

Depth-habitat reorganization of planktonic foraminifera across the Albian/Cenomanian boundary

Atsushi Ando, Brian T. Huber, and Kenneth G. MacLeod

Abstract.—New mid-Cretaceous stable isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) records of multiple planktonic foraminiferal species and coexisting coccoliths from Blake Nose (western North Atlantic) document a major depth-ecology reorganization of planktonic foraminifera. Across the Albian/Cenomanian boundary, deep-dwelling *Praeglobotruncana stephani* and *Rotalipora globotruncanoides* adapted to living at a shallower depth, while, at the same time, the population of surface-dwelling *Paracostellagerina libyca* declined. Subsequently, the opportunistic species *Hedbergella delrioensis* shifted to a deep environment, and the deep-dwelling forms *Rotalipora montsalvensis* and *Rotalipora reicheli* first appeared. The primary paleoenvironmental cause of the observed changes in planktonic adaptive strategies is uncertain, yet their coincidence with an earliest Cenomanian cooling trend reported elsewhere implicates the importance of reduced upper-ocean stratification. Although there has been an implicit assumption that the species-specific depth habitats of fossil planktonic foraminifera were invariant through time, planktonic paleoecology is a potential variable. Accordingly, the possibility of evolutionary changes in planktonic foraminiferal depth ecology should be a primary consideration (along with other environmental parameters) in paleoceanographic interpretations of foraminiferal stable isotope data.

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Introduction

Paleoceanographic reconstruction of the mid-Cretaceous (Aptian–Turonian; 125–89 Ma) has been an essential component in enhancing our knowledge of the Earth's surface environments during greenhouse climates. Among various proxy records for marine paleoenvironments, stable oxygen and carbon isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) of foraminifera have long received particular attention because the combined planktonic (surface- to deep-dwelling) and benthic data can quantitatively illustrate the thermal and physical evolution of the vertical water column. It was during the 1990s that integrative foraminiferal isotope data from multiple deep-sea sections became available for reconstruction of mid-Cretaceous latitudinal thermal structures (Sellwood et al. 1994; Huber et al. 1995; Price et al. 1998; Fassell and Bralower

1999). Subsequent data generated from clay-hosted foraminifera exhibiting exceptional “glassy” preservation (sensu Sexton et al. 2006) have yielded significant insights into mid-Cretaceous paleoceanography. The major achievements include reconciliation of the so-called cool tropics paradox (Norris and Wilson 1998; Wilson and Norris 2001), establishment of the Turonian hyperthermal period (Huber et al. 2002; Norris et al. 2002; Wilson et al. 2002; Bice et al. 2003; see also Bornemann et al. 2008), and recognition of short-term intensification (Erbacher et al. 2001) or destabilization (Wilson and Norris 2001; Petrizzo et al. 2008) of vertical stratification.

Another important aspect of recent advances in foraminiferal isotopic study is renewed interest in depth-related paleoecology of mid-Cretaceous planktonic foraminifera, upon

which paleoceanographic reconstructions are based. Traditionally, the strategy for depth-ecology ranking of planktonic taxa was twofold: (1) comparison with modern morphological counterparts (small, simple, globular, *Globigerina*-like groups are attributed to the shallow-dwelling assemblage, whereas large, ornamented, flattened, *Globorotalia*-like groups are attributed to the deep-dwelling assemblage [Hart 1980, 1999; Caron and Homewood 1983; Premoli Silva and Sliter 1999]); and (2) biogeographic distributions (taxa common in epicontinental shelf settings are attributed to the shallow-dwelling assemblage, whereas taxa that dominated in pelagic settings are attributed to the deep-dwelling assemblage [Hart and Bailey 1979; Leckie 1987]). Although these approaches have long been considered appropriate and were generally supported by available stable isotope data, a growing number of exceptions have been documented by recent measurements of glassy foraminifera (Norris and Wilson 1998; Wilson and Norris 2001; Bornemann and Norris 2007; Petrizzo et al. 2008). For example, the Albian genus *Planomalina*, which by its single-keeled morphology would be identified as a thermocline dweller, exhibits isotopic features of an upper-ocean habitat. Despite such findings, the primary focus of recent foraminiferal isotopic studies has been the determination of interspecies $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ differences at a particular locality and time interval, with little effort to improve our understanding of the planktonic foraminiferal paleoecology.

To refine and provide meaningful systematization for the paleoecological model of mid-Cretaceous planktonic foraminifera, this study presents new multispecies stable isotope data from the Albian–Cenomanian (A–C) transition of Ocean Drilling Program (ODP) Site 1050 on Blake Nose, western North Atlantic (Fig. 1). Specifically, by exploiting comparative stable isotope data from the coexisting coccolith-dominant fine (<63 μm) sediment fraction (hereafter referred to as the coccolith-rich fraction) to give a photic zone reference value, we provide a robust case for a dramatic reorganization of planktonic foraminiferal depth ecology in this

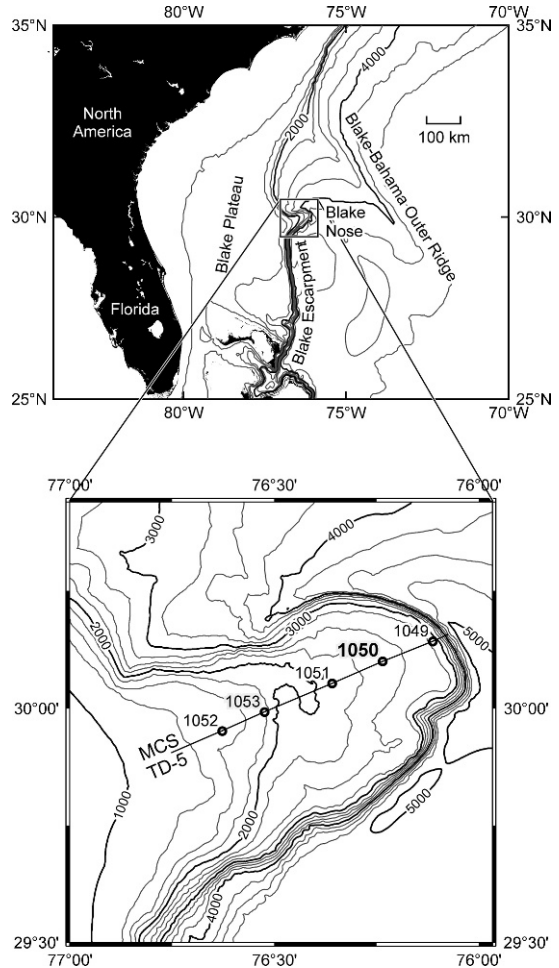


FIGURE 1. Map showing ODP Leg 171B sites on Blake Nose, a submarine bulge on the continental slope off northern Florida, subtropical western North Atlantic. The Cenomanian paleolatitude of this depth transect is $\sim 25^\circ\text{N}$ (Ogg and Bardot 2001). MCS TD-5, multichannel seismic reflection line TD-5.

period. We propose that such a phenomenon, which has been largely overlooked (notable exceptions are Miocene globorotaliids [Hodell and Vayavananda 1993; Norris et al. 1993, 1996] and Eocene hantkeninids [Coxall et al. 2000]), constituted an important factor in the evolutionary paleoecology of planktonic foraminifera.

Paleoceanographic Background

The A–C transition witnessed the first phase of the highest sea level and warmest global temperatures during the Cretaceous (e.g., Leckie et al. 2002; Wilson et al. 2002). In

response to latest Albian Oceanic Anoxic Event (OAE) 1d, fossil calcareous plankton exhibited contrasting population dynamics, with planktonic foraminifera experiencing a major faunal turnover and calcareous nannoplankton remaining relatively static (Leckie et al. 2002). Systematic A–C paleoceanographic studies carried out at North Atlantic ODP Sites 1050 and 1052 of the Blake Nose depth transect (Fig. 1) (Wilson and Norris 2001; Watkins et al. 2005; Petrizzo et al. 2008) and Deep Sea Drilling Project (DSDP) Site 547 off Morocco (Nederbragt et al. 2001) have revealed that stratigraphic distribution of planktonic foraminifera in both regions and of nannofossils in the eastern North Atlantic are consistent with the global compilation by Leckie et al. (2002). In the western North Atlantic, on the other hand, nannoplankton at the time of OAE 1d suffered local extinctions of 20% of taxa (biased to deep-dwelling representatives), preceded by a long-term increase in high-fertility indicative taxa, suggesting regional upwelling and/or deep mixing (Watkins et al. 2005). Instability in the vertical structure of the western North Atlantic (e.g., thermocline shoaling and “stratification collapse”) during the late Albian, potentially a result of the fluctuating proto-Gulf Stream system, has been particularly well documented by high-resolution multispecies $\delta^{18}\text{O}$ records of foraminifera at Site 1052 (Wilson and Norris 2001; Petrizzo et al. 2008). Still, the proposed forcing mechanisms of OAE 1d are site-specific, resulting from increased primary productivity with disrupted stratification as proposed for the western North Atlantic (Watkins et al. 2005), and/or elevated runoff leading to enhanced stratification and poor bottom-water oxygenation, such as in the Mediterranean Tethys (Vocontian Basin, France) (Bornemann et al. 2005).

Regarding the A–C paleotemperature trend, the planktonic $\delta^{18}\text{O}$ records at Site 1052 indicate extremely warm subtropical sea-surface temperatures (SSTs) of up to 32°C in the late Albian, followed by cooling in the early Cenomanian (Wilson and Norris 2001; Petrizzo et al. 2008). A similar SST trend can be seen in the $\delta^{18}\text{O}$ profile of hemipelagic

marls at Site 547 (Nederbragt et al. 2001), and it is further reproduced by long-term TEX_{86} thermometry from organic carbon-rich sediments of ODP Site 1258, Demerara Rise, equatorial Atlantic (Forster et al. 2007a). Such a similarity between independent SST proxies at distant sites implicates the global nature of the A–C warming-to-cooling trend.

It is worthwhile summarizing the mode of coccolith occurrence at Blake Nose (Sites 1050 and 1052) examined by Watkins et al. (2005) because the compositional variation in calcareous nannofossils (especially the ratio of surface- to deep-dwelling taxa) is often considered an obstacle when using the coccolith-rich fraction for paleoceanographic analysis. Of 164 taxa identified at the A–C transition, 105 species occur through the entire examined range; 3 species of which (*Watznaueria barnesiae*, *Zeughrabdotus moulladei*, *Biscutum constans*) are high in abundance (total 30–40% of the assemblage). Taxa subjected to local turnover (mainly in a narrow interval between OAE 1d black shale deposition and the A/C boundary) include 22 species. Of these, nannoconids and braarudospheres (both specialized to the lower photic zone or thermocline) are marked by relatively large compositional changes. For the interval examined by this study (Site 1050; 100.5–97.9 Ma), however, neither of these groups is common (<5%), so the nannofossil assemblage should be representative of the upper photic zone.

Material and Methods

The material used is from Cores 25–27 (part) (538.97–559.25 m below the seafloor [mbsf]) of ODP Site 1050 (Hole 1050C) (Figs. 1, 2). The water-depth of this site is presently 2297 m (Shipboard Scientific Party 1998) and the mid-Cretaceous paleo-water-depth is inferred to be ~1500 m (Norris et al. 1998: p. 6). In this upper Albian–lower Cenomanian interval, previous biostratigraphic treatments have recognized abundant, well-preserved planktonic foraminifera documenting a long-term faunal turnover (Bellier and Moullade 2002; Petrizzo and Huber 2006). In terms of planktonic foraminiferal zonation, this interval encompasses

the *Rotalipora appenninica* Zone (*Planomalina buxtorfi* Subzone) to *Rotalipora globotruncanoides* Zone. The base of the latter zone at 553.24 mbsf (this study; see Appendix for further notes on biostratigraphy) has been accepted as defining the A/C stage boundary (= Lower/Upper Cretaceous Series boundary) (Kennedy et al. 2004). The lithology of Hole 1050C changes from claystone below to chalk above the A/C boundary. A coring gap at 556.6–558.0 mbsf (Core 25/26), in which an unconformity is present, translates to a sedimentation gap of ~0.8 Myr based on the graphic correlation with shallower Site 1052 (Petruzzo and Huber 2006; Petruzzo et al. 2008). It explains the limited occurrence of the OAE 1d black shales at this site as compared to Site 1052 (Wilson and Norris 2001; Petruzzo et al. 2008).

A total of 33 samples, including some that were previously examined by Huber et al. (2002), were processed for stable isotope analysis. Each sample was treated with dilute H_2O_2 solution, wet-sieved at 63 μm , and oven-dried at $<50^\circ C$. All dominant planktonic foraminiferal taxa were picked from a narrow sieve fraction (212–300 μm) to minimize potential artifacts from the ontogenetic effects (Norris and Wilson 1998). For *Hedbergella*, a finer sieve fraction (180–212 μm) was used occasionally when insufficient numbers of larger specimens were present. Stable isotope and Sr/Ca data for the coccolith-rich fraction, obtained from the wash-water via settling and decantation, were reported by Ando et al. (2009).

Isotope ratio measurements of the isolates of individual planktonic species, with typically four to six specimens in each analysis, were performed by using a Thermo FinniganTM DeltaPlus mass spectrometer with an on-line automated carbonate reaction Kiel III device at the Biogeochemistry Isotope Laboratory, University of Missouri. Data are reported as per mil deviation relative to the Vienna Peedee belemnite (VPDB) standard after normalization based on the difference between the within-run average of NBS 19 and its recommended value ($\delta^{13}C = -1.95\text{‰}$; $\delta^{18}O = 2.20\text{‰}$). Replicate measurements of NBS 19 yielded long-term external precision

(1 SD) better than $\pm 0.03\text{‰}$ for $\delta^{13}C$ and $\pm 0.06\text{‰}$ for $\delta^{18}O$. For selected levels, foraminiferal preservation was investigated using a HITACHI S-3500N scanning electron microscope (SEM) at Pusan National University.

The planktonic foraminiferal temperature scale adopted herein (Fig. 2) is based on equation (1) of Bemis et al. (1998) along with commonly used assumptions, including a mean seawater $\delta^{18}O$ value of -1‰_{SMOW} (which corresponds to -1.27‰ for seawater in the paleotemperature equation) for an ice-free Earth (Shackleton and Kennett 1975) and a latitudinal seawater $\delta^{18}O$ gradient at $25^\circ N$ paleolatitude similar to that of the present day (Zachos et al. 1994). The use of this equation is for consistency with Wilson and Norris (2001), Norris et al. (2002), and other relevant literature. The rationale of these authors was that equation (1) is based on non-symbiotic species of cultured planktonic foraminifera, but it was actually derived from symbiont-bearing *Orbulina universa*. Nonetheless, equation (1) is considered most appropriate (Bemis et al. 1998) and has been applied to Pleistocene paleoceanographic analyses using non-symbiotic planktonic taxa (e.g., Zuraida et al. 2009).

Results

Stable Isotopic Trends.—Systematic secular trends are present in both $\delta^{18}O$ and $\delta^{13}C$ among multiple species of planktonic foraminifera and the coccolith-rich fraction (Fig. 2). A distinct positive $\delta^{13}C$ shift in the uppermost Albian (by $+0.6\text{‰}$ [$1.9\text{--}2.5\text{‰}$]) in the coccolith-rich fraction corroborates previous results of Petruzzo et al. (2008), and is also consistent with data reported from nearby Site 1052 (Wilson and Norris 2001; Petruzzo et al. 2008). In addition, the $\delta^{13}C$ shift correlates well with the uppermost Albian $\delta^{13}C$ records reported from around the globe, in both marine carbonates and terrestrial organic matter (Ando and Kakegawa 2007, and references therein). Such a globally reproducible $\delta^{13}C$ trend could be attributed to (1) the dynamic isotopic equilibrium between the upper-ocean dissolved inorganic carbon (DIC) and atmospheric CO_2 within the ocean-atmosphere system, and (2) the fact that the $\delta^{13}C$ compo-

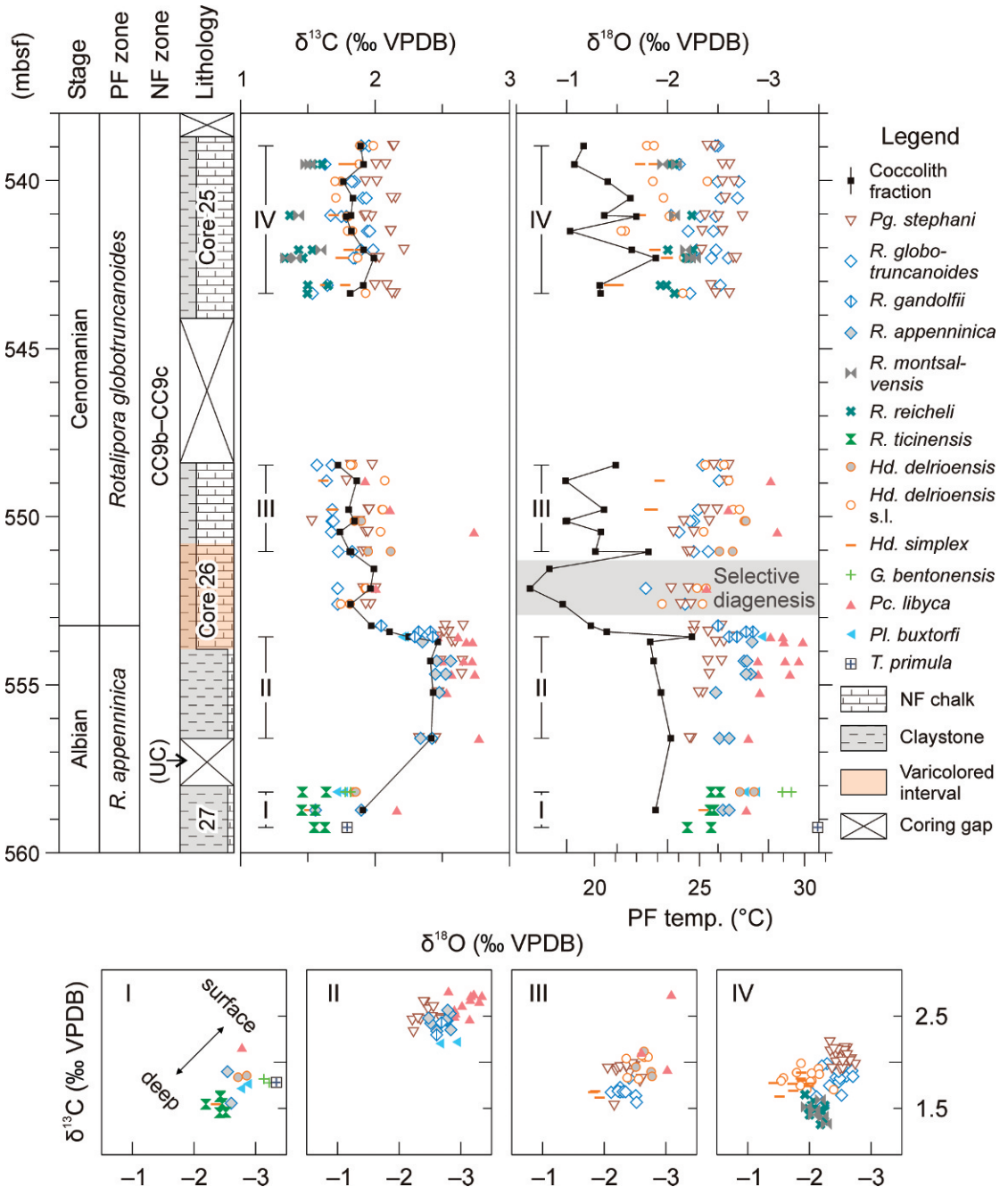


FIGURE 2. Stable isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) composition of multispecies planktonic foraminifera (PF) and coccolith-rich fraction at the Albian-Cenomanian transition of ODP Site 1050, plotted against sub-bottom depth (mbsf) (data partly from Huber et al. 2002). Plots shown on bottom are $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ relationships for four discrete intervals, phases I to IV (coccolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values are relatively invariant in each phase). The planktonic foraminiferal zonation is from this study and the nannofossil (NF) zonation is from Watkins et al. (2005). The pronounced positive $\delta^{18}\text{O}$ anomaly (shaded) is due to selective diagenesis at a varicolored lithology as supported by SEM and Sr/Ca evidence (see text). Note that the PF temperature scale may underestimate paleotemperatures by up to $\sim 5^\circ\text{C}$ owing to diagenetic overprints (Fig. 4). Abbreviations: *Pg.*, *Praeglobotruncana*; *R.*, *Rotalipora*; *Hd.*, *Hedbergella*; *G.*, *Globigerinelloides*; *Pc.*, *Paracostellagerina*; *Pl.*, *Planomalina*; *T.*, *Ticinella*; UC, unconformity; VPDB, Vienna Peedee belemnite. See color version of this figure in the online PDF format of this paper.

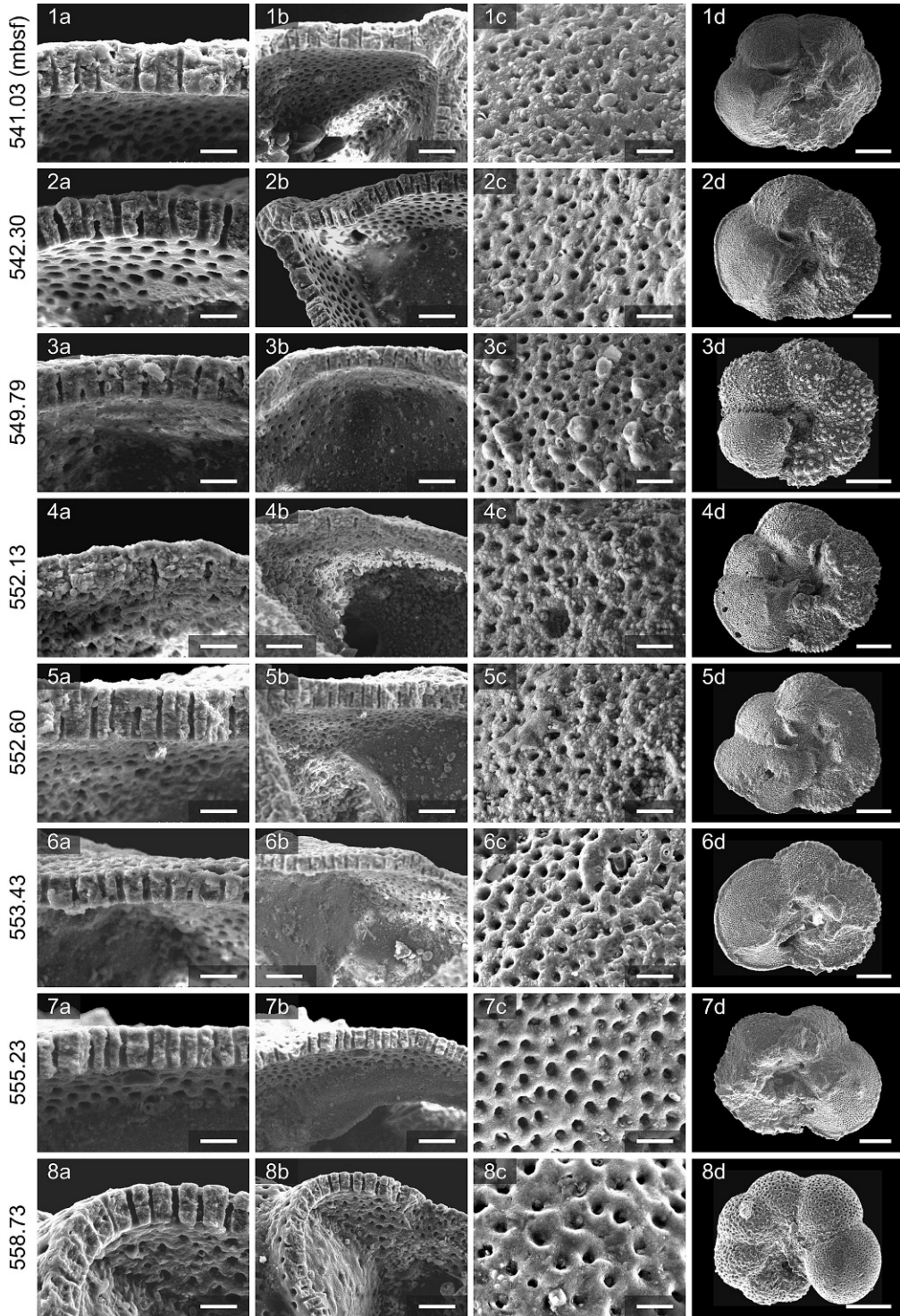


FIGURE 3. SEM images (Pt-Pd coated) of selected specimens of planktonic foraminifera: (1) ODP Sample 1050C-25R-2, 83–87 cm; (2) ODP Sample 1050C-25R-3, 60–64 cm; (3) ODP Sample 1050C-26R-1, 139–141 cm; (4) ODP Sample 1050C-26R-3, 73–76 cm; (5) ODP Sample 1050C-26R-3, 120–122 cm; (6) ODP Sample 1050C-26R-4, 53–55 cm; (7) ODP Sample 1050C-26R-5, 83–86 cm; (8) ODP Sample 1050C-27R-1, 73–76 cm. Their respective sub-bottom depths are shown on left. a = close-up of wall cross-section (usually the penultimate chamber); b = same field as (a) with lower magnification

sition in pelagic carbonates is relatively unaffected by burial diagenetic processes (i.e., recrystallization and cementation) (e.g., Ando et al. 2008).

The $\delta^{18}\text{O}$ records are characterized by a remarkable positive $\delta^{18}\text{O}$ anomaly at the A–C transition (by $\sim +1.6\%$ [-2.2 to -0.6%] in the coccolith-rich fraction). If this is a primary signal that is interpreted in terms of $\delta^{18}\text{O}$ paleothermometry, this $\delta^{18}\text{O}$ event at Site 1050 signifies a cooling of SSTs by $\sim 6^\circ\text{C}$. This finding is impressive because the trend is similar to the aforementioned SST proxies of foraminiferal $\delta^{18}\text{O}$ and TEX_{86} . However, evidence for selective diagenesis does not support the potential A/C cooling event in our Site 1050 $\delta^{18}\text{O}$ data (see below).

Diagenetic Assessment.—SEM study shows that foraminiferal preservation covaries with lithologies and $\delta^{18}\text{O}$ values (Figs. 3, 4). Specimens from upper Albian claystones, for which most negative $\delta^{18}\text{O}$ values are recorded, are excellently preserved and rated as quasi-glassy; each individual is mostly translucent, but partly frosty (Fig. 3[7,8]). Specimens from the lower Cenomanian chinks are more or less frosty under a stereomicroscope, while they are still essentially hollow and translucent when moistened. For these frosty specimens, SEM images show that secondary calcite is present, mainly as micron-scale crystals but occasionally as discrete rhombs. The poorest preservation is identified at 552.13 mbsf in a varicolored chalk interval, with interior chamber surfaces exhibiting an extensive overgrowth of fine euhedral calcite crystals (Fig. 3[4]). Around this level, where $\delta^{18}\text{O}$ values are the highest among the sample set, sediments are partially indurated.

Strong $\delta^{18}\text{O}$ –Sr/Ca covariation ($R^2 = 0.81$) for the coccolith-rich fraction (Fig. 4) can be interpreted as indicating a diagenetic component in the $\delta^{18}\text{O}$ trend of the examined

interval (Ando et al. 2009). Sr/Ca ratios are known as useful indicators of the extent of pelagic carbonate diagenesis (e.g., Veizer 1983; Marshall 1992; Ando et al. 2006), because Sr is biologically enriched in the original unaltered calcite test and eliminated systematically from the solid phase via recrystallization as a consequence of the low distribution coefficient into inorganic calcite ($D_{\text{Sr}} \ll 1$). The view that Sr/Ca is controlled by coccolithophorid paleoproductivity has also been advanced (e.g., Stoll and Bains 2003), but the magnitude of diagenetic Sr/Ca shift is greater than that attributable to paleoproductivity.

With concurrent SEM and Sr/Ca evidence, the positive $\delta^{18}\text{O}$ shift across the A/C boundary should be taken as an artifact of selective diagenesis within the varicolored lithology. This shift is predictable at a low-latitudinal setting in which recrystallization generates isotopically heavier secondary calcites through interaction with colder bottom and/or pore waters (e.g., Schrag et al. 1995; Crowley and Zachos 2000). In theory, the original $\delta^{18}\text{O}$ composition of coccolith calcite can be derived by extrapolating the exponential regression curve back to the primary coccolith Sr/Ca ratio (Fig. 4B). Because this “backstripping” (Marshall 1992) implicitly assumes that the primary absolute $\delta^{18}\text{O}$ values in coccoliths were uniform over the examined interval, it is only a first-order approximation. Besides, the mean primary Sr/Ca ratio in ancient coccoliths is still not well constrained. With these caveats, assuming that the diagenetic shift in planktonic foraminiferal $\delta^{18}\text{O}$ composition draws an exact parallel with the coccolith-rich fraction and that the primary Sr/Ca ratio in the coccolith-rich fraction is around 1.5 mmol/mol (Stoll and Bains 2003), foraminiferal paleotemperatures (Fig. 2) are underestimated by up to $\sim 5^\circ\text{C}$ in the early Cenomanian.

←

showing chamber interior; c = close-up of pored external chamber surface; d = whole specimen view from which (c) is taken. All specimens were picked from the 212–300 μm fraction. Images (a,b) and (c,d) are taken from different specimens. Species name: 1d, 2d, 5d = *Rotalipora globotruncanoides*; 3d = *Praeglobotruncana stephani*; 4d, 6d = *Rotalipora gandolfii*; 7d = *Rotalipora appenninica*; 8d = *Ticinella* sp. Scale bars, 10 μm in a, c; 20 μm in b; 100 μm in d.

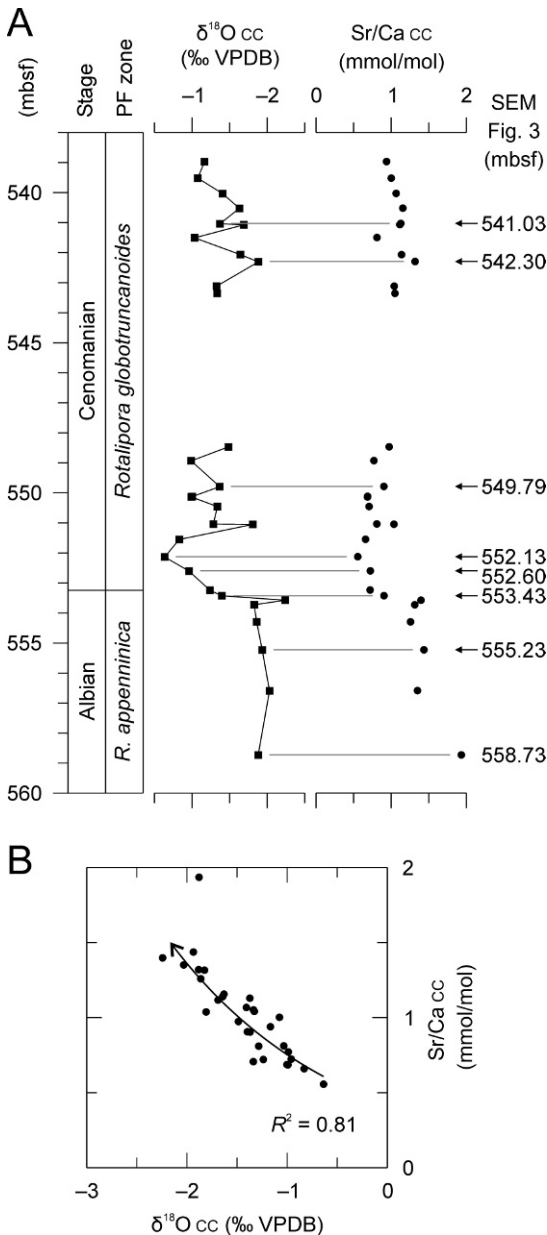


FIGURE 4. Stratigraphic variations in $\delta^{18}\text{O}$ values and Sr/Ca ratios (A) and their cross-plot (B). Sr/Ca data from Ando et al. (2009). The regression curve is an exponential function (excluding one data point of Sr/Ca = 1.93 mmol/mol at 558.73 mbsf). Arrowed end of regression curve points to the near-original coccolith Sr/Ca ratio (=1.5 mmol/mol; see text).

Isotopic Ecological Ranking and Its Problem.—Some diagenetic shifts in the mean values notwithstanding, each of the planktonic foraminiferal taxa (14 species from seven genera) is isotopically distinct. It seems evident that

paleoecologically significant interspecies $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ differences have not been obscured by diagenetic overprints. It is known that such primary isotopic offsets are well retained, even in cases where there is much extensive recrystallization (Sexton et al. 2006).

Interspecies isotopic offsets are more clearly illustrated in the $\delta^{18}\text{O}$ – $\delta^{13}\text{C}$ relationships (Fig. 2), which are shown with respect to four discrete intervals, phases I to IV; note that the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of coccolith-rich fraction are relatively invariant in each phase. In general, each cross-plot exhibits an array of data distribution trending from the upper right to lower left, which is ascribed to geochemical expression of the development of species-specific depth ecology (e.g., Pearson 1998). Specifically, given that the vertical gradients of temperatures and $\delta^{13}\text{C}$ of DIC in the modern oceans were similarly established in the geologic past, the low $\delta^{18}\text{O}$ and high $\delta^{13}\text{C}$ values (toward the upper right in the cross-plot) are inferred to indicate the formation of calcite test in warm, ^{13}C -enriched surface water, whereas the high $\delta^{18}\text{O}$ and low $\delta^{13}\text{C}$ values (toward the lower left) indicate calcification in cool, ^{13}C -depleted subsurface water. The usual “J-shaped” $\delta^{18}\text{O}$ – $\delta^{13}\text{C}$ pattern (Pearson 1998; Pearson et al. 2001) is ambiguous in our data, and this fact is ascribed to the absence of symbiotic ^{13}C -enrichment in any of the taxa analyzed (Norris and Wilson 1998; Bornemann and Norris 2007).

At this point, the next anticipated step would typically be to choose “guide species” whose isotopic signals might track surface and deep settings. The convention most commonly used for this purpose is to attribute the taxa with the lowest $\delta^{18}\text{O}$ and highest $\delta^{13}\text{C}$ values to shallow-dwelling assemblage, whereas those with the highest $\delta^{18}\text{O}$ and lowest $\delta^{13}\text{C}$ values to deep-dwelling assemblage. Upon examination of the isotopic patterns among all the taxa, however, it is clear that neither practice would be appropriate.

The salient feature of our data set is that the ecological ranking as suggested by stable isotopes is not consistent through time. Inconsistency in rank ordering is particularly

evident for *Praeglobotruncana stephani*, *R. globotruncanoides* (including its direct ancestors, *appenninica* and *gandolfii*), and *Hedbergella delrioensis*. Initially in the Albian (phases I, II), *Pg. stephani* and *R. appenninica-gandolfii* were probably deep dwelling, because their $\delta^{18}\text{O}$ values are clearly higher than those of the dominant surface dwellers of this period, *Ticinella primula* and *Paracostellagerina libyca* (Wilson and Norris 2001; Petrizzo et al. 2008). During the early Cenomanian (phase IV), though, *Pg. stephani* and *R. globotruncanoides* typically registered the lowest $\delta^{18}\text{O}$ values in the assemblages, showing their marked upper-ocean preference. By contrast, *Hd. delrioensis* shows a reverse trend, as its initially low (shallow) $\delta^{18}\text{O}$ signals (phases I, III) shifted to higher, thermocline values in the early Cenomanian (phase IV).

Discussion

Solving Enigmatic Foraminiferal Isotopic Patterns with Coccoliths.—The observed isotopic signatures of changing depth ecology are unexpected in light of the current knowledge of mid-Cretaceous planktonic foraminifera. In particular, the inferred shallow habitat of *R. globotruncanoides* is most surprising because it is at odds with the long-held consensus that the single-keeled rotaliporids were the representatives of deep, thermocline dwellers (Caron and Homewood 1983; Leckie 1987; Jarvis et al. 1988; Norris and Wilson 1998; Hart 1999; Premoli Silva and Sliter 1999). Predictable objection to such finding is that *R. globotruncanoides* remained in the deep habitat, whereas other species adapted to a much deeper habitat, while surface-dwelling species were absent at that time. It could also be argued that we missed inclusion of surface-dwellers in our analyses despite a thorough multispecies survey. Foraminiferal data by themselves cannot rule out such arbitrary interpretations, and this is a limitation of foraminiferal isotopic studies that have depended solely on *relative* interspecies $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ differences.

In order to avoid this limitation and to independently estimate foraminiferal depth habitats through time, we take advantage of the coexisting coccolith-rich fraction as an

indicator of surficial marine $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values. Compared with planktonic foraminifera that can actively change their habitat preferences through their life cycles, coccolithophorids are calcite-secreting photosynthetic algae restricted to the photic layer by their autotrophic nutritional mode. In fact, a recent Miocene case study by Ennyu et al. (2002) has strengthened the significance of coccolith stable isotopes as tracers of upper-ocean paleoceanographic properties.

Our coccolith-rich fraction $\delta^{18}\text{O}$ data display a systematic offset relative to coeval planktonic foraminifera (Fig. 2). The observed $\delta^{18}\text{O}$ offset is in accord with the known magnitude of the coccolithophorid vital effect (biologically induced disequilibrium in isotope fractionation) derived through culture experiments ($\sim +1.1\%$ from equilibrium calcite at 25–30°C [Dudley et al. 1986; Ennyu et al. 2002]).

We expect that $\delta^{13}\text{C}$ values in coccoliths approximate the equilibrium calcite $\delta^{13}\text{C}$ values with upper-ocean DIC, because our coccolith-rich fraction and planktonic foraminiferal $\delta^{13}\text{C}$ data are highly consistent each other (Fig. 2). However, the coccolithophorid vital effect in $\delta^{13}\text{C}$ is still unclear. Limited $\delta^{13}\text{C}$ data from culture experiments and Quaternary size-sorted $<38\ \mu\text{m}$ sediment delineated significant interspecies variation as large as 5‰ (Paull and Thierstein 1987; Ziveri et al. 2003). Further, published $\delta^{13}\text{C}$ trends in the Quaternary coccolith-rich fraction were inconsistent with that of coexisting planktonic foraminifera (*Globigerina bulloides*) (Dudley and Nelson 1989), and were difficult to correlate from one site to another (Paull and Thierstein 1990).

Stoll (2005) has shed new insights on the $\delta^{13}\text{C}$ composition of coccoliths from the geologic past. She identified the closely matched $\delta^{13}\text{C}$ trends between near-monogenic isolates (fine [3–5 μm] and coarse [8–12 μm] fractions) of Paleogene coccoliths, and argued that the interspecies differences in coccolithophorid $\delta^{13}\text{C}$ vital effect should have been minimal. The proposed mechanisms that explain this finding were the larger coccolithophorid cell diameter and/or a different DIC acquisition strategy relative to

extant taxa under increased $p\text{CO}_2$ conditions. Each of the taxonomically separated Paleogene coccoliths analyzed by Stoll (2005) was isotopically indistinguishable from coeval subbotinid planktonic foraminifera, an observation that allowed her to postulate that calcification by ancient coccolithophorids was nearly in equilibrium with the $\delta^{13}\text{C}$ compositions in seawater.

New Depth-Ecology Model.—We propose an updated paleoecological model of planktonic foraminifera by considering the simple isotopic differences relative to the coccolith-rich fraction ($= \Delta\delta_{\text{PF-CC}}$) as shown in Figure 5A. The assumptions used are threefold: first, the coccolithophorid vital effects were $\sim +1.1\%$ for $\delta^{18}\text{O}$ and $\sim 0\%$ for $\delta^{13}\text{C}$ relative to equilibrium calcite (Ennyu et al. 2002; Stoll 2005); second, seasonal paleoceanographic dynamics of mid-Cretaceous subtropical western North Atlantic are compatible with those of the present day (Gruber et al. 2002); and third, coccolith stable isotopes mirror a “seasonal window” during the spring bloom rather than the annual mean (Ennyu et al. 2002).

We determine that: (1) taxa with $\Delta\delta^{18}\text{O}_{\text{PF-CC}} \approx -1.1$ and $\Delta\delta^{13}\text{C}_{\text{PF-CC}} \approx 0$ (e.g., *R. globotruncanoides*) have dominated in the same water mass inhabited by coccolithophorids, and hence they are spring mixed-layer dwellers; and (2) taxa more depleted in ^{18}O and enriched in ^{13}C (reflecting higher temperatures and seasonal ^{13}C -enrichment in DIC [$\Delta\delta^{18}\text{O}_{\text{PF-CC}} < -1.1$; $\Delta\delta^{13}\text{C}_{\text{PF-CC}} > 0$]; e.g., *Pg. stephani* [phases III, IV], *Pc. libyca*) are summer mixed-layer dwellers. Intraspecific isotopic variations are high for cases (1) and (2), and this is taken as an isotopic feature diagnostic of planktonic foraminifera in the upper-ocean setting in which intra- and inter-annual perturbations in temperatures and salinity are significant (e.g., Rohling et al. 2004; Petrizzo et al. 2008). Further, (3) taxa substantially enriched in ^{18}O and depleted in ^{13}C ($\Delta\delta^{18}\text{O}_{\text{PF-CC}} \gg -1.1$; $\Delta\delta^{13}\text{C}_{\text{PF-CC}} \ll 0$) with small intraspecific isotopic variations (e.g., *R. ticinensis*, *R. reicheli* and *R. montsalvensis*) would be thermocline dwellers.

In contrast to the above cases (1) to (3) for which straightforward interpretations are

possible, we also recognize that (4) *R. appenninica* and *Pg. stephani* (both phase II) and (5) *Hd. delrioensis* and *Hedbergella simplex* in phase IV present contradictory cases. This is because habitat information from $\Delta\delta^{13}\text{C}_{\text{PF-CC}}$ points to a shallow setting, whereas that from $\Delta\delta^{18}\text{O}_{\text{PF-CC}}$ suggests a deep setting. As concerns case (4) in phase II, the apparent reduction of a $\delta^{13}\text{C}$ gradient is noteworthy (Fig. 5A). During this period, as has been suggested by local nannoplankton extinction, the water column over Blake Nose became less stratified (Watkins et al. 2005) (see “Paleoceanographic Background” above). At the same time, planktonic foraminiferal interspecies $\delta^{13}\text{C}$ variation is somewhat small (Petrizzo et al. 2008; ca. 99.9–99.6 Ma in their age-model). Thus, in light of the absence of a typical upper-ocean $\delta^{13}\text{C}_{\text{DIC}}$ gradient (probably indicating upwelling), *R. appenninica* and *Pg. stephani* in phase II were deep-dwelling according to $\delta^{18}\text{O}$ data. For case (5), the isotopic record of *Hd. delrioensis* may represent the opportunistic ecological behavior of this species, which is reported to vary from one locality to another (e.g., Wilson et al. 2002). Such an enigmatic isotopic feature recalls that of another Late Cretaceous opportunist, *Heterohelix globulosa* (e.g., Bornemann and Norris 2007), the proposed ecological strategy of which is adaptation to the oxygen minimum zone (Huber et al. 1995; MacLeod et al. 2000, 2001). If such a *globulosa*-like strategy applies to *Hd. delrioensis*, it draws a parallel with the case of *Hd. simplex*, which has also been interpreted to prefer oxygen-deficient environments (Coxall et al. 2007). Nevertheless, habitat preference in the oxygen minimum zone should be illustrated by the most negative $\delta^{13}\text{C}$ values within the assemblage (Boersma and Premoli Silva 1989; Coxall et al. 2007), the isotopic features that cannot be seen in *Hd. delrioensis* and *Hd. simplex* (phase IV). We therefore consider an alternative explanation for the $\delta^{13}\text{C}$ feature of *Hd. delrioensis* and *Hd. simplex* (phase IV) in terms of seasonality, such that their calcification may have occurred exclusively during spring when the vertical $\delta^{13}\text{C}$ gradient disappears. In any case, we infer that a shift in depth ecology to a thermocline-depth oc-

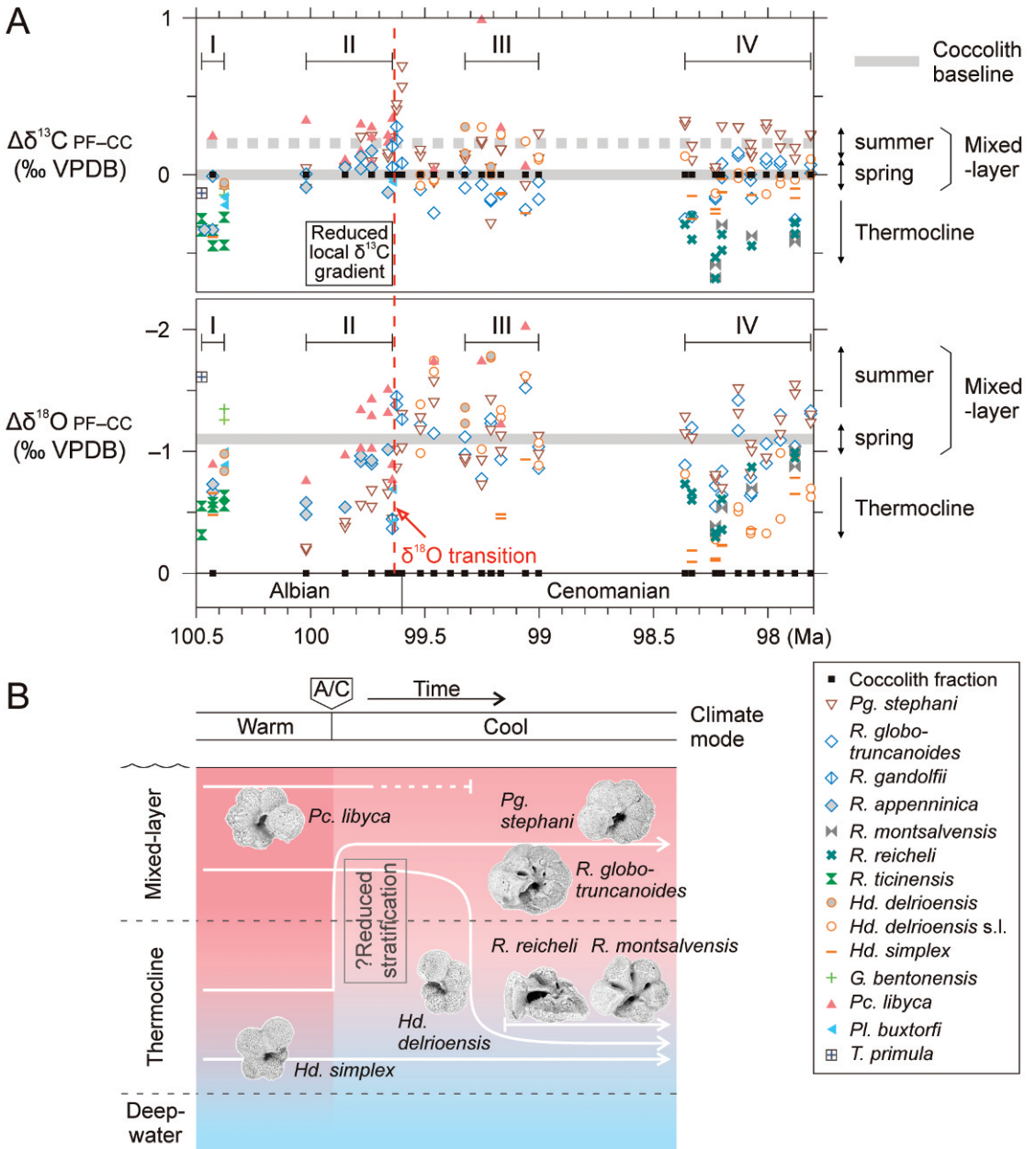


FIGURE 5. A, Isotopic difference of planktonic foraminifera relative to the coccolith-rich fraction ($\Delta\delta^{18}\text{O}_{\text{PF-CC}}$ and $\Delta\delta^{13}\text{C}_{\text{PF-CC}}$), plotted against numerical age. For information, the coccolith data series ($\Delta\delta = 0$) is also shown. For phase I, a single coccolith-rich fraction data point (558.73 mbsf) is used to derive $\Delta\delta_{\text{PF-CC}}$ values for the rest of the two levels. The “coccolith baseline” represents disequilibrium-corrected $\Delta\delta$ values of the coccolith-rich fraction, which is equal to $\Delta\delta^{18}\text{O}_{\text{PF-CC}} = -1.1\text{‰}$ and $\Delta\delta^{13}\text{C}_{\text{PF-CC}} = 0\text{‰}$. This baseline denotes the level of equilibrium calcite during the major coccolithophorid growth period (i.e., spring bloom). The dotted thick gray line represents a $\delta^{13}\text{C}$ offset from the baseline by $\sim+0.2\text{‰}$, which corresponds to a $\delta^{13}\text{C}$ increase in the upper-ocean DIC during summer (Gruber et al. 2002). Age assignment of late Albian around phase I (Core 27) is based on Petrizzo et al. (2008). The latest Albian–Cenomanian numerical age scale is derived by linear inter- and extrapolation of two datums: FO of *R. globotruncanoides* (=99.6 Ma [Ogg et al. 2004]) at 553.24 mbsf; and onset of MCE I $\delta^{13}\text{C}$ excursion (=95.83 Ma; Ando et al. 2009, and references therein) at 523.14 mbsf. B, Schematic illustration of reconstructed depth-ecology reorganization and faunal turnover of planktonic foraminifera across the Albian/Cenomanian (A/C) boundary. Seasonality in foraminiferal occurrence (see text) is not considered. See color version of this figure in the online PDF format of this paper.

curred with *Hd. delrioensis*, as revealed by $\delta^{18}\text{O}$ values.

Evolutionary Paleocological Implications.—The new depth-habitat reconstruction highlights the hitherto unknown mechanisms for the evolutionary paleoecological dynamics of mid-Cretaceous planktonic foraminifera (Fig. 5B). At the A/C boundary, when a cooler climate mode might have been initiated (see “Paleoceanographic Background”), the initially deep-dwelling *Pg. stephani* and the *R. globotruncanoides* lineage shifted rapidly to the mixed-layer (“ $\delta^{18}\text{O}$ transition” in Fig. 5A), plunging a surface-dwelling *Pc. libyca* into decline and finally extinction; alternatively, a decline in the population of *Pc. libyca* might have facilitated the invasion toward the surface habitats by *Pg. stephani* and *R. globotruncanoides*. Later on, the deeper environment was marked by immigration of the opportunistic *Hd. delrioensis*, as well as speciation of *R. reicheli* and *R. montsalvoensis*. This reestablished rotaliporid depth ecology has been shown to persist into the middle Cenomanian (Ando et al. 2009).

This study further advances the recently advocated view that there exists no particular relationship between test morphology and environment of fossil planktonic foraminifera (see “Introduction”). Thus, comparative morphology with respect to extant taxa does not help understand their depth ecology. Our isotopic evidence for a deeper habitat of *Hedbergella* also calls for the reexamination of biogeographically inferred depth-ecology models (Hart and Bailey 1979; Leckie 1987); the dominance of this taxon in the epicontinental shelf setting might not have been simply the function of shallow-depth preference, but instead represents adaptation to a peculiar water-mass condition, such as a salinity anomaly.

Previous studies of foraminiferal isotopic paleoecology around the A–C transition cannot be compared directly with our results owing to the absence of concurrent stable isotope measurements of the coccolith-rich fraction or to the questionable state of foraminiferal preservation. Regarding data from the uppermost Cenomanian of DSDP Site 551, northeastern Atlantic (Gustafsson et

al. 2003), the isotopic signal of *Rotalipora greenhornensis* (= direct descendant of *R. globotruncanoides*) appears to indicate its deeper habitat. In addition, limited data (foraminifera only, without coccolith-rich fraction) from DSDP Site 511, southern Atlantic, register the $\delta^{18}\text{O}$ values of *Praeglobotruncana* close to those of benthic foraminifera (Huber et al. 1995; Bice et al. 2003). Clearly, further effort is necessary to investigate the spatio-temporal evolution of planktonic foraminiferal depth stratification through the Late Cenomanian on a global scale.

Mid-Cretaceous diversification of planktonic foraminifera has been modeled in light of adaptation of large, ornamented, *K*-mode specialists into a deeper, oligotrophic environment (Hart 1980, 1999; Caron and Home-wood 1983; Premoli Silva and Sliter 1999). The evolution of *R. reicheli* and *R. montsalvoensis* observed herein conforms to this view, yet our results highlight the importance of an adaptive strategy in a reverse sense from the deep to the surface. Given that reduced upper-ocean stratification is a reasonable paleoceanographic consequence of a cool climate mode for this period (Nederbragt et al. 2001; Wilson and Norris 2001; Petrizzo et al. 2008), the weakening of a hydrographic barrier might have spurred the upward migration of deep-dwelling species (Fig. 5B). This inference of weakened stratification at the time of depth-ecology organization (“ $\delta^{18}\text{O}$ transition” to phase III [Fig. 5A]) can be supported by the limited thermocline data of *Hd. simplex* showing smaller vertical $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ gradients during phase III. With regard to this point, the planktonic $\delta^{18}\text{O}$ record in subsequent phase IV implies the resumption of a stratified water column, but available $\delta^{18}\text{O}$ data do not clarify whether the climate modes were different between phases III and IV.

The observed case of an upward shift in depth ecology resembles that of Eocene hantkeninids (Coxall et al. 2000). The hantkeninid evolution took place from sub-thermocline to thermocline to surface mixed-layer over <5 Myr, and was accompanied by speciation as manifested by marked changes in chamber extension and shape, for which a

functional morphological explanation in response to changing paleoceanographic properties is possible (Coxall et al. 2000). Therefore, the hantkeninid evolutionary paleoecology cannot be directly cited as a model case for the A/C wholesale depth-habitat reorganization, characterized by its remarkable rapidity and by the absence of speciation (for *Praeglobotruncana*, *Hedbergella*) or less pronounced evidence for it (for *R. gandolfii* → *R. globotruncanoides*). A depth-habitat shift without speciation, in turn, does not allow application of the existing depth parapatry model (Norris 2000). In the absence of gametogenetic calcification in Cretaceous taxa (Bornemann and Norris 2007), it is likely that extinct planktonic foraminifera indeed lacked strategies for enhancing reproductive isolation, and that they instead possessed high flexibility in niche selection.

Paleoceanographic Implications.—This study clearly shows that, for appropriate paleoceanographic reconstructions by means of stable isotopes of planktonic foraminifera, determination of their evolutionary paleoecological dynamics should be of primary consideration; any paleoceanographic application may be flawed without firm knowledge of the underlying ecological and evolutionary dynamics of fossil planktonic taxa. An example is given for A–C paleoceanographic change at contemporary Site 1052. As summarized above (see “Paleoceanographic Background”), the closely matched $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values between surface-dwelling *Pc. libyca* and deep-dwelling “*Rotalipora* spp.” were taken as evidence for stratification collapse by Wilson and Norris (2001) and Petrizzo et al. (2008). Although the likelihood of this transient paleoceanographic event is acceptable for a latest Albian time slice (i.e., *R. appenninica* Zone), it is untenable to interpret the persistence of such homogenized vertical ocean structure into the early Cenomanian, as implied by Wilson and Norris (2001: Fig. 2), because the rotaliporid species analyzed by these authors (*R. globotruncanoides*) is here redefined as a surface dweller.

Our findings may also concern current understanding of the paleoceanographic evolution across the Cenomanian/Turonian (C/

T) boundary (93.5 Ma). Expansion of the oxygen minimum zone has been a paramount hypothesis to account for the C/T paleoceanographic event, as manifested principally by the selective extinction of the “deep-dwelling” genus *Rotalipora* (Jarvis et al. 1988). However, such a prerequisite is worthy of reexamination because the rotaliporid species that went extinct include *greenhornensis* and *deeckeii* (Ando and Huber 2007), which are descendants of surface-dwelling *R. globotruncanoides* (see also Gale et al. 2000). Another remarkable aspect of the C/T global change is significant warming of deep water as revealed by benthic foraminiferal stable isotopes (Huber et al. 1999), yet, for the same reason, such deep-water changes may not be sufficient to explain the rotaliporid extinction. Instead, it is worthwhile investigating the possibility that a transient cooling (Forster et al. 2007b) may have played a role in C/T planktonic foraminiferal extinction and turnover, by analogy with this study showing that the A/C depth-habitat reorganization was coupled with a cooler climate mode.

Conclusions

New stable isotope records of multispecies planktonic foraminifera and the coccolith-rich fraction from Blake Nose (western North Atlantic) have shown that a wholesale depth-habitat reorganization and turnover of planktonic foraminifera occurred during the mid-Cretaceous. The foraminiferal events include rapid adaptation to living at a surface habitat by initially deep-dwelling *Pg. stephani* and the *R. globotruncanoides* lineage across the A/C boundary, which might have caused or might have been induced by the decline of surface-dwelling *Pc. libyca*. After a while (~1 Myr), vertical migration to a deep environment occurred in the opportunistic *Hd. delrioensis*, at the same time as speciation of deep-dwelling *R. montsalvensis* and *R. reicheli*. We infer that the observed adaptive strategy and evolution among the planktonic foraminifera were in response to a cooling episode started at the A–C transition. The remarkable flexibility in depth-habitat selection of planktonic foraminifera is unexpected, but such evolutionary paleoecological dy-

namics can be established objectively by using the coccolith-rich fraction as an independent indicator of surficial-marine $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values.

Our results strongly support the increasing isotopic evidence against the traditional model of planktonic foraminiferal depth ecology based on comparison to modern morphological counterparts and biogeographic distribution. Further, the new view differs from any other previous studies in proposing that the "stationary" paleoecological model of mid-Cretaceous planktonic foraminifera is obsolete. Most notable is the case for the genus *Rotalipora*. Although all rotaliporid species have long been believed to be deep-dwelling and the sum category of "*Rotalipora* spp." is used to indicate the deep thermocline environments, our study clearly shows their dramatic shift in depth ecology, together with surface-to-deep intrageneric ecological variation.

Our finding is of considerable significance to the general field of paleoceanography based on stable isotope analysis of fossil planktonic foraminifera. Among the several assumptions needed for paleoceanographic application of planktonic foraminiferal stable isotopes are ambient seawater $\delta^{18}\text{O}$ composition, salinity, pH or alkalinity, and diagenetic alteration. Here we shall add the depth-ecology shift as a hitherto unaddressed but crucial factor that needs to be addressed before developing paleoceanographic reconstructions.

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Appendix

Biostratigraphic and Taxonomic Notes

This study yielded some improvements upon previous biostratigraphic treatments of the Cenomanian of Site 1050 (Bellier and Moullade 2002; Petrizzo and Huber 2006), and are briefly summarized here. We place the first occurrence (FO) datum of *R. globotruncanoides* at 553.24 mbsf by following the rotaliporid taxonomy of Ando and Huber (2007). The FO of *R. reicheli* is recognized at 543.36 mbsf, but it is not used to define the *R. reicheli* Zone. This level is significantly below the onset of MCE 1 $\delta^{13}\text{C}$ excursion (\approx base of the Middle Cenomanian Substage) at 523.14 mbsf (Ando et al. 2009). At this site, *R. reicheli* occurs at two separate stratigraphic intervals in Core 25 (543.36–539.52 mbsf) and Core 23 (526.06–520.67 mbsf). The older occurrence is at odds with the representative Tethyan planktonic foraminiferal biostratigraphy (e.g., Caron and Spezzaferri 2006). This discrepancy is presumably due to an incomplete zonal scheme (cf. Coccioni and Galeotti 2003), an ambiguous species concept of *R. reicheli*, and/or an unknown paleoceanographic control.

Importantly, the lower Cenomanian foraminiferal record at Site 1050 is marked by the common occurrence of relatively small *R. montsalvensis*, certainly representing its early evolutionary stage (Fig. A1) (its FO level may fall within a coring gap between Cores 25 and 26). This form, not previously known in the classic Tethyan localities, is typified by possessing weakly developed periumbilical ridges that fringe the broad poreless chamber surfaces around the umbilicus. From the “relict” ornamental element it could be considered a phyletic link with the *R. globotruncanoides*-like ancestor. This observation, together with that of *R. reicheli*, points to an unknown paleoceanographic control resulting in a fundamental bioprovincial disparity between the thermocline assemblages in the western North Atlantic and Mediterranean Tethys, at least during a part of the mid-Cretaceous.

This new insight into the early evolution of *R. montsalvensis*, in turn, calls into question the recent emendation of the rotaliporid genera by González-Donoso et al. (2007), who assigned an independent generic rank to the *montsalvensis-cushmani* lineage on the basis of the assumption that it has evolved from ?*Praeglobotruncana*. Further efforts are in progress to generate actual stratophenetic fossil evidence to solve the phylogenetic and genus-level taxonomic problems. Until then, the long-held tradition that all rotaliporid species are placed in the single genus *Rotalipora* is retained herein.

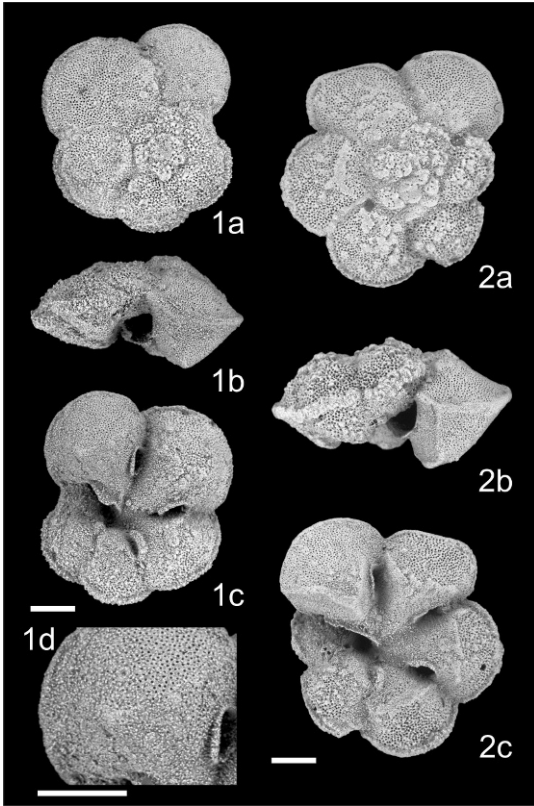


FIGURE A1. SEM images of the early evolutionary forms of *Rotalipora montsalvoensis*. a = spiral, b = edge, and c = umbilical views. (1) ODP Sample 1050C-25R-3, 142–146 cm (543.12 mbsf). Note broad, nearly poreless surface near umbilicus, being fringed by weakly developed periumbilical ridge (1d). (2) ODP Sample 1050C-25R-3, 60–64 cm (542.30 mbsf). Periumbilical ridges that extend to the chamber anterior and merge with the equatorial keel are clearly seen. All scale bars, 100 μm .