coincide with the major OAEs (Figure 7). Foraminiferal evolutionary patterns clearly show that the highest rates of speciation and/or extinction occur at or near the OAEs. For the calcareous nannofossils the highest rates of turnover occur at OAE1a in the early Aptian and OAE2 at the Cenomanian/Turonian boundary. In addition to the major OAEs, additional perturbations in the ocean-climate system may have occurred during the mid-Aptian, late Albian, and the mid-Cenomanian on the basis of accelerated evolutionary activity in both the planktic foraminifera and the calcareous nannoplankton.

#### 4.2. Planktic Foraminiferal Size and Trophic Ecology

[32] Planktic foraminiferal size varied significantly during the mid-Cretaceous (Figure 8). During the late Barremian, all species were <250  $\mu\text{m}$  with an average size of 168  $\mu\text{m}$ . Average size steadily increased toward the late

Aptian in parallel with increasing diversity (Figures 4 and 6) and morphological variety and complexity [Leckie, 1989]. The average size of planktic foraminifera reached 330  $\mu\text{m}$  by the late Aptian with the largest taxon (*Globigerinelloides algerianus*) attaining maximum diameters of  $\sim 700 \mu\text{m}$ . Planktic foraminiferal size and diversity both crashed across the Aptian/Albian boundary; at this time the average size dropped to 230  $\mu\text{m}$ . Average test size steadily rose to 400  $\mu\text{m}$  by the end of the Albian in parallel with the trend in diversity. Cenomanian and Turonian planktic foraminifera are similar to late Albian taxa in their overall range of size.

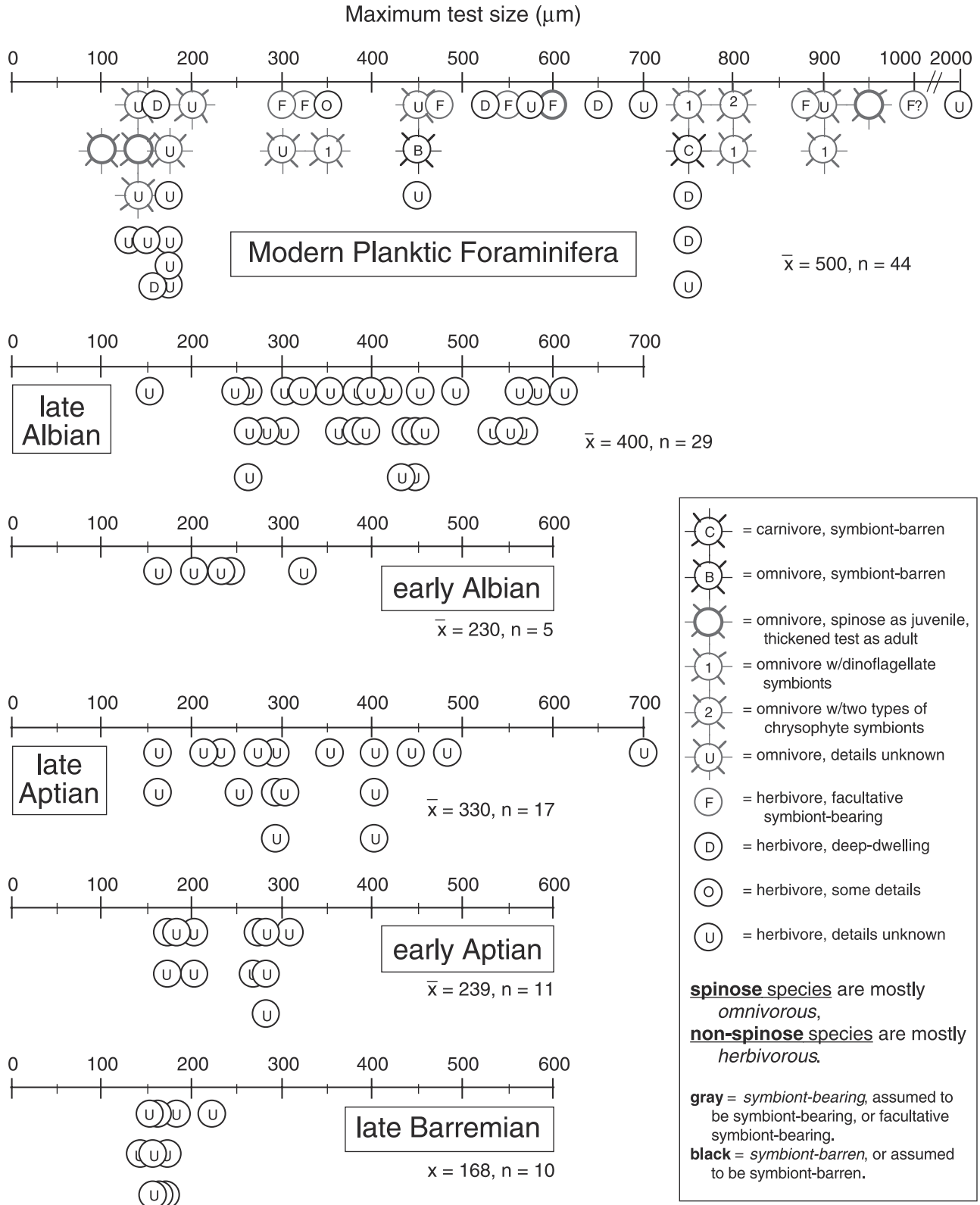
[33] By comparison with extant species of planktic foraminifera the mid-Cretaceous planktic foraminifera are much smaller (Figure 8). Note the wide range of size and implied trophic diversity of modern taxa (e.g., the average adult maximum diameter, on a spine-free basis, of the 44 extant species is  $\sim 500 \mu\text{m}$ ; range is  $\sim 100\text{--}2000 \mu\text{m}$ ). Nearly half (19 of 44) of all modern planktic foraminifera bear long spines that provide infrastructure to support the sticky rhizopodial network used to snare particulate organic matter or prey and/or to deploy photosymbionts. In addition, the modern taxa show a diverse array of feeding strategies, many of which were probably unavailable to mid-Cretaceous taxa, including a variety of photosymbioses and carnivory of microcrustaceans such as copepods [Hemleben *et al.*, 1989; Laybourn-Parry, 1992] (Figure 8). For example, ultrastructural evidence indicates that none of these ancient species had spines, and isotopic data suggest that no mid-Cretaceous species contained photosymbionts [Norris and Wilson, 1998], although very few species have been analyzed with the appropriate isotopic technique to critically evaluate for photosymbionts [e.g., D'Hondt and Arthur, 1995; Norris, 1996, 1998].

#### 4.3. Planktic Foraminiferal Isotope Paleoecology and Upper Water Column Stratification

[34] Several studies have utilized isotopic analyses of individual mid-Cretaceous planktic foraminiferal species for the purposes of assessing paleoecology, water column structure, and/or productivity [e.g., Corfield *et al.*, 1990; Huber *et al.*, 1995, 1999, 2002; Norris and Wilson, 1998; Fassell and Bralower, 1999; Erbacher *et al.*, 2001]. Our results show that latest Aptian age planktic foraminifera (*Ticinella bejaouaensis* zone) were probably weakly stratified in the upper water column on the basis of a 0.58–0.62‰ difference between the lightest (*Ticinella bejaouaensis*) and heaviest (*Globigerinelloides aptiense*)  $\delta^{18}\text{O}$  values (Figures 9g and 9h and Table 3). The planktic-benthic isotopic gradients also show that the water column was weakly stratified with deep/intermediate water temperatures of  $\sim 10^{\circ}\text{--}11^{\circ}\text{C}$  and salinity corrected surface water temperatures (SSTs) of  $\sim 14^{\circ}\text{--}17^{\circ}\text{C}$ .

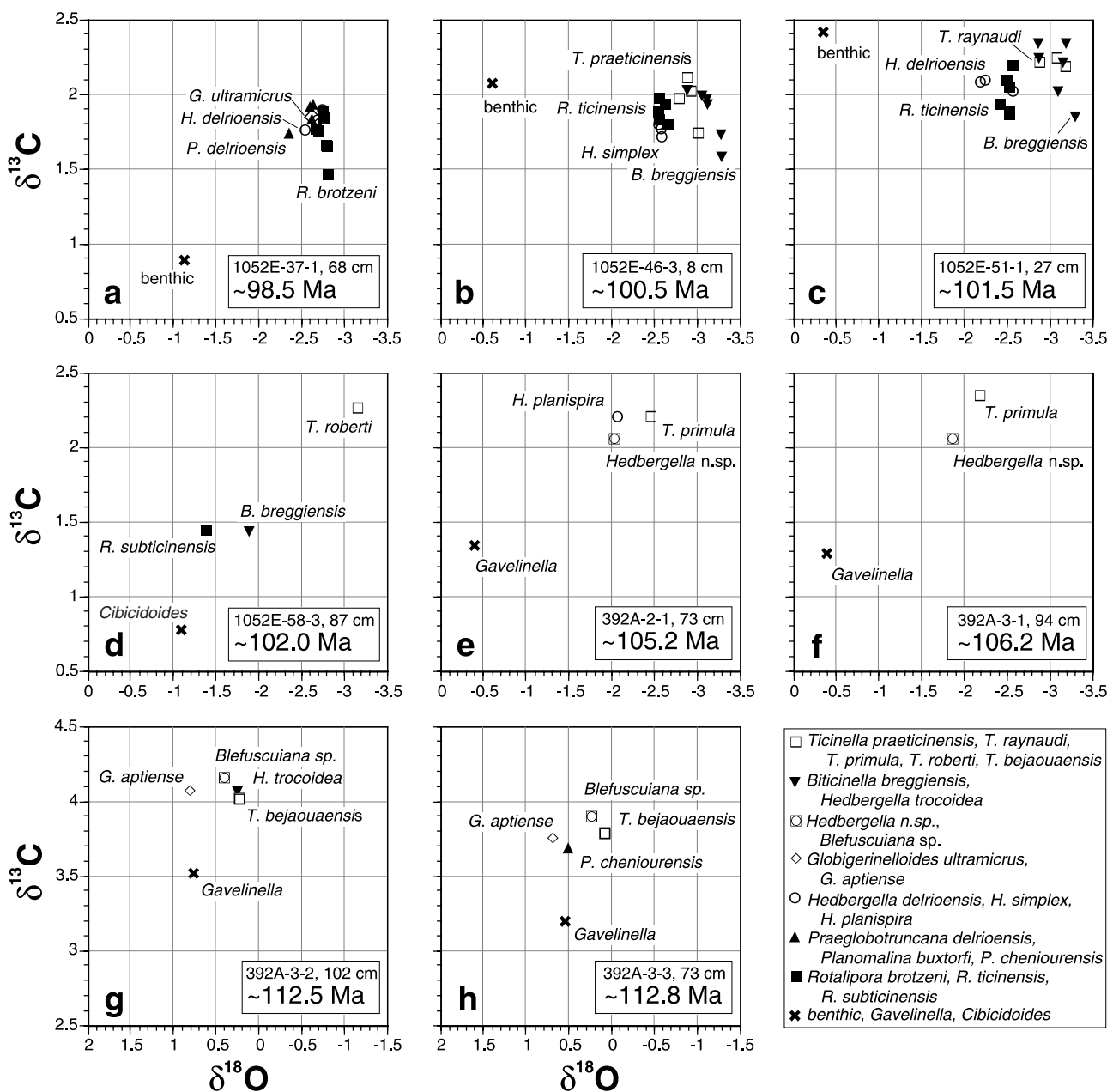
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**Figure 7.** (opposite) Plankton evolutionary events relative to the OAEs showing percentage of species first appearances (speciation) or disappearances (extinction) through 1 million year increments. Radiolarian data are from *Erbacher and Thurow* [1997]. Planktic foraminiferal and calcareous nannofossil extinction and speciation data are based on this study (Figure 6). For planktic foraminifera, larger triangles represent  $\geq 19\%$  change, and smaller triangles represent 15–19% for calcareous nannofossils, larger triangles represent  $>4\%$  change, and smaller triangles represent 3–4%. Note that the highest rates of plankton turnover (extinction plus speciation) occur at or near the major OAEs.



**Figure 8.** Comparison of mid-Cretaceous and modern planktic foraminiferal size and trophic strategies. Data for modern planktic foraminifera are from Hemleben et al. [1989]; mid-Cretaceous data are from Longoria [1974], Leckie [1984], Coccioni and Premoli Silva [1994], and R. M. Leckie, unpublished data from ODP Hole 641C). Data are also presented on Figure 10.

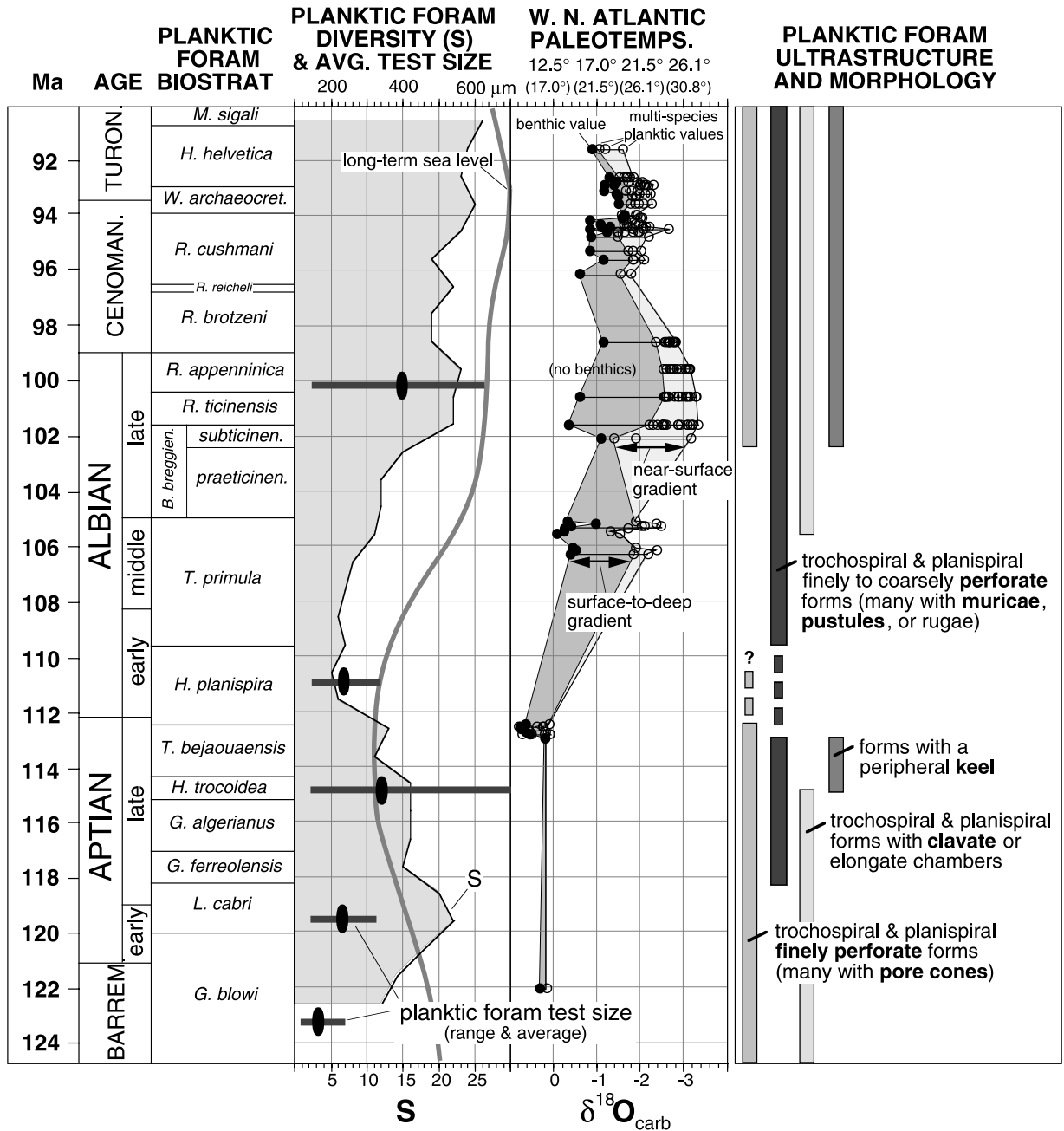




**Figure 9.** Stable isotopic data for multispecies mid-Cretaceous planktic foraminifera from Blake Nose in the western North Atlantic. (a–d) Data from the upper Albian-basal Cenomanian of ODP Hole 1052E (data are from Norris and Wilson [1998]; multiple data points for each species represent different size fractions). (e–h) New data from the uppermost Aptian and middle Albian of DSDP Site 392A (Table 3).

By late middle Albian time (upper *Ticinella primula* zone), salinity-corrected SSTs had risen to  $\sim 25^{\circ}$ – $28^{\circ}\text{C}$ , and deep/intermediate water temperatures in the western North Atlantic had risen to  $\sim 14^{\circ}$ – $17^{\circ}\text{C}$  (middle Albian data from the same site by Fassell and Bralower [1999] show benthic temperatures as low as  $12.5^{\circ}\text{C}$  and salinity-corrected SSTs as low as  $\sim 22^{\circ}\text{C}$ ). While upper water column isotopic gradients remained weak ( $0.30$ – $0.45\text{‰}$ ), the surface to deep water gradient of  $1.78$ – $2.08\text{‰}$  indicates that the water column was significantly more stratified at this location by middle Albian time (Figures 9e and 9f).

[35] When integrated with other published records from the Blake Nose in the western North Atlantic [Norris and Wilson, 1998; Fassell and Bralower, 1999; Huber et al., 1999], the isotopic data show clear evidence for increasing stratification of the upper water column during latest Aptian through Albian time in parallel with increasing planktic foraminiferal diversity and test size (Figure 10). Not only did deep water temperature rise during the Albian, but both the planktic-benthic and interplanktic species  $\delta^{18}\text{O}$  gradients ( $0.46$ – $1.79$  and  $1.67$ – $2.95\text{‰}$ , respectively [Norris and Wilson, 1998]) increased with rising sea level and rising



**Figure 10.** Paleotemperature estimates based on benthic (solid circles) and multispecies planktic (open circles) foraminiferal data from the Blake Nose in the western North Atlantic [Norris and Wilson, 1998; Fassell and Bralower, 1999; Huber et al., 1999; this study]. Planktic foraminiferal paleotemperature estimates have been corrected for salinity (values in parentheses) following Zachos et al. [1994]. Calculations are based on the equation of Erez and Luz [1983] assuming  $\delta_{water} = -1.0\text{‰}_{smow}$  for a nonglacial world [Shackleton and Kennett, 1975]. Note the following: (1) the decrease in planktic foraminiferal test size and diversity across the Aptian/Albian boundary is associated with a fundamental change in foraminiferal ultrastructure, (2) planktic foraminiferal simple diversity (species richness) and average test size generally track the pattern of long-term rising sea level and warming during the Albian (species of Cenomanian and Turonian planktic foraminifera are very similar to late Albian species in test size), (3) relatively cool surface and deep water temperatures during the latest Barremian and latest Aptian give way to a warming trend in both deep water and surface waters through the Albian, (4) the sharp increase in  $\delta^{18}O_{planktic}$  gradient in the late Albian is associated with a marked increase in planktic foraminiferal diversity, (5) increased water column stratification by the late Albian marks the onset of widespread deposition of calcareous ooze (chalk) with rising sea level, and (6) latest Aptian to early Turonian sea surface temperatures track the long-term trend of global sea level.

sea surface temperatures (Figures 9a–9d), indicating that the water column in the western North Atlantic became well stratified by early late Albian time. Sea surface temperatures peaked in the late Albian with values exceeding 30°C [Norris and Wilson, 1998]. Water column stratification persisted through the Cenomanian-Turonian [Norris and Wilson, 1998; Huber et al., 1999].

## 5. Discussion

### 5.1. The Evolutionary Record of Mid-Cretaceous Plankton

[36] Calcareous nannoplankton and radiolarians have a rich history back to the Triassic and earlier. By contrast, the planktic foraminifera experienced their first major radiations from tiny ancestors (with test diameters <100 µm) during the Early Cretaceous [Tappan and Loeblich, 1973; Banner and Desai, 1988; Sliter, 1989b; Coccioni et al., 1992; Coccioni and Premoli Silva, 1994; BouDagher-Fadel et al., 1997; Premoli Silva and Sliter, 1999]. The evolutionary patterns of the planktic foraminifera and other plankton show that this period of overall diversification was punctuated by episodes of extinction and speciation; the highest rates of turnover occurred at or near the OAEs (Figure 7). In the planktic foraminifera a reversal in the general trend of increasing size and morphological variety and complexity occurred during latest Aptian-early Albian OAE1b when the average shell diameter decreased sharply to <250 µm and diversity plummeted (Figure 10).

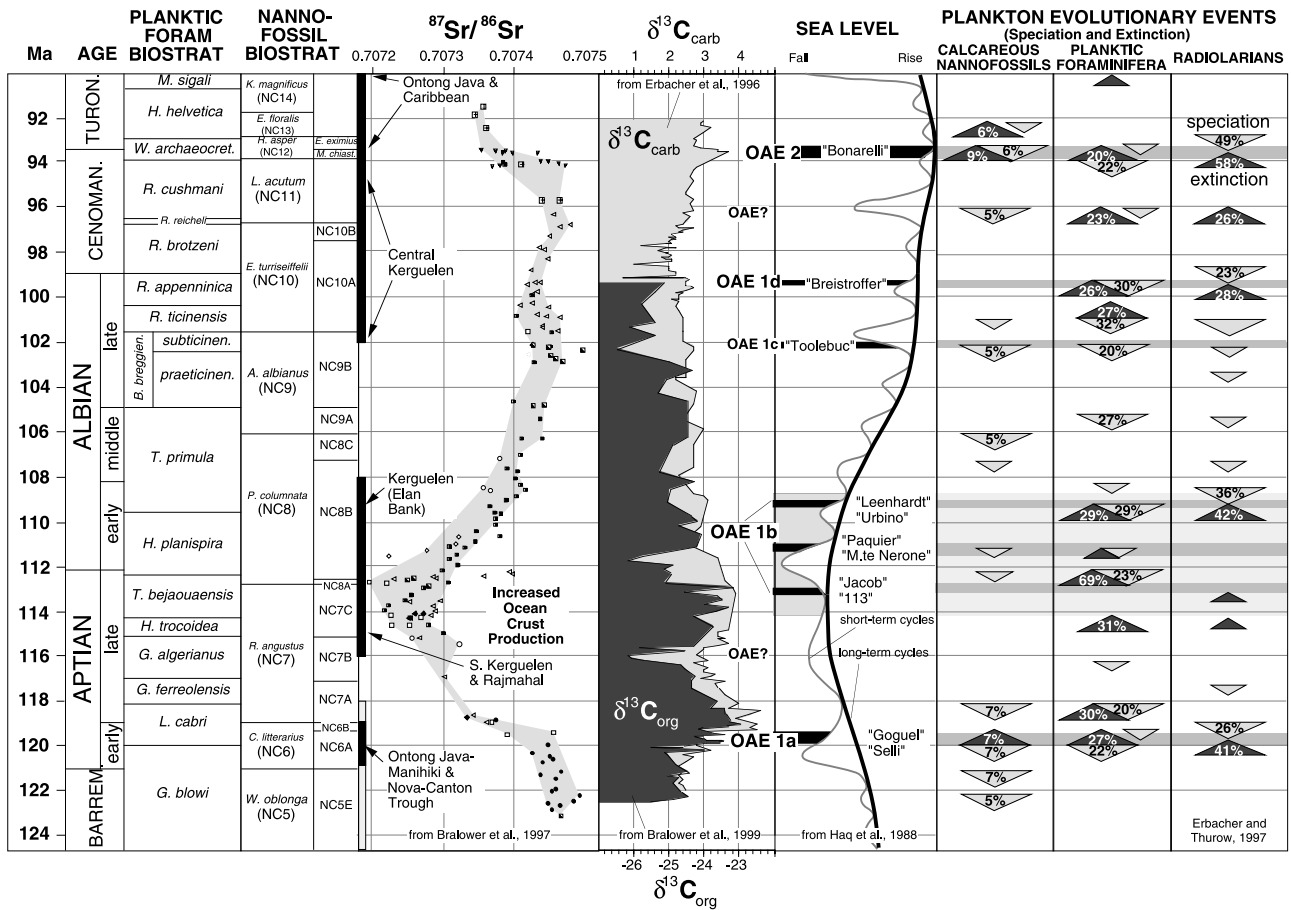
[37] Although relatively little is known about the ecology of mid-Cretaceous planktic foraminifera, we can make inferences about trophic strategy on the basis of the size of these ancient species. In the modern plankton, only the smallest protists (nannoplankton: 2–20 µm; microplankton: 20–200 µm) benefit energetically by consuming bacteria (picoplankton: 0.2–2 µm). For example, autotrophic nannoplankton and picoplankton (including cyanobacteria) and heterotrophic bacteria are consumed by heterotrophic flagellates, which in turn are consumed by ciliates and small sarcodines [Azam et al., 1983; Laybourn-Parry, 1992; Jumars, 1993; Rivkin et al., 1996]. The tiny test size of planktic foraminifera in the Early Cretaceous and during OAE1a and OAE1b may in large part reflect limited trophic strategies and the availability of food resources, with bacterivory as a likely feeding strategy in the smallest taxa. Many species of small benthic foraminifera are known to graze on heterotrophic bacteria living on and within the sediments [Lee, 1980; Lipps, 1983; Goldstein, 1999]. Small planktic foraminifera, by analogy, are also likely to exploit heterotrophic bacteria, aerobic photoheterotrophic bacteria [Fenchel, 2001; Kolber et al., 2001], and/or cyanobacteria by suspension feeding or by adapting a pseudobenthic lifestyle on marine snow or other organic-rich flocs, which are heavily colonized by bacteria [Azam, 1998; Azam and Long, 2001]. Other important food sources of these early planktic foraminifera likely included phytoplankton and flagellates such as the bacterivorous choanoflagellates (~2–10 µm in size [Laybourn-Parry, 1992; Jumars, 1993]).

[38] The nannoconids, an extinct group of heavily calcified calcareous nannoplankton, were the dominant pelagic

carbonate producers of the Early Cretaceous. However, this group experienced a two-stage perturbation during the Aptian (Figure 6). The early Aptian “nannoconid crisis” was the more dramatic of the two events and was associated with the emplacement of LIPs in the Pacific as a precursor to OAE1a [Erba, 1994; Larson and Erba, 1999]. We hypothesize that the Pacific superplume eruption in the early Aptian resulted in reduced carbonate availability ( $\text{CO}_3^{2-}$ ) associated with increased  $\text{CO}_2$  and lowered pH. Accordingly, this created a deleterious effect on the heavier calcifying forms like the nannoconids in addition to altering nutricline, thermocline, and plankton ecosystem dynamics as suggested by Erba [1994].

[39] The first occurrence of the aberrant planktic foraminiferal species *Leupoldina cabri*, with its distinctive club-like chambers, is nearly coincident with the “nannoconid crisis” and the onset of OAE1a [Premoli Silva et al., 1999]. Leupoldinids dominate the low-abundance, low-diversity planktic foraminiferal assemblages during the Selli event in Italy. It has been suggested that taxa with radially elongate chambers, such as *L. cabri*, may have been adapted to low-oxygen conditions in the upper water column [BouDagher-Fadel et al., 1997; Premoli Silva et al., 1999]. Planktic foraminifera experienced a marked turnover in the early Aptian immediately following OAE1a (Figure 7), which was followed by increasing test size and morphological complexity during the middle to late Aptian [Leckie, 1989; Premoli Silva and Sliter, 1999]. A cooler climate in the early late Aptian (*Globigerinelloides algerianus* biozone [Weissert and Lini, 1991; Weissert et al., 1998]) may have created cooler deep waters and stronger water column density gradients thereby facilitating the diversification of planktic foraminifera at this time [e.g., Caron and Home-wood, 1983; Leckie, 1989; Premoli Silva and Sliter, 1999].

[40] Toward the end of the Aptian the total range of *Planomalina cheniourensis*, the first keeled planktic foraminifer, coincides with a nannoconid resurgence referred to as the “*Nannoconus truittii* acme” [Erba, 1994] (Figure 6). The widespread distribution of the *N. truittii* assemblage has been attributed to warming surface waters [Mutterlose, 1989]. A second nannoconid “minicrisis” coincides with the extinction level of *P. cheniourensis* during the latest Aptian (within the *Ticinella bejaouaensis* biozone) marking the onset of falling sea level [Bréhéret, 1994], global cooling [Weissert and Lini, 1991; Weissert et al., 1998], and a protracted interval of organic carbon burial (OAE1b) that spans the Aptian/Albian boundary (Figure 1). Increased ocean crust production near the end of the Aptian and during the early Albian may have affected planktic ecosystems in a manner similar to OAE1a, including the loss of the heaviest calcified nanofossils and planktic foraminifera. The relatively cool paleotemperature estimates for this time interval may also reflect lower seawater pH associated with elevated levels of submarine volcanism and increasing atmospheric  $p\text{CO}_2$  [Zeebe, 2001]. Planktic foraminifera suffered their greatest rates of extinction and turnover across the Aptian/Albian boundary (Figure 11). The radiolarians were likewise affected while the calcareous nannoplankton, other than the nannoconids, were largely unaffected. Foremost was a major evolutionary change in the ultrastructure



**Figure 11.** Summary of the major geochemical, tectonic, sea level, and plankton evolutionary events associated with the mid-Cretaceous oceanic anoxic events. Note the concentration of evolutionary turnover events (speciation plus extinction) with the OAEs. Also note that OAE1a, OAE1b, and OAE2 are temporally associated with increased submarine volcanic activity as indicated by the lower  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios [Bralower *et al.*, 1997], and all three are linked to increased burial of marine organic matter [e.g., Arthur *et al.*, 1987; Erbacher *et al.*, 1996; Larson and Erba, 1999]. We hypothesize that submarine volcanism and hydrothermal activity at the spreading centers helped to fuel the elevated levels of marine productivity during the OAEs by way of iron fertilization of the water column. In addition to submarine volcanism the strontium isotope record is also influenced by continental weathering and runoff [e.g., Jones and Jenkyns, 2001], and the rise in  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios during the Albian may in large measure record increased weathering rates with rising sea level and global warming despite the elevated level of ocean crust production that sustained high global sea level through much of the Late Cretaceous. The high productivity associated with OAE1d may have been facilitated by an ocean already preconditioned by dissolved iron.

of planktic foraminiferal tests. This was a watershed event in planktic foraminiferal evolution as the trochospirally coiled taxa with small pores, many with distinctive pore mounds, were replaced by taxa with larger pores and smooth walls (Figure 10).

[41] During middle and late Albian time the planktic foraminifera diversified rapidly, particularly during the late Albian when keeled morphologies reappeared [Leckie, 1989; Premoli Silva and Sliter, 1999] (Figures 6 and 10). There was a pronounced increase in the degree of calcification in many taxa between the middle and late Albian as well as a continued increase in size, diversity, and morphological complexity. The development of muricæ (spikes of calcite) on species of the genera *Hedbergella*, *Rotalipora*,

and *Praeglobotruncana*, *rugae* (rows of calcite) on *H. libyca*, and peripheral keels, raised sutures, and/or adumbilical ridges on species of *Rotalipora*, *Praeglobotruncana*, and *Planomalina* illustrate the propensity for calcification by late Albian time. This pattern of evolutionary change in the planktic foraminifera tracks the overall trend of rising sea level and global warming. Stable isotopic evidence points to exploitation of the uppermost water column by way of depth stratification in the mixed layer and along the thermocline as density gradients within the upper ocean, and between the surface and deep ocean increased [Norris and Wilson, 1998] (Figures 9 and 10). A major phase of turnover affecting the planktic foraminifera and radiolarians coincides with OAE1d in the latest Albian. The collapse of



density gradients during OAE1d [Wilson and Norris, 2001] may account for increased rates of extinction and speciation in both of these groups.

[42] The productivity event of OAE2 (Cenomanian/Turonian boundary) had a major effect on the radiolarians and calcareous nannoplankton. The latter group experienced their largest turnover of the mid-Cretaceous [Bralower, 1988] (Figure 11). Deeper-dwelling planktic foraminifera were the most severely affected by OAE2 as evidenced by the loss of the genus *Rotalipora*, possibly due to the expansion of the oxygen minimum zone into thermocline waters [Hart, 1980; Wonders, 1980; Leckie, 1985, 1989]. Alternatively, abrupt warming of deep waters, to nearly 20°C at middle bathyal depths, may have caused a breakdown of the thermocline thereby effectively eliminating the niche of the deeper-dwelling species [Huber *et al.*, 1999]. The extinction of deep-sea benthic foraminifera across the Cenomanian/Turonian boundary [Kaiho *et al.*, 1993; Kaiho and Hasegawa, 1994; Kaiho, 1998] may be related to this warming event analogous to the deep-sea benthic foraminiferal extinction associated with the Paleocene-Eocene thermal maximum [Tjalsma and Lohmann, 1983; Kennett and Stott, 1991; Thomas and Shackleton, 1996].

## 5.2. Submarine Volcanism

[43] Vermeij [1995] hypothesized that massive submarine volcanism and hydrothermal activity coupled with rising sea level and CO<sub>2</sub>-induced global warming were the principal triggers to the major biosphere-scale revolutions of the Phanerozoic, including the rise of mineralized planktic protists during the Mesozoic. He argued that when raw materials and energy (especially temperature) become available to organisms at unusually high rates, opportunities for evolutionary innovation and diversification are enhanced through increased access to nutrients and adaptation. Nutrients are made available to the marine plankton through continental weathering, upwelling of deep and/or intermediate waters, and volcanism. Biological activity, including nutrient recycling, is strongly temperature-dependent [Brasier, 1995; Vermeij, 1995]. Therefore trends in global temperature and sea level tend to run parallel with marine productivity and diversification. The mid-Cretaceous was one of those times, and submarine volcanism was an integral part of plankton resource economics through its influence on increased CO<sub>2</sub>, global temperatures, and nutrient supply to the ocean [Vogt, 1989].

[44] The <sup>87</sup>Sr/<sup>86</sup>Sr ratio of seawater decreased markedly during three intervals of the mid-Cretaceous corresponding with OAE1a, OAE1b, and OAE2 [Bralower *et al.*, 1997; Jones and Jenkyns, 2001] (Figure 11). These authors interpreted the lowered (less radiogenic) values as episodes of effusive emplacement of oceanic plateaus (mantle plumes) or hydrothermal activity associated with increased ocean crust production. Other studies have proposed important linkages between increased submarine volcanism (hydrothermal activity), primary productivity, and black shale deposition [Vogt, 1989; Bralower *et al.*, 1994; Erba, 1994; Ingram *et al.*, 1994; Sinton and Duncan, 1997; Kerr, 1998; Larson and Erba, 1999]. Hydrothermal vents associated with spreading centers are major sources of dissolved

iron and other biolimiting metals to the ocean and minor sources of phosphorus [Froelich *et al.*, 1982; Vermeij, 1995]. Horizontal and vertical advection of limiting nutrients and trace elements, particularly iron, may have provided important catalysts for marine productivity during times of elevated rates of seafloor spreading and submarine volcanism, particularly for locations or times of weak water column stratification.

[45] Large-scale ocean thermohaline circulation and wind-driven upwelling play a major role in supplying nutrients to the euphotic zone of the world ocean. Well-developed density stratification in the low latitudes of the modern ocean coupled with seasonal stratification in the midlatitudes greatly limits the vertical advection of nutrients. These conditions create relatively focused zones of elevated primary productivity in coastal and high-latitude waters and in narrow bands of wind-driven oceanic divergence. In contrast, the reduced equator-to-pole temperature gradients of the mid-Cretaceous ocean created generally weaker water column density gradients. Such conditions provided an opportunity for greater rates of vertical advection of nutrients at times of increased water mass production. For example, mesoscale eddies [Falkowski *et al.*, 1991; McGillicuddy and Robinson, 1997; McGillicuddy *et al.*, 1998; Williams and Follows, 1998; Oschlies and Garcon, 1998; Siegel *et al.*, 1999], driven in part by the sinking of warm, saline waters, may have induced intermittent upwelling and lateral advection of nutrients in the upper layers of the mid-Cretaceous ocean. Planetary Rossby waves are also effective mechanisms for the delivery of nutrients to the surface ocean [Siegel, 2001; Uz *et al.*, 2001]. Hydrothermal megaplumes generated at the spreading centers and oceanic plateaus may have also contributed to decreased water column stratification and nutrient injection to the euphotic zone [Vogt, 1989; Baker *et al.*, 1995; Palmer and Ernst, 1998].

[46] Rates of seafloor spreading were 40–50% greater during the mid-Cretaceous than they are today [Richter *et al.*, 1992]. Earlier studies have suggested that spreading rates accelerated during the Aptian [Kominz, 1984; Larson, 1991a, 1991b]. The low <sup>87</sup>Sr/<sup>86</sup>Sr isotopic ratios of the late Aptian may mark the onset of increased ridge crest volcanism (Figure 11). Accelerated rates of seafloor spreading and/or increased ridge length during the latest Aptian initiated the long-term Albian-Turonian eustatic rise of sea level [Kominz, 1984; Haq *et al.*, 1988; Larson, 1991a, 1991b] and global warming [Huber *et al.*, 1995; Clarke and Jenkyns, 1999; Ferguson *et al.*, 1999; Frakes, 1999]. According to the hypothesis of Stanley and Hardie [1998], increased hydrothermal activity associated with faster spreading rates reduced oceanic Mg/Ca and preconditioned the ocean for the spread of pelagic carbonate on continental margins and in epicontinental seas with rising sea level.

## 5.3. Iron Fertilization and Sustained Productivity During OAEs

[47] Cyanobacteria contribute substantially to primary productivity in nutrient-poor, oligotrophic waters [Cho and Azam, 1988; Laybourn-Parry, 1992; Falkowski *et al.*,

1998], and colonies of cyanobacteria support diverse assemblages of consortial organisms, including protists [e.g., *Glover et al.*, 1988; *Capone et al.*, 1997]. Iron availability greatly enhances nitrogen fixation by cyanobacteria [*Codispoti*, 1997; *Falkowski*, 1997], and it stimulates increased production in the eukaryotic phytoplankton [*Martin and Fitzwater*, 1988; *Martin et al.*, 1994; *Coale et al.*, 1996a, 1996b; *Frost*, 1996]. The heterotrophic bacteria of the microbial loop compete with prokaryotic and eukaryotic autotrophs for this limiting micronutrient [*Kirchman*, 1996]. Iron facilitates greater efficiency of carbon metabolism in the heterotrophic bacteria; when iron is available, greater bacterial biomass is produced and available for consumption by bacterivores and higher trophic levels of the grazing food chain [*Azam et al.*, 1983; *Azam*, 1998]. When iron is limited, more of the dissolved organic carbon consumed by the bacteria is respired to CO<sub>2</sub> [*Kirchman*, 1996; *Tortell et al.*, 1996].

[48] In the modern ocean, it is the larger phytoplankton cells, principally the diatoms, that show the greatest productivity response to increased iron availability [*Martin et al.*, 1994; *Coale et al.*, 1996a, 1996b; *Longhurst*, 1996]. However, diatoms did not reach their pinnacle of importance in marine food webs until the Cenozoic [*Harwood and Nikolaev*, 1995]. One of the few diatomaceous deposits known from the mid-Cretaceous occurs near Antarctica and is of Aptian/Albian boundary age [*Gersonde and Harwood*, 1990; *Harwood and Gersonde*, 1990], a time roughly coincident with OAE1b, onset of Rajmahal-Kerguelen Plateau volcanism, and higher rates of seafloor spreading (Figure 11).

[49] Iron limitation is widespread in the ocean today, including the subtropical gyres as well as high-nutrient, low-chlorophyll regions [*Falkowski et al.*, 1998; *Behrenfeld and Kolber*, 1999]. Mechanisms that enhance iron availability, such as increased aeolian dust deposition during the Last Glacial Maximum [*Martin*, 1990] or, as we and others suspect, iron fertilization by submarine volcanism during the mid-Cretaceous, can result in increased rates of primary productivity. However, in a warm Cretaceous world, elevated rates of denitrification in low-oxygen environments may have limited the availability of fixed nitrogen required by the eukaryotic autotrophs [*Codispoti*, 1997; *Falkowski*, 1997], or phosphate may have become limited by elevated abundances of nitrogen-fixing cyanobacteria [*Codispoti*, 1989; *Toggweiler*, 1999; *Tyrell*, 1999].

[50] We suggest that the availability of iron at times of heightened submarine volcanism and oceanic crustal production stimulated and sustained the production of nitrogen-fixing cyanobacteria and improved the efficiency of the microbial loop, both of which facilitated greater export production during the OAEs. Elevated trace metal abundances in OAE1a and OAE2 strata suggest a linkage between these OAEs and submarine volcanism [*Orth et al.*, 1993; *Sinton and Duncan*, 1997; *Kerr*, 1998; *Larson and Erba*, 1999]. Of these two events it is possible that only OAE1a was directly triggered by submarine volcanism and iron fertilization as suggested by *Larson and Erba* [1999].

[51] We hypothesize that increased ocean crust production and hydrothermal activity beginning in the late Aptian

(Figure 11) were indirectly responsible for stimulating and sustaining widespread production of marine organic matter during the broad OAE1b event. By contrast, the subsequent OAEs were likely initiated by changing forcing factors. For example, beginning in the Albian, an increasingly stratified water column limited the availability of nutrients to the oceanic photic zone, thereby altering planktic ecosystem structure, reducing export production, and providing a positive feedback for the global warming that persisted through much of the Late Cretaceous. OAE1d (latest Albian) and OAE2 were likely triggered by ocean-climate events that affected ocean circulation and/or water column stratification, but in order to sustain marine productivity for 10<sup>4</sup>–10<sup>5</sup> years and disrupt the global carbon cycle we suspect that elevated rates of hydrothermal activity indirectly contributed to these events.

#### 5.4. Ocean Circulation, Rising Sea Level, and Chalk Deposition

[52] Reduced export production after the early Albian was closely related to rising sea level, global warming, and increased upper water column stratification. Planktic and benthic foraminiferal isotopic data from the western North Atlantic (Blake Nose) show that sea surface temperatures (SSTs) rose rapidly during the Albian (Figure 10). In addition, isotopic gradients of the upper water column (based on multispecies planktics) as well as planktic-benthic comparisons show that the water column became increasingly stratified during the Albian. Because temperature has such an important effect on metabolic rates [e.g., *Brasier*, 1995; *Vermeij*, 1995], increased SSTs would be expected to result in decreased export production because greater nutrition (food supply) is required by warm water organisms compared with cooler water taxa. Coupled atmosphere-ocean general circulation models with two different biogeochemical schemes predict that rising levels of CO<sub>2</sub> and global warming will cause increased ocean stratification leading to reduced nutrient supply to the euphotic zone and increased light efficiency (longer growing season), with both effects causing a reduction in export production [*Bopp et al.*, 2001].

[53] There is a striking parallel between the rapid radiation of angiosperms on land and the diversification of calcareous plankton during Albian time [e.g., *Hickey and Doyle*, 1977; *Retallack and Dilcher*, 1986; *Lidgard and Crane*, 1988; *Crane et al.*, 1995]. According to *Tappan* [1986], the evolution of land plants during the Phanerozoic limited the delivery of land-derived nutrients to the marine plankton. The partitioning of nutrients between the land and the marine environment may have been further exacerbated during times of higher eustatic sea level owing to the sequestering of organic matter and nutrients in coastal wetlands and estuaries. In addition, the growth of warm, oxygen-poor epicontinental seas may have increased the rate of denitrification, thereby further limiting the availability of fixed nitrogen for oceanic phytoplankton [*Codispoti*, 1997; *Falkowski*, 1997]. Nutrient limitation would have favored primary productivity by cyanobacteria, coccolithophorids, and other picoautotrophs and nanoflagellates [*Laybourn-Parry*, 1992; *Jumars*, 1993; *Falkowski et al.*, 1998].

The initiation of widespread chalk deposition by the late Albian signals the spread of warm, oligotrophic, stratified seas, which persisted through Late Cretaceous time. This marks a fundamental shift in the ecosystem structure of oceanic plankton communities as near-surface waters of the euphotic zone became stratified and nutrient-starved.

[54] A widespread upper to middle bathyal (500–1000 m) oxygenation event in the late early or early middle Albian age sediments at Site 1049 in the western North Atlantic and at Site 511 on Falkland Plateau in the South Atlantic abruptly terminates dysoxic to anoxic conditions at these two widely separated sites. This event suggests that an intermediate water connection between the North and South Atlantic Ocean basins may have existed by early Albian time. If this connection involved the introduction of dense (saline) northern South Atlantic water into the North Atlantic basin at this time [e.g., *Arthur and Natland, 1979*], the Coriolis effect would have directed the strongest flow of intermediate or deep water northward along the margin of northwest Africa. The prominent unconformity in the Albian section of Site 545 may be the consequence of erosion by eastern boundary currents (Figure 2). Later deep water oxygenation events occurred at or near the end of the Cenomanian stage [*Tucholke and Vogt, 1979; Summerhayes, 1981*].

[55] The beginning of the end of black shale deposition in both the North and South Atlantic Ocean basins was not simply the consequence of changing trophic dynamics in the plankton and reduced export production; the end of dysoxic and anoxic conditions was also related to changing tectonic gateways and sill depths with the opening of the Atlantic [e.g., *de Graciansky et al., 1982; Summerhayes, 1987; Weissert and Lini, 1991*]. The propensity for black shale deposition in the basins of the Atlantic and European Tethys became progressively minimized during Albian-Cenomanian time. The OAEs of the latest Albian and Cenomanian/Turonian boundary were triggered by different tectonic and ocean-climate circumstances than the early Aptian and latest Aptian–early Albian events. The consequences of long-term rising sea level and global warming during Albian-Turonian time included (1) creation of epicontinental seas and other gateways to the high latitudes, (2) partitioning of nutrients between flooded coastal plains, epicontinental seas, and the open ocean, (3) changes in oceanic circulation and water mass sources as epicontinental seas linked Tethys with the higher latitudes and as the deepwater gateway between the North and South Atlantic continued to open, (4) changes in the hydrologic cycle and continental weathering, and (5) increasing water column stratification and nutrient partitioning between surface and deep waters. Taken together, the cumulative effects of climate, ocean fertility, ocean circulation, water column stratification, and carbonate chemistry controlled plankton populations and their capacity to produce organic carbon and/or carbonate.

## 6. Conclusions

[56] Turnover (extinction plus speciation) in the planktic foraminifera closely tracks that of the radiolaria, and both

groups of heterotrophic protists display the greatest rates of turnover at or near the major OAEs. The autotrophic calcareous nannoplankton were most strongly affected by the early Aptian OAE1a (Selli event) and the Cenomanian/Turonian boundary OAE2 (Bonarelli event). These two events were the most widespread of the OAEs; both were short-lived and associated with increased marine productivity and active submarine volcanism. The eruption of the Ontong Java superplume was a precursor to OAE1a, and the combined influences of faster seafloor spreading rates and/or other submarine volcanism occurred during the time of OAE2. We propose that increased marine productivity during latest Aptian–early Albian OAE1b was also linked to increased ridge crest volcanism and hydrothermal activity as indicated by reduced (less radiogenic)  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios. However, OAE1b encompasses a protracted interval of organic carbon burial in contrast to the black shales of OAE1a and OAE2. A number of different mechanisms created the conditions necessary to accumulate the multiple but geographically restricted black shale events of OAE1b. However, the large carbon isotopic excursions (up to 3‰) during late Aptian–early Albian time (*Ticinella bejaouaensis-Hedbergella planispira* biozones) indicate that this interval was associated with significant disruptions in the global carbon cycle.

[57] The OAEs were extraordinary events driven by extraordinary forcing factors. Each was associated with pronounced carbon isotopic excursions ( $>1.5\text{--}2\text{‰}$ ) and elevated rates of plankton turnover indicating a broad impact on the ocean-climate system, despite the variable geographic distribution of black shale deposition, but how could the ocean be affected on a global scale, and how could elevated marine productivity be sustained for  $10^4\text{--}10^5$  years? We conclude that the mid-Cretaceous OAEs were linked to submarine volcanic activity. We hypothesize that the emplacement of oceanic plateaus and increased ridge crest hydrothermal activity indirectly helped to fuel and sustain the elevated levels of marine productivity during the OAEs by way of iron fertilization of the water column. Global warming associated with increased submarine volcanism also contributed to higher productivity by way of intensified chemical weathering on the land and greater flux of nutrients to the ocean. Perhaps only OAE1a was directly triggered by submarine volcanism, but we suggest that active hydrothermal activity, in particular, indirectly helped to sustain marine productivity on a global scale during the OAEs. Transgression also facilitated the production of marine organic matter and its burial and preservation as condensed intervals of black shale deposition.

[58] Changing nutrient availability and/or upper water column structure were the causes of plankton turnover at or near the OAEs. However, excess  $\text{CO}_2$  associated with submarine volcanism may have reduced carbonate availability and seawater pH, thereby contributing to the loss of calcareous plankton during the early Aptian and latest Aptian–early Albian OAEs. For example, the heavily calcified nannofossils (the nannoconids) were seriously affected by the ocean-climate changes associated with OAE1a, and both nannoconids and the largest and most heavily calcified planktic foraminifera were either eradicated or severely



depleted at the onset of OAE1b. In contrast, the deepest-dwelling planktic foraminifera not necessarily the most heavily calcified taxa were eradicated during OAE2 at the Cenomanian/Turonian boundary. This event was likely caused by an expanded oxygen minimum zone associated with elevated productivity and/or by the decay of the thermocline due an abrupt deep-sea warming event. The turnover event associated with OAE1d in the latest Albian was likewise triggered by a collapse of upper water column stratification due to surface water cooling or an intermediate water warming event.

[59] Greater ocean crust production in the late Aptian initiated a long-term trend of rising sea level and warming global climate, both of which peaked in the early Turonian (~92–93 Ma). The rising  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios during the Albian record increasing continental weathering rates with rising sea level and global warming despite the increased ridge crest volcanism that sustained high global sea level through much of the Late Cretaceous. In addition, the deepening gateway between the basins of North and South Atlantic figured prominently in surface and intermediate water ocean circulation by early Albian time and deep water ventilation by Cenomanian/Turonian boundary time.

[60] OAE1b in the latest Aptian-early Albian was a watershed event in the evolution of planktic foraminifera. This interval also marks the beginning of the end of widespread black shale deposition and the initiation of chalk deposition. According to the hypothesis of Stanley and

Hardie [1998], greater rates of hydrothermal activity through the spreading centers altered ocean carbonate chemistry to favor calcite-secreting plankton and other organisms. The marked increases in planktic foraminiferal size and degree of calcification during the Albian support this hypothesis. The spread of pelagic carbonate deposition with rising sea level in the Albian also signals a changing planktic trophic regime dictated by increased thermal and fertility gradients. Fundamental changes in circulation, water column structure, nutrient partitioning, and plankton ecosystem dynamics in the post-Aptian ocean favored stratified, oligotrophic to mesotrophic, diverse, carbonate-based pelagic and benthic ecosystems that came to characterize the widespread chalk seas of the Late Cretaceous.

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