

# Macroevolutionary History of the Planktic Foraminifera

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## Keywords

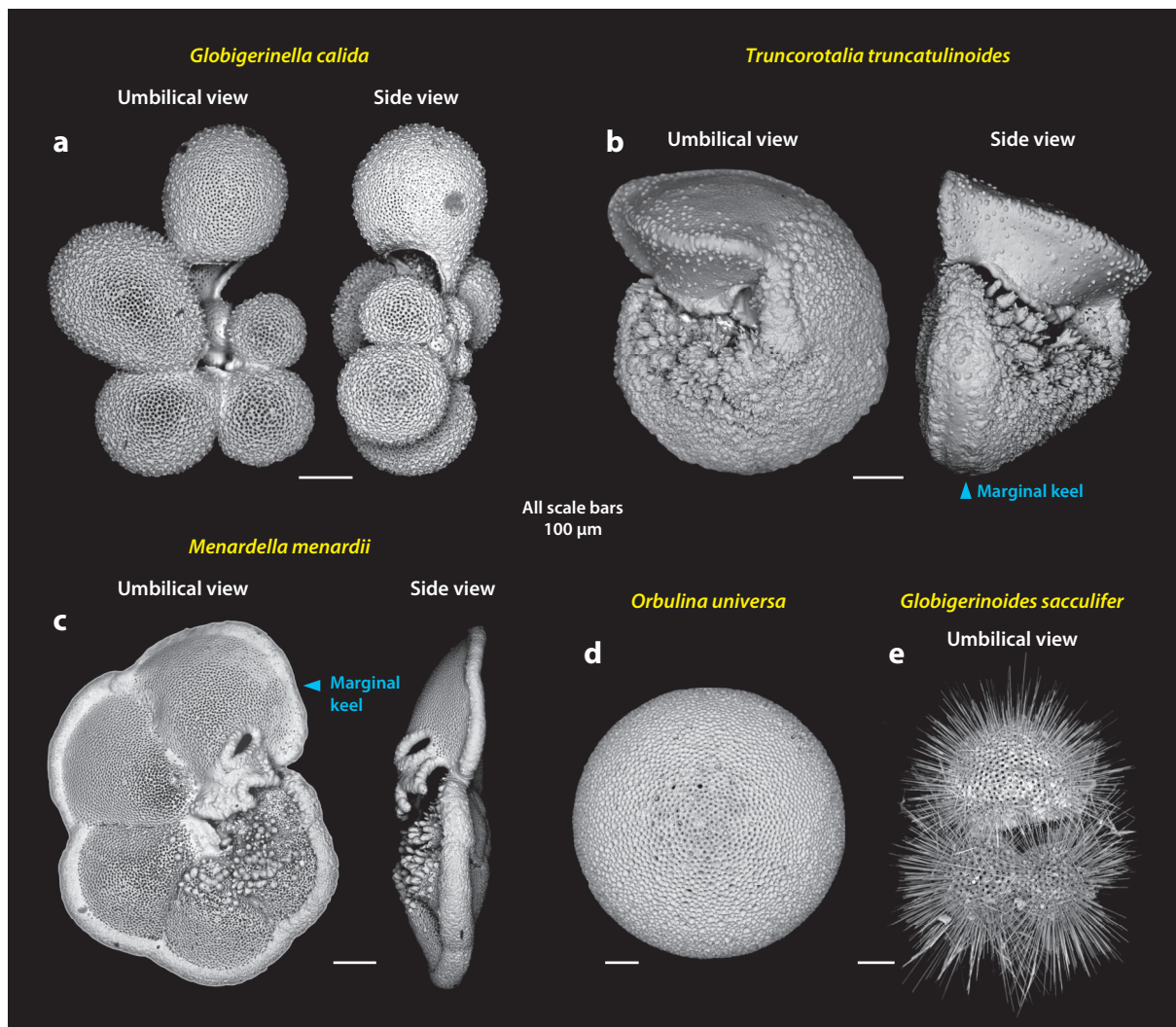
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## Abstract

Planktic foraminifera are an abundant component of deep-sea sediment and are critical to geohistorical research, primarily because as a biological and geochemical system they are sensitive to coupled bio-hydro-lithosphere interactions. They are also well sampled and studied throughout their evolutionary history. Here, we combine a synoptic global compilation of planktic foraminifera with a stochastic null model of taxonomic turnover to identify statistically significant increases in macroevolutionary rates. There are three taxonomic diversifications and two distinct extinctions in the history of the group. The well-known Cretaceous–Paleogene extinction is of unprecedented magnitude and abruptness and is linked to rapid environmental perturbations associated with bolide impact. The Eocene–Oligocene boundary extinction occurs due to a combination of factors related to a major reorganization of the global climate system. Changes in ocean stratification, seawater chemistry, and global climate recur as primary determinants of both macroevolutionary turnover in planktic foraminifera and spatiotemporal patterns of deep-sea sedimentation over the past 130 Myr.

## 1. INTRODUCTION

Planktic foraminifera are an exclusively marine group of amoeboid protists that grow minute (<1 mm) tests composed of calcite ( $\text{CaCO}_3$ ). Test construction generally follows a simple pattern of accretionary growth, with successive chambers coiled into a spiral, but there are myriad variations on this basic theme (**Figure 1**). Owing to their high dispersal capacity (Norris 2000), planktic foraminifera have colonized virtually every area in one of the largest biomes on the planet—the epipelagic realm (0–200 m water depth) of the ocean. The absolute flux of biogenic debris from the epipelagic realm to the ocean bottom varies over time and across space, but the accumulation



**Figure 1**

Scanning electron micrographs of select species of modern planktic foraminifera. Specimens *a*, *c*, and *e* are from a sediment trap deployed in the equatorial Pacific Ocean (2,284 m water depth). Specimens *b* and *d* are from Quaternary sediments atop Blake Ridge (2,790 m water depth) in the northwest Atlantic Ocean (piston core CH-15-00-PC9).

of debris on the seafloor has produced a rich sedimentary record both of ocean/climate change and of biological evolution. Of the many different kinds of microfossils preserved in the sedimentary archive, planktic foraminifera are among the most geographically widespread and abundant.

Because of their abundance and diversity of form, the evolutionary history of planktic foraminifera has received considerable attention from taxonomists and biostratigraphers across their entire 170-Myr evolutionary history (e.g., Masters 1977, Bolli et al. 1985). This history spans episodes of major tectonic plate reorganization, global atmospheric and oceanic circulation changes, prolonged and abrupt climate change, varying global sea levels, and cataclysmic bolide impact. Because plankton populations are exposed to even the shortest-duration changes in Earth's surface environment, the evolutionary history of the foraminifera is closely intertwined with the physical environmental history of the ocean-climate system. In addition, many species of planktic foraminifera have biogeographic ranges that stretch across multiple ocean basins (Lipps 1970, Bé & Tolderlund 1971, Bé 1977); hence, environmental perturbations of a global scale are generally required to extirpate them (Wei & Kennett 1986, Peters et al. 2013).

The relatively complete fossil record, expansive biogeographic ranges, rich and well-documented evolutionary history, and sheer abundance in the geological record make the planktic foraminifera ideal for evolutionary and biostratigraphic studies (e.g., Prothero & Lazarus 1980, Berggren et al. 1995, Gradstein et al. 2004). Moreover, the advent of analytical techniques for extracting the paleoceanographic information recorded by the chemistry of their calcite tests has made them a powerful tool for studying past ocean/climate conditions (Hemleben et al. 1989). The utility of planktic foraminifera for evolutionary and paleoceanographic studies has been further enhanced by neontological studies, which have characterized the life history strategies, ecological affinities, trophic behaviors, population structures and dynamics, and biochemistries of many extant species (Hemleben et al. 1989). Thus, the stratigraphic ranges, species-level biological systematics, and phylogenetic relationships of planktic foraminifera are unusually well documented in comparison with many other fossil organisms.

Here, we use a synoptic data set consisting of the taxonomic names, classifications, and global stratigraphic ranges of all published species of planktic foraminifera to generate genus- and species-level macroevolutionary histories for the past 170 Myr. We then discuss the many relationships between this history and known variability in the ocean-climate system. We are not alone in providing a thorough account of the evolutionary history of planktic foraminifera, and many fine overviews exist (e.g., Berggren 1969, Wei & Kennett 1986, Tappan & Loeblich 1988, Collins 1989, Ezard et al. 2011, Lloyd et al. 2011). This review differs from others primarily in that macroevolutionary quantities are compared with a null model of taxon ranges that enables us to identify time intervals with statistically significant deviations from background rates of species origination and extinction (e.g., Raup & Sepkoski 1982). We then relate these significant taxonomic rate excursions to well-known changes in the Earth system as well as to macrostratigraphic patterns that describe variability in the spatial and temporal distribution of deep-sea sedimentation.

## 2. METHODS

### 2.1. Data Set

We used authoritative taxonomic atlases and electronic data sets to derive taxa and the times of their first and last appearance in the fossil record. Stratigraphic ranges for Mesozoic species were taken primarily from the CHRONOS database (<http://www.chronos.org>; accessed 2008), with additions and modifications (Caron 1985, Boudagher-Fadel et al. 1997, Premoli Silva & Sliter 1999, Leckie et al. 2002, Georgescu et al. 2008, Huber & Leckie 2011). Three published

Supplemental Material

atlases (Toumarkine & Luterbacher 1985, Olsson et al. 1999, Pearson et al. 2006) served as the primary sources for Paleogene species. Likewise, ranges of Neogene species were compiled from several widely used atlases (Saito et al. 1981, Kennett & Srinivasan 1983, Bolli & Saunders 1985). In addition, species and ranges were cross-referenced with PLANKRANGE (<http://palaeo.gly.bris.ac.uk/Data/plankrange.html>).

The combined data set consists of a list of valid species and numerical ages for their first and last appearance. In the literature, these can be resolved to a single biostratigraphic zone, in this case the planktic foraminiferal biozonation scheme of Gradstein et al. (2004). Because a well-established planktic foraminiferal biozonation does not exist for the Jurassic and earliest Cretaceous, stratigraphic stage boundaries were used for these time intervals. The operational timescale used here has 90 intervals (**Figure 2**), which vary in duration from 0.1 to 6.7 Myr (median 1.5 Myr). If the Jurassic and earliest Cretaceous are omitted, there are 82 bins with a median duration of 1.45 Myr. Care was taken to avoid duplicate entries stemming from multiple references and synonymies. For additional discussion of the data set and methods used to assemble it, see the **Supplemental Methods** and **Supplemental Figure 1** (follow the **Supplemental Material** link in the online version of this article or at <http://www.annualreviews.org/>).

## 2.2. Analysis

Taxonomic rates of evolution were calculated using per capita per million year rates (Foote 2000). Origination metrics  $p$  and  $\hat{p}$  and extinction metrics  $q$  and  $\hat{q}$  are defined as

$$p = -\ln(N_{bt}/N_t) \quad (1)$$

$$\hat{p} = -\ln(N_{bt}/N_t)/\Delta t \quad (2)$$

$$q = -\ln(N_{bt}/N_b) \quad (3)$$

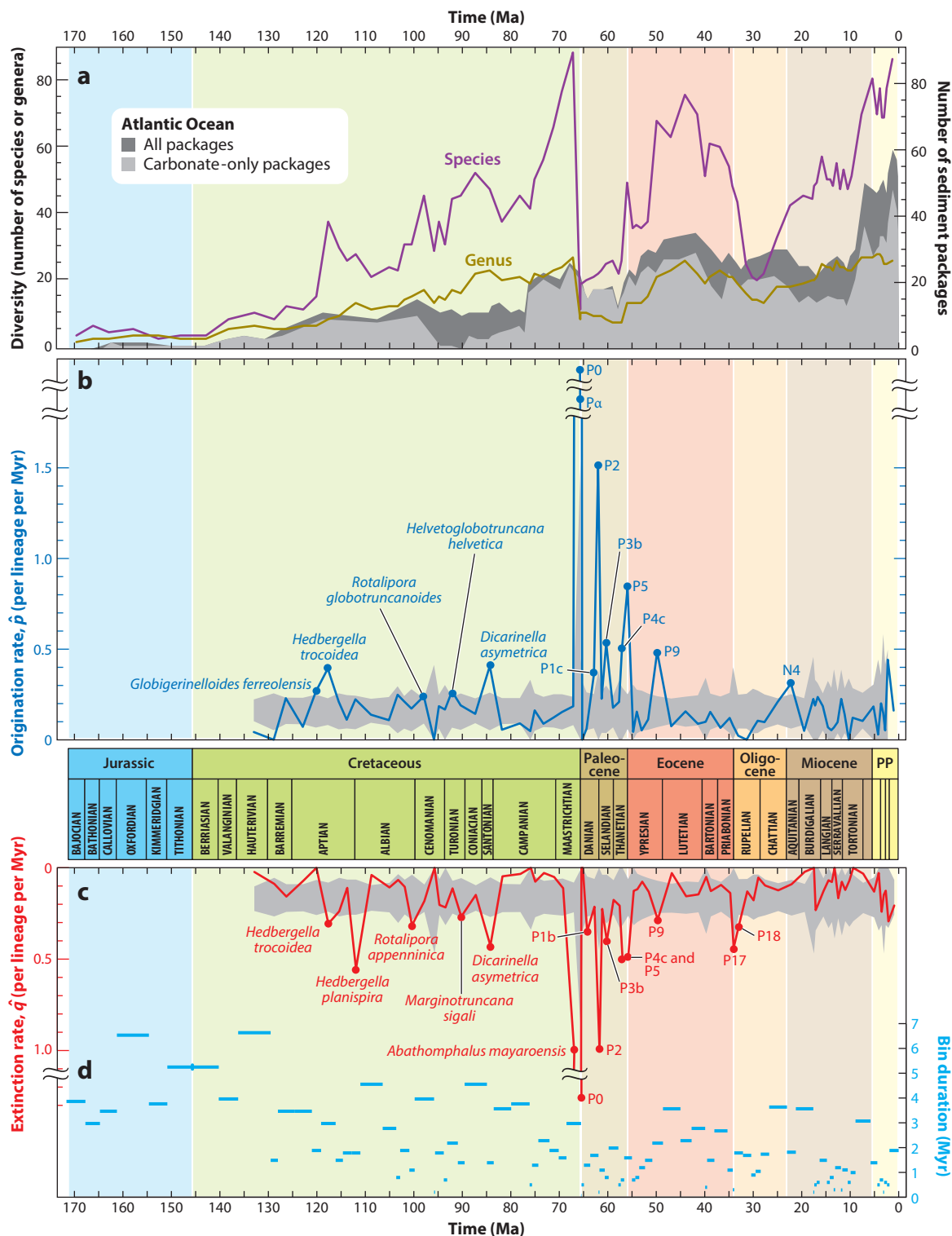
$$\hat{q} = -\ln(N_{bt}/N_b)/\Delta t, \quad (4)$$

where  $N_{bt}$  is the number of taxa with ranges that cross both the bottom and top zone boundaries (range through),  $N_t$  is the number of taxa with ranges that cross only the top zone boundary (originations + range through),  $N_b$  is the number of taxa with ranges that cross only the bottom zone boundary (extinctions + range through), and  $\Delta t$  is the zone duration measured in millions of years.

Null expectations for  $\hat{p}$  and  $\hat{q}$  that account for variability in both the temporal binning scheme used here and the empirical durations of species were generated using a Monte Carlo approach. In each iteration, all species were assigned random times of first appearance, while their original durations were preserved. Simple rules were followed to confine the randomized species ranges to the empirical timescale (e.g., randomized lineages could be extant, but they could not extend

### Figure 2

Macroevolutionary history of the planktic foraminifera and Atlantic basin macrostratigraphy. (a) Diversity and number of sediment packages. (b) Origination rates,  $\hat{p}$  (blue line). (c) Extinction rates,  $\hat{q}$  (red line). The gray envelope shows the 95% confidence limit on rates derived from a randomization model. Zones with significantly high rates are highlighted with a filled circle and zone name (see **Table 1**). (d) Bin duration. Abbreviation: PP, Plio-Pleistocene.



into the future). Rates of extinction and origination were then recalculated for the randomized data using the same temporal binning scheme. Confidence limits were generated by repeating the randomization 5,000 times and calculating the 95% range of rates in each binned time interval (**Figure 2b,c**). Zones in which the observed  $\hat{p}$  and/or  $\hat{q}$  values fell outside of the randomization envelope were identified as statistically different from a null model of randomly distributed stratigraphic ranges (**Table 1**). Because the Jurassic and early Cretaceous had few taxa, we omitted this interval from the analysis of macroevolutionary rates, but we show diversity results for the sake of completeness. All computations and analyses were performed in the R software environment (R Dev. Core Team 2008).

### 3. RESULTS

#### 3.1. Species Diversity

There are three diversifications and two large drops in planktic foraminifera diversity, with several second-order fluctuations superimposed on this first-order diversity trend (**Figure 2a**). Species diversity slowly increases in the early Cretaceous (Berriasian–Barremian), then rises more quickly during the Aptian, only to drop at the Aptian–Albian boundary. Species-level diversity recovers during the late Albian and Cenomanian, drops again across the Cenomanian–Turonian boundary, and then increases for a third time during the Turonian and Coniacian. There is a short-lived decrease in diversity across the Santonian–Campanian boundary, but diversity increases dramatically during the ensuing Campanian and Maastrichtian.

The Cretaceous–Paleogene (K–Pg) boundary represents the largest and most abrupt decline in diversity in the history of planktic foraminifera (**Figure 2a**). After a rapid increase directly after the boundary, diversity remains low throughout most of the Paleocene. It then rises at the close of the Paleocene, only to drop again during the earliest Eocene. The mid-Eocene is typified by a rapid increase in species diversity followed by a decline across the Eocene–Oligocene (E–O) boundary to a minimum in the early Oligocene. Diversity gradually increases during the rest of the Oligocene and into the Miocene, but plateaus during the mid-Miocene, after which time it continues to increase until near the Miocene–Pliocene boundary. Following a brief decline and a period of fluctuation, diversity increases modestly to its present-day level. Diversity today is comparable to the diversity maxima in the Cretaceous and Paleogene. Thus, there is no overall long-term increase in the species-level diversity of the planktic foraminifera.

#### 3.2. Genus Diversity

Genus diversity generally mirrors the species-level pattern, although genus-level changes are, as expected, muted (**Figure 2a**). Two notable deviations between the species- and genus-level records are apparent. First, the rise and fall in species diversity observed during the Aptian is not paralleled by similar changes in genus diversity. Instead, genus diversity increases nearly monotonically during the Aptian. Second, the modest increase in species diversity observed during the Paleocene corresponds to a comparably modest decline in the number of genera.

#### 3.3. Origination Rate

**Table 1** reports all statistically significant increases in origination rate, here defined as time intervals with observed rates of origination that exceed the 95% bounds generated by the randomization of the times of species origination. During the Cretaceous, there are five such increases, whereas



**Table 1** Extinction and origination rate values that exceed the limits of the stochastic null model

| Epoch or stage | Extinctions                          |                              |  | Originations                               |                               |   | Zone duration<br>(Myr) |
|----------------|--------------------------------------|------------------------------|--|--|-------------------------------|---|------------------------|
|                | Zone                                 | Extinctions<br>(per lineage) | Extinction rate,<br>$\hat{q}$ (per lineage<br>per Myr) | Zone                                       | Originations<br>(per lineage) | Origination rate,<br>$\hat{p}$ (per lineage<br>per Myr) |                        |
| Miocene        | —                                    | —                            | —  | N4   | 0.573                         | 0.313   | 1.83                   |
| Oligocene      | P18                                  | 0.583                        | 0.324  | —  | —                             | —   | 1.8                    |
| Eocene         | P17                                  | 0.134                        | 0.445  | —  | —                             | —   | 0.3                    |
| Eocene         | P9                                   | 0.582                        | 0.265  | P9   | 1.007                         | 0.458   | 2.2                    |
| Eocene         | P5                                   | 0.799                        | 0.499  | P5   | 1.358                         | 0.849   | 1.6                    |
| Paleocene      | P4c                                  | 0.357                        | 0.510  | P4c  | 0.357                         | 0.510   | 0.7                    |
| Paleocene      | P3b                                  | 0.325                        | 0.407  | P3b  | 0.431                         | 0.538   | 0.8                    |
| Paleocene      | P2                                   | 0.194                        | 0.971  | P2   | 0.305                         | 1.527   | 0.2                    |
| Paleocene      | —                                    | —                            | —  | P1c  | 0.636                         | 0.374   | 1.7                    |
| Paleocene      | P1b                                  | 0.460                        | 0.353  | —  | —                             | —   | 1.3                    |
| Paleocene      | —                                    | —                            | —  | P $\alpha$                                 | 0.747                         | 10.674  | 0.07                   |
| Paleocene      | P0                                   | 0.511                        | 17.028   | P0   | 1.099                         | 36.620  | 0.03                   |
| Maastrichtian  | <i>Abathomphalus<br/>mayaroensis</i> | 2.904                        | 0.968  | —  | —                             | —   | 3                      |
| Santonian      | <i>Dicarinella asymetrica</i>        | 0.606                        | 0.433  | <i>Dicarinella asymetrica</i>              | 0.575                         | 0.411   | 1.4                    |
| Turonian       | <i>Marginothracana sigali</i>        | 0.379                        | 0.271  | —  | —                             | —   | 1.4                    |
| Turonian       | —                                    | —                            | —  | <i>Helvetoglobotruncana<br/>helvetica</i>  | 0.593                         | 0.270   | 2.2                    |
| Cenomanian     | —                                    | —                            | —  | <i>Rotulipora<br/>globotruncanoides</i>    | 0.969                         | 0.242   | 4                      |
| Albian         | <i>Rotulipora appenninica</i>        | 0.351                        | 0.319  | —  | —                             | —   | 1.1                    |
| Aptian/Albian  | —                                    | —                            | —  | <i>Hedbergella planispira</i>              | 0.405                         | 0.225   | 1.8                    |
| Aptian         | <i>Hedbergella trocoldea</i>         | 0.916                        | 0.305  | <i>Hedbergella trocoldea</i>               | 1.344                         | 0.448   | 3                      |
| Aptian         | —                                    | —                            | —  | <i>Globigerinelloides<br/>ferreolensis</i> | 0.511                         | 0.269   | 1.9                    |

Shaded rows indicate zones with significantly high rates of both extinction and origination.

during the Cenozoic there are nine (**Figure 2b**). Most of the Cenozoic events occur in the Paleocene; only one (earliest Miocene) is observed during the Neogene. Background origination rates are unusually low during the latest Cretaceous (Campanian–Maastrichtian) and late Paleogene (mid-Eocene to early Oligocene).

### 3.4. Extinction Rate

There are six statistically significant extinction events in the Cretaceous, and nine in the Cenozoic (**Figure 2c**). Curiously, there are no intervals with significantly high rates of extinction in the Neogene. Background extinction rates typically remain near the lower portion of the envelope, and there are several time intervals (Albian, Campanian, Maastrichtian, and Miocene) during which  $\hat{q}$  values fall below the 95% confidence limits, indicating significantly less extinction than expected under a null model of randomly distributed species ranges.

### 3.5. Effect of Taxonomic Level

Genera are widely assumed to be reasonable proxies for species-level macroevolutionary patterns in the fossil record, but there have been few quantitative assessments of the validity of this assumption. In planktic foraminifera, species- and genus-level origination rates ( $p$ ,  $r = 0.623$ ) and extinction rates ( $q$ ,  $r = 0.883$ ) are positively correlated; extinction is more strongly positively correlated between genus and species levels than is origination. Family-level origination ( $p$ ,  $r = 0.415$ ) and extinction ( $q$ ,  $r = 0.745$ ) rates are also correlated with species-level rates, but more weakly so; the difference in correlation between extinction and origination rates is even stronger at the family level than it is at the genus level. These results support the view that macroevolutionary patterns among genera are a reasonable, though far from perfect, proxy for species-level patterns. However, the species-level data do suggest that genus-level extinction rates tend to be more reflective of species-level rates than are origination rates.

## 4. DISCUSSION

Numerous studies have independently documented major radiations of planktic foraminifera during the Cretaceous, early Paleogene, and Neogene periods (e.g., Cifelli 1969, Tappan & Loeblich 1988, Norris 1991). Each of these radiations culminates in comparable diversity maxima, as well as large diversity declines across the K–Pg and E–O boundaries (**Figure 2a**). The fidelity of the fossil record to the empirical macroevolutionary history of the group is also likely to be higher than is typically associated with the marine invertebrate fossil record (e.g., Foote 2000, Alroy 2014). For example, abrupt extinction pulses appear to be smeared backward in time when the preservation of stratigraphic ranges is incomplete (Foote 2000), resulting in underestimated rates in the time interval of true extinction and overestimated rates in the preceding time intervals. The planktic foraminifera appear to lack this type of extinction distortion; for example, empirical rates of extinction prior to the end-Cretaceous mass extinction are actually very low (**Figure 2c**), implying that few lineage durations have been artificially truncated by incomplete preservation prior to their true end-Cretaceous extinction events. Additionally, the so-called pull of the Recent—whereby extinction rates artificially decrease toward the Recent due to the extension of discontinuous stratigraphic ranges of extant species to the present day (Foote 2000)—does not appear to manifest in the planktic foraminifera. The lack of these aforementioned artifacts related to incomplete preservation is consistent with the view that the fossil record of planktic foraminifera is unusually well preserved and generally well sampled. Indeed, almost all known living species have a rich fossil



record, and even many delicate forms are known from deep-sea sediment samples. The number of individual sampling locations required to capture the vast majority of living species in the ocean is also in the single digits (Peters et al. 2013), indicating that sampling overall is likely to be very complete both today and throughout most of the group's history. This does not, however, rule out the more insidious possibility that rates of taxonomic evolution have been distorted as a result of artificial nomenclatural changes along continuously evolving lineages (i.e., pseudoextinction; Smith & Patterson 1988).

What follows is a discussion of the macroevolutionary events identified as statistically significant in the history of the planktic foraminifera. Because environmental change is widely accepted as driving macroevolutionary change in the planktic foraminifera (e.g., Cifelli 1969, Lipps 1970, Frerichs 1971, Hart 1980, Stanley et al. 1988, Leckie et al. 2002, Schmidt et al. 2004), this discussion is coupled with a treatment of important shifts in the ocean-climate system and related biological systems, as well as macrostratigraphic results for the deep-sea sedimentary record in the Atlantic basin.

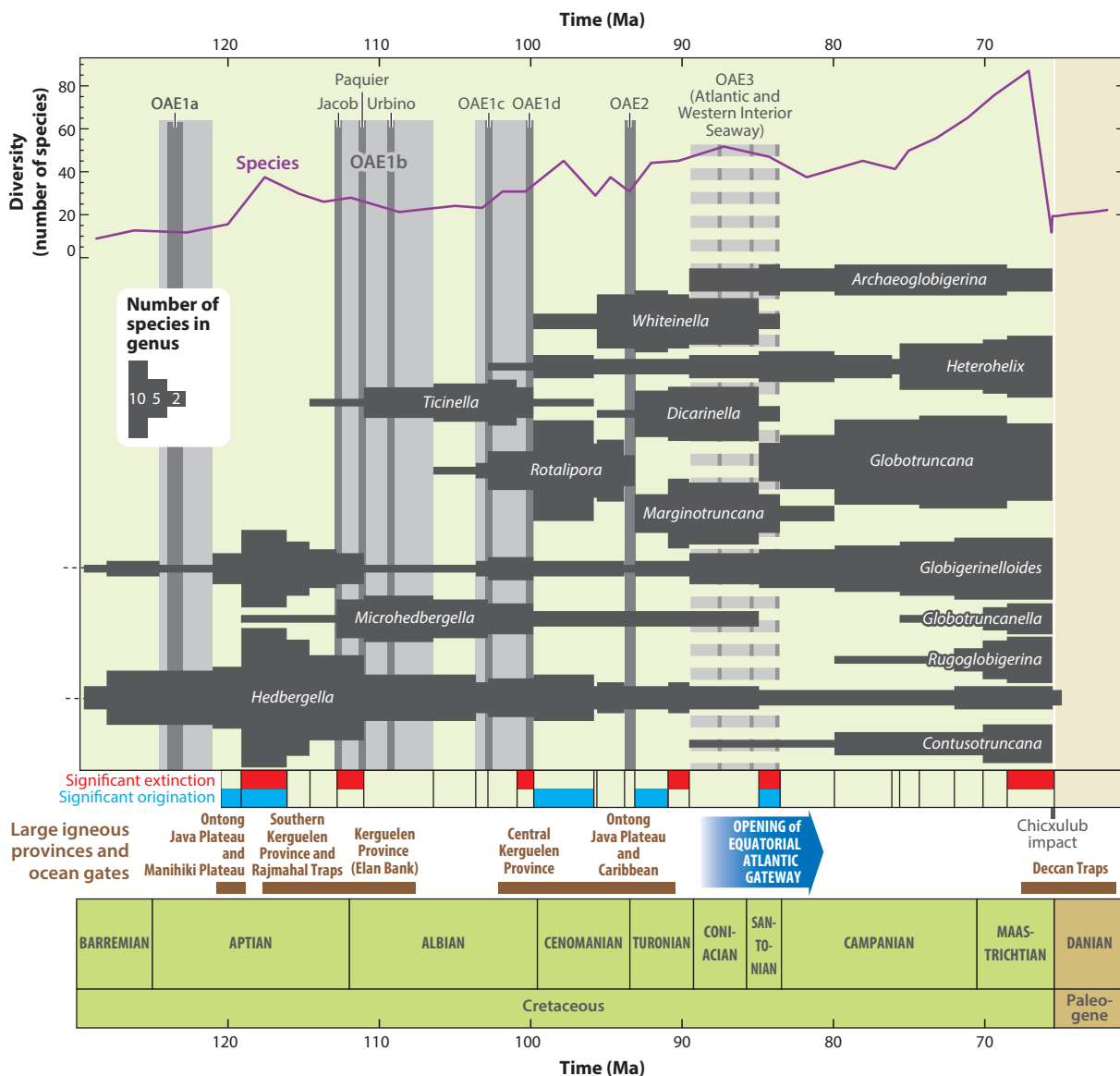
#### 4.1. Cretaceous

Planktic foraminifera increase in global abundance during the Cretaceous, ultimately becoming a major source of deep-sea carbonate sediment by the Late Cretaceous (Premoli Silva & Sliter 1999). This Cretaceous increase in abundance and the associated taxonomic radiation occur at a time when the configuration of the ocean basins was undergoing major reorganization (e.g., Berggren & Hollister 1974, Poulsen et al. 2001), and when numerous large igneous provinces (LIPs) were being formed on the ocean floor (Larson 1991). During this time, elevated concentrations of atmospheric CO<sub>2</sub> are thought to have sustained a long-term greenhouse climate, with minimal or absent polar ice sheets (Caldeira & Rampino 1991, Freeman & Hays 1992, Berner 1994, Barron et al. 1995). Tectonic and climatic factors resulted in the formation of vast shallow epicontinental seaways (Haq et al. 1987, Kauffman & Caldwell 1993, Miller et al. 2005). In extreme cases, physical factors, perhaps operating in conjunction with biological productivity, conspired to induce oceanic anoxic events (OAEs), which are prominently recorded by widespread carbonaceous shale deposits and pronounced fluctuations in sedimentary stable carbon isotope ( $\delta^{13}\text{C}$ ) records (e.g., Schlanger & Jenkyns 1976, Jenkyns 1980, Scholle & Arthur 1980).

The Cretaceous radiation of planktic foraminifera is not a monotonic rise in diversity, and previous studies have divided the Cretaceous radiation into successive faunal associations (Bandy 1967, Premoli Silva & Sliter 1999). These associations partition the Cretaceous radiation into four primary diversifications: the late Aptian, late Albian–early Cenomanian, Turonian–Santonian, and Campanian–Maastrichtian (**Figure 2a**). In general, each of these is coincident with long-term variations seen in global compilations of benthic foraminiferal stable isotope records, corroborating the view that secular variation in the ocean-climate system strongly influenced planktic foraminiferal macroevolution (Friedrich et al. 2012). Most conceptual models devised to explain these diversifications, and intervening extinctions, have invoked changes in oceanic thermal stratification and pelagic trophic structure (e.g., Hart 1980, Caron & Homewood 1982). Premoli Silva & Sliter (1999) described how each diversification was interrupted by pulses of extinction and/or faunal turnover associated with major oceanographic changes, many of which coincided with OAEs. Many of these previously recognized events register as significant increases in both origination ( $\hat{p}$ ) and extinction ( $\hat{q}$ ) rates in this study.

The first statistically significant event in our analysis is an increase in  $\hat{p}$  during the *Globigerinelloides ferreolensis* Zone of the late Aptian (**Figure 2b**). This origination pulse is followed by a significant turnover event (**Figure 2b,c**) during the *Hedbergella trocoidea* Zone that results in an

overall increase in diversity (Figure 2a). The late Aptian diversification is largely confined to the genera *Hedbergella* and *Globigerinelloides* (Figure 3). The hedbergellids are thought to have been eurytopic opportunists with varied depth habitats and an affinity for eutrophic conditions (Norris & Wilson 1998, Premoli Silva & Sliter 1999, Friedrich et al. 2008), whereas stable isotope data suggest that the globigerinelloidids occupied the deeper parts of the mixed layer (Petrizzo et al.



**Figure 3**

Cretaceous species diversity (purple line) and spindle diagrams for select genera. The height of each spindle scales to the number of species in that genus per time interval. Vertical dark gray bars delimit the timing of oceanic anoxic events (OAEs) that occurred within time intervals highlighted by lighter gray vertical bars. Intervals with significant origination (light blue) and extinction (red) are indicated by rectangles along the abscissa. Important tectonic and paleoceanographic events are noted along the Cretaceous timescale.

2008). The prevailing view is that the development of a strongly stratified surface ocean and the expansion of oligotrophic conditions drove the late Aptian diversification (Leckie 1989, Premoli Silva & Sliter 1999). According to this model, a thermally stratified water column increased the vertical partitioning of plankton populations and fostered the evolution of stenotopic species with narrowly defined depth ecologies.

The late Aptian diversification is short lived. Diversity drops across the Aptian–Albian boundary due to a large increase in extinction rate (**Figure 2c**). This extinction event marks an important turning point in the history of planktic foraminifera in which many large, heavily calcified species are replaced by depauperate faunas consisting of diminutive *Microhedbergella* species (Leckie 1989, Premoli Silva & Sliter 1999, Huber & Leckie 2011). The coincidence of the end-Aptian extinction with OAE1b suggests a causal relationship (Bréhéret 1994). OAE1b involved multiple episodes of organic carbon burial, much of which centered on strata referred to as the Niveau Paquier and Niveau Killian (~112–113 Ma) in the Tethyan and North Atlantic regions (Arthur et al. 1990, Erba 1994, Kennedy et al. 2000). Thus, the spread of dysaerobic-to-anaerobic conditions and the expansion of the oxygen minimum zone (OMZ) are thought to have played a role in this extinction (Bréhéret et al. 1986, Erbacher et al. 1999, Premoli Silva & Sliter 1999). The prevalence of eurytopic microhedbergellids following the end-Aptian has been cited as evidence for eutrophic conditions due to increased ocean overturning during OAE1b (Leckie 1989, Premoli Silva & Sliter 1999). However, multispecies foraminiferal stable isotope records from the northwestern Atlantic seemingly contradict this hypothesis by suggesting that surface-ocean stratification impeded ocean overturning and enhanced organic carbon preservation in tectonically isolated basins throughout the North Atlantic Ocean (Erbacher et al. 2001, Huber et al. 2011).

The limited areal extent of the carbonaceous shales belies the global scope of OAE1b; many deep-sea sections spanning the Aptian–Albian boundary are truncated by a hiatus caused by intense and widespread carbonate dissolution (Bréhéret et al. 1986, Premoli Silva et al. 1989, Huber & Leckie 2011). Potential forcing mechanisms for this change in deep-sea carbonate sedimentation are increased volcanogenic CO<sub>2</sub> emissions sourced by the emplacement of the Kerguelen Plateau LIP (Leckie et al. 2002) and/or a change in ocean circulation patterns. The relatively low values registered by marine strontium isotope (<sup>87</sup>Sr/<sup>86</sup>Sr) records across the Aptian–Albian boundary are evidence for LIP volcanism and increased rates of oceanic crust production (Bralower et al. 1997, Jones & Jenkyns 2001). Moreover, the decrease in planktic foraminiferal test sizes suggests that CO<sub>2</sub>-induced ocean acidification may have inhibited biocalcification (Leckie et al. 2002). However, evidence for rapid carbon input, such as an abrupt decrease in δ<sup>13</sup>C, has not been found. In general, the δ<sup>13</sup>C of inorganic and organic carbon decreases across OAE1b (Weissert et al. 1998, Bralower et al. 1999, Gröcke et al. 1999), but the timing and magnitude of this isotopic shift remain unclear due to the widespread stratigraphic break at the Aptian–Albian boundary (Gröcke et al. 1999, Kennedy et al. 2000, Huber et al. 2011). Because the hiatus and extinctions are roughly synchronous, one could assume that a decline in diversity was caused by poor preservation; however, the sweeping changes to pelagic sedimentation and irrevocable faunal changes imposed by the end-Aptian extinction are also consistent with a common-cause extinction mechanism, whereby patterns of sedimentation and biological turnover are both caused by environmental perturbations (Peters 2005, Hannisdal & Peters 2011, Peters et al. 2013).

The diversification that occurs through the Albian and Cenomanian stages is punctuated by significant extinction during the *Rotalipora appenninica* Zone (**Figure 2c**) and is followed by significant origination during the *Rotalipora globotruncanoides* Zone (**Figure 2b**). This end-Albian event has been recognized by earlier studies, and it is associated with cyclic black-shale deposition culminating in OAE1d (also known as Breistrofer) within the Tethys and North Atlantic regions (Premoli Silva & Sliter 1999, Nederbragt et al. 2001, Leckie et al. 2002). OAE1d is considered

to have been a global perturbation because carbonaceous sediments and a positive  $\delta^{13}\text{C}$  excursion occur at the Albian–Cenomanian boundary in many marine records globally (Wilson & Norris 2001, Jarvis et al. 2006). The end-Albian turnover that occurred within the radiolarians (Erbacher & Thurnow 1997) further attests to the global extent of OAE1d.

Study of deep-sea records straddling OAE1d has revealed that this was a period of sequential first and last occurrences (Petrizzo et al. 2008). The balance of extinctions and originations resulted in a substantial change in taxonomic composition (i.e., turnover), with species diversity subsequently increasing during the Cenomanian (**Figure 2a**). Key elements of this turnover are the first appearances of three genera (*Praeglobotruncana*, *Paracostellagerina*, and *Planomalina*) (**Figure 3**) and the last occurrences of two long-ranging genera (*Ticinella* and *Biticinella*), as well as the extinction of the short-lived genus *Planomalina* near the end of OAE1d (Petrizzo et al. 2008). The depth habitats of these genera, as inferred from their stable isotope signatures, indicate that mixed-layer-dwelling species were most strongly affected (Petrizzo et al. 2008). Further, multispecies stable oxygen and carbon isotope records through OAE1d indicate that black shale deposition coincided with a marked warming of intermediate (mid-bathyal) waters and a collapse in surface-ocean thermal stratification in the northwestern Atlantic (Wilson & Norris 2001). Thus, this event is thought to reflect a transient shift toward more eutrophic conditions, possibly due to increased vertical mixing within a weakly stratified surface ocean (Wilson & Norris 2001, Petrizzo et al. 2008).

The extinction of *Rotalipora* and *Thalmaninella* during the onset of OAE2 in the latest Cenomanian (Wonders 1980, Leckie 1985, Caron et al. 2006) sets the stage for a period of rapid turnover and increasing diversity during the Turonian stage (**Figure 2a**). This is reflected by a significant origination rate in the aftermath of OAE2 (*Helvetoglobotruncana helvetica* Zone) followed by a significant extinction rate during the ensuing *Marginotruncana sigali* Zone (**Figure 2b**). Over the course of the Turonian, faunas dominated by large whiteinellids are succeeded by diverse assemblages consisting of hedbergellids, biserial heterohelicids, and a variety of keeled genera such as the dicarinellids, praeglobotruncanids, and marginotruncanids (Bandy 1967, Premoli Silva & Sliter 1999). This faunal shift also entails the early evolution of biserial genera with flattened tests (*Lae-vibetorobelix*) and supplementary apertures (*Pseudoguembelina*) (Nederbragt 1991). Clavate genera (*Clavibedbergella*, *Hastigerinella*, and *Shackoina*) with ecological affinities for OMZ conditions are also common in Turonian faunas (Coxall et al. 2007, Friedrich et al. 2008).

This episode of macroevolutionary change corresponds to a sea-level highstand (Kauffman 1985, Huber et al. 1999) during the height of the mid-Cretaceous thermal maximum (Clarke & Jenkyns 1999, Friedrich et al. 2012), when extremely warm tropical surface-ocean (32–36°C) and deep-ocean (~20°C) temperatures prevailed (Wilson et al. 2002, Friedrich et al. 2012). Extreme polar warmth (30–32°C) during the late Turonian is also indicated by planktic foraminiferal  $\delta^{18}\text{O}$  records from the Southern Ocean (Bice et al. 2003). The hothouse conditions of the Turonian are believed to have fostered the reestablishment of a thermally stratified surface ocean and the suppression and/or contraction of the OMZ (Premoli Silva & Sliter 1999), which reopened deeper habitats that had been previously occupied by *Rotalipora* and *Thalmaninella* during the late Albian and Cenomanian (Leckie 1985, Jarvis et al. 1988).

The Santonian has long been recognized as a period of wholesale taxonomic turnover that affected all trophic groups within the planktic foraminifera (Wonders 1980). Significant increases in both origination and extinction rates within the *Dicarinella asymetrica* Zone support this view (**Figure 2b,c**). This turnover entailed the extinction of many planktic taxa (whiteinellids, dicarinellids, and marginotruncanids) at the close of the Santonian, and diversification of the genera *Globotruncana*, *Globotruncanita*, and *Contusotruncana* during the early Campanian (**Figure 3**).

Species-specific stable isotope data suggest that the depth ecologies of many keeled taxa may have changed during the Santonian turnover. For instance, most species of the double-keeled genus

*Globotruncana* register stable isotope values indicative of deep-water ecologies (e.g., Douglas & Savin 1978), yet the species *Globotruncana bulloides* consistently yields a stable isotope signal (low  $\delta^{18}\text{O}$ , high  $\delta^{13}\text{C}$ ) reflective of a shallow-water habitat in Campanian sections from Tanzania (Falzoni et al. 2013). Moreover, the same study (Falzoni et al. 2013) reported stable isotope values for Santonian marginotruncanids consistent with a shallow-water habitat, whereas the  $\delta^{18}\text{O}$  of Turonian marginotruncanids is more consistent with calcification in colder, deep waters (Huber et al. 1999).

Relating this turnover to ocean-climate change via traditional means has been hampered by a widespread stratigraphic hiatus at the Santonian–Campanian boundary (Norris et al. 2001); however, this extensive unconformity also signals a major reorganization of deep-ocean circulation was likely a driver of the evolution of planktic foraminifera (Ando et al. 2013). Neodymium isotopic records support an ocean circulation change by suggesting that the Southern Ocean became a focus of deep-water formation (Robinson et al. 2010). Additional evidence for ocean-climate change is derived from a benthic foraminiferal  $\delta^{18}\text{O}$  record suggesting abrupt cooling of deep-sea temperatures by as much as  $\sim 5\text{--}6^\circ\text{C}$  across the Santonian–Campanian boundary (Ando et al. 2013).

The timing of the Santonian turnover is roughly correlative with the termination of OAE3, which is generally considered to be the last of the major OAEs (Jenkyns 1980). OAE3 was a protracted event (Coniacian–Santonian) that involved the deposition of numerous, localized black shales throughout the tropical Atlantic Ocean and adjacent basins (Wagreich 2012). The termination of OAE3 during the early Campanian has been attributed to increased exchange and ventilation of deep-water masses via the progressive opening of the equatorial gateway between the North and South Atlantic Ocean basins (Friedrich et al. 2012). Thus, it has been postulated that the Santonian turnover within the planktic foraminifera may reflect tectonically forced changes in ocean circulation (Premoli Silva & Sliter 1999).

The most pronounced increase in Cretaceous diversity occurs during the Campanian and Maastrichtian stages (**Figure 2a**), but this diversification is driven by a decrease in extinction rate, not an increase in origination rate (**Figure 2c**). The latest Cretaceous diversity increase unfolds at a time when atmospheric  $\text{CO}_2$  was declining (Berner 1994) and global climate was cooling (Barerra & Savin 1999, Cramer et al. 2009). Thus, the oceans are thought to have become more modern-like by the Maastrichtian, which possibly led to more oligotrophic conditions in the tropics (Premoli Silva & Sliter 1999). A few genera, most notably those with serial tests (*Racemiguembelina* and *Pseudoguembelina*), evolved a symbiotic relation with photosynthetic autotrophs at this time (D'Hondt & Zachos 1998, Houston et al. 1999), a strategy that is particularly advantageous in nutrient-depleted waters (Hemleben et al. 1989). A survey of the stable isotopic compositions of Late Cretaceous taxa indicates that photosymbiosis did not evolve until the Campanian or Maastrichtian (Bornemann & Norris 2007); hence, this adaptive strategy for coping with oligotrophic conditions likely played a role, albeit a minor one, in promoting a latest-Cretaceous increase in diversity.

## 4.2. The Cretaceous–Paleogene Boundary and Danian Recovery

The end-Cretaceous extinction devastates planktic foraminifera (**Figure 2a**), with  $\sim 95\%$  of all species becoming extinct (**Table 1**). Because of the longer-than-average duration of the final Cretaceous zone ( $\sim 3$  Myr), the percent kill estimate does include species that probably went extinct before the actual boundary event. Nonetheless, it is clear that the K–Pg is the most important extinction in the entire history of the group (Arenillas et al. 2000). The dramatic, geologically instantaneous nature of this crisis is well explained by an asteroid impact (Alvarez et al. 1980,

Schulte et al. 2010). The short impact winter from aerosols and ejecta (Vellekoop et al. 2014), followed by warming induced by vaporized carbonates and sulfate aerosols (Kring 2007), is witnessed by a global drop in organic matter flux and carbonate sedimentation (D'Hondt 2005). Many of these effects lasted on the order of hundreds of years (Kring 2007), whereas patterns of deep-sea carbonate sedimentation may have been perturbed for up to 4 Myr (D'Hondt 2005).

Only five species in our compilation cross the K–Pg boundary, but the Danian Zones P0 and P $\alpha$  see a rapid recovery in planktic foraminifera. Diminutive taxa with microperforate wall textures are the most diverse group in the earliest Danian (e.g., Olsson et al. 1992, Hull et al. 2011), and the discovery that some modern microperforate species are both planktic and benthic (tychopelagic) suggests that this versatile lifestyle may have been key to survival during the K–Pg impact event (Darling et al. 2009). Several properties of the microperforate genus *Zeauvigerina* suggest a tychopelagic lifestyle during the Danian (Leckie 2009); however, isotopic evidence for mode of life is equivocal for this genus during the Danian, though later zeauvigerinid species are clearly planktic (D'Haenens et al. 2012). Danian faunas dominated by tiny microperforate taxa are succeeded by early photosymbiotic *Praemurica* species starting at ~63.5 Ma (Birch et al. 2012), though this succession appears not to have been globally synchronous (Hull et al. 2011). The rather rapid reestablishment of photosymbiosis in the aftermath of the end-Cretaceous mass extinction is intriguing given that it took nearly 90 Myr for this ecological strategy to first evolve during the Cretaceous. The short-lived dominance of the diminutive microperforates exemplifies the fast turnover within the Paleocene (Table 1).

### 4.3. Cenozoic

The Cenozoic witnesses both the Paleogene and the Neogene radiations, which are separated by a diversity decline during the Oligocene (Figure 2a). Although the Paleogene and the Neogene have broadly similar patterns of diversity, there are substantial differences in rates of origination and extinction (Collins 1989). Perhaps most obvious is the greater number of statistically significant rate excursions during the Paleogene (eleven) compared with the Neogene (one). The traditional explanation for this pattern is that rapid speciation directly after the bolide impact was promoted by the recolonization of niches vacated during the K–Pg extinction (Smit 1982). It is also possible that anagenesis and corresponding artificial extinction caused by nomenclatural change contributed to the increase in origination rate during the Paleocene (e.g., Pearson 1993), but this would not account for the overall increase in diversity observed during the Paleocene. It is therefore likely that anagenesis, and the artificial taxonomic nomenclatural changes it promotes, does contribute to some of the observed taxonomic turnover documented here, but this nomenclatural artifact must affect both extinction and origination equally and cannot be the sole cause of high rates of origination observed during Zones P0, P $\alpha$ , and P5.

The reestablishment of photosymbiosis in the aftermath of the K–Pg mass extinction, particularly during Subzone P3a, may have also promoted diversification. Photosymbionts are important in several Paleogene genera, including *Acarinina*, *Morozovella*, and *Igorina* (D'Hondt et al. 1994, Kelly et al. 1996a, Norris 1996), and the first evidence for photosymbiosis during the Cenozoic can be placed at ~63.5 Ma within *Praemurica* (Birch et al. 2012). Ezard et al. (2011) explicitly included photosymbiosis in their analysis of Cenozoic planktic foraminifera macroevolutionary dynamics and found that ecology (including photosymbiosis) is the strongest sole predictor of clade growth, although the inclusion of climate, standing diversity, and other ecology-related factors results in the best explanatory models.

Both origination and extinction rates increase significantly in Zone P5 (Figure 2b,c), which coincides with the Paleocene–Eocene Thermal Maximum (PETM), the most rapid and extreme



perturbation to the Earth system after the end-Cretaceous. Foraminiferal stable isotope and minor elemental ratio (Mg/Ca) records show that deep-ocean temperatures rapidly increased by  $\sim 5^{\circ}\text{C}$  (Zachos et al. 2001), with sea-surface temperatures increasing at low and high latitudes by  $\sim 5^{\circ}\text{C}$  and  $\sim 8^{\circ}\text{C}$ , respectively (Kennett & Stott 1991, Zachos et al. 2003). Hallmarks of the PETM are a negative  $\delta^{13}\text{C}$  excursion, widespread carbonate dissolution, and a major benthic foraminiferal mass extinction (Dickens et al. 1995, Zachos et al. 2005, Thomas 2007). Together, these lines of evidence signal massive carbon input into the ocean-atmosphere system with resultant ocean acidification (Dickens et al. 1997, Zeebe et al. 2009).

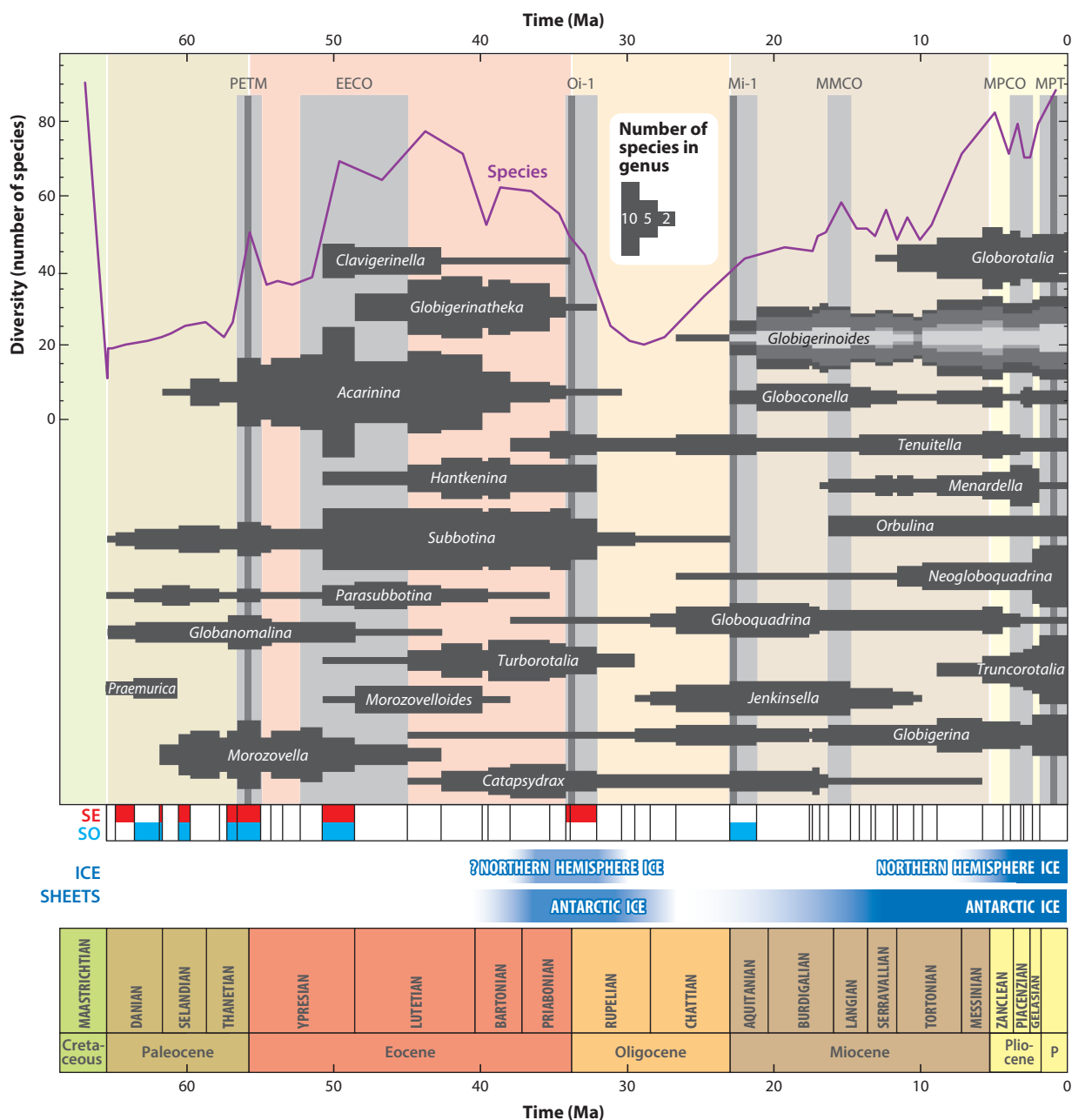
Unlike the mass extinction event suffered by benthic foraminifera, tropical planktics respond to PETM conditions through a rapid diversification among mixed-layer-dwelling taxa (morozovellids, acarininids) and a temporary collapse of populations of the thermocline-dwelling genus *Subbotina* (Kelly et al. 1996b). An interesting aspect of the short-lived morphospecies restricted to the PETM interval (i.e., excursion taxa) is weak calcification of their tests. For instance, the transition from heavily calcified *Morozovella velascoensis* into the transitory excursion form *Morozovella allisonensis* during the early stages of the PETM, when carbonate undersaturation was most severe, is followed by the reappearance of the heavily calcified *M. velascoensis* morphotype as PETM conditions waned (Kelly et al. 1996b). This pattern of morphological variation is consistent with the view that ocean acidification inhibited biocalcification during the PETM. High-latitude planktic faunas were also affected by PETM conditions. In the Weddell Sea region, the PETM interval is marked by a brief incursion of warm-water morozovellids and a turnover in the taxonomic composition of acarininids (Kelly 2002).

A significant increase in both extinction ( $\hat{q}$ ) and origination ( $\hat{p}$ ) occurs at the end of the early Eocene during Zone P9 (**Figure 2b,c**; **Table 1**). This increase in macroevolutionary rates takes place after the flurry of evolutionary activity within the Paleocene, and is unlikely to be directly related to recovery from mass extinction. Excess origination over extinction gives rise to one of the largest single increases in species diversity in the record (**Figure 2a**), and several genera undergo notable changes during this time. For example, *Acarinina* experiences a large species-level turnover, the number of species within *Subbotina* roughly doubles, and *Hantkenina* makes its debut (**Figure 4**). This interval is directly after the Early Eocene Climate Optimum (EECO) and begins the protracted downturn to the icehouse of the Oligocene, a long-term cooling that well accounts for the observed increase in the number of species in the cooler-water genus *Subbotina*. *Claviger-inella* and *Hantkenina* likely lived within the OMZ below high productivity zones in equatorial and coastal waters (Coxall et al. 2007).

The second radiation ends during the mid-Eocene, with diversity reaching approximately 80 species, slightly lower than the preceding Maastrichtian peak. This diversity peak, reproduced by other workers (e.g., Tappan & Loeblich 1988, Ezard et al. 2011), is not observed on sampling-corrected diversity curves (Lloyd et al. 2012, Cermeño et al. 2013). For example, the sampling-standardized diversity curve generated by Lloyd et al. (2012) is broadly similar to that presented here, but the peak Cretaceous diversity documented here (**Figure 2a**) is actually higher than that in the Eocene or Pliocene. By contrast, the diversity curve generated by Cermeño et al. (2013) is strikingly different, with 30 fewer species in the Eocene and a nadir at the E–O boundary rather than in the mid-Oligocene. This discrepancy is puzzling. Sampling standardization via shareholder quorum subsampling (Alroy 2010) generates comparable Cretaceous diversity trends, but at the same time dramatically reduces Cenozoic changes in diversity. Simpler rarefaction-type analysis yields curves that are comparable to raw diversity curves, though only when ignoring the Paleogene. If, however, the record of planktic foraminiferal diversity has not been strongly biased by variability in sampling, as we argue above, then there must be something unique to the Paleogene that explains these differences. One factor could be an increase in global provinciality,

which would affect the underlying heterogeneity of the target population being sampled and therefore the total number of sampling locations that are required to capture all foraminiferal species.

Species diversity drops during the late mid-Eocene (~40 Ma), probably due to extinctions among several mixed-layer taxa (**Figure 2a**), most notably the gradual decline of acarininids and extinction of the genus *Morozovelloides* (Sexton et al. 2006). Following this diversity decline, several



major groups of planktic foraminifera suffer extinction across the E–O boundary, an event that is registered in morphospecies-based compilations as well as reconstructed phylogenies (e.g., Aze et al. 2011, Ezard et al. 2011). Though extinction rates are significantly positive in both Zones P17 and P18 (**Figure 2c**), the downturn in diversity is more sustained, with a loss in species from ~40 until ~30 Ma. This event and its decrease in diversity are amplified by the effect of low origination rates (**Figure 2b**). Thus, it is perhaps more accurate to refer to this as both an extinction event and a prolonged interval of loss by attrition (e.g., Bambach 2006).

The late Eocene to early Oligocene was an interval of gradual climate change that culminated in the initiation of episodic Northern Hemisphere glaciation (Eldrett et al. 2007) and a major expansion of Antarctic ice sheets, as signaled by a prominent increase in foraminiferal  $\delta^{18}\text{O}$  records, referred to as the Oi-1 event (Miller et al. 1987). The Oi-1 event represents a shift from the Eocene greenhouse to the Oligocene icehouse (see Coxall & Pearson 2007 for a review), which was likely triggered by a lowering of atmospheric  $p\text{CO}_2$  levels (DeConto et al. 2008). It follows that decreased origination rates may be connected to a longer climate trend, whereas the increase in extinction is connected to the Oi-1 event. This can be seen in the differential survival of the genera *Hantkenina* and *Subbotina* (**Figure 4**). All species within *Hantkenina* undergo a near-synchronous extinction (Wade & Pearson 2008), whereas *Subbotina* species are gradually lost over ~5 Myr. This difference may have emerged due to the ecologies of these two taxa; the genus *Subbotina* had an affinity for cool thermocline waters (Boersma et al. 1987), whereas the genus *Hantkenina* likely inhabited OMZs associated with high productivity zones (Coxall et al. 2007, Wade & Pearson 2008).

The Oi-1 event reflects a period of dramatic environmental change that entailed a major sea-level fall (Katz et al. 2008), deepening of the calcite compensation depth (Coxall et al. 2005), and expansion of the Antarctic ice sheet (Zachos et al. 2001). The longer cooling trend has been linked to a major reorganization in oceanic circulation, which altered the paleobiogeographic ranges of plankton (Haq et al. 1977). The steepening of latitudinal temperature gradients during this climatic transformation likely enhanced ocean overturning, which would have reduced ocean stratification and the number of depth niches available to planktic species (Cifelli 1969, Boersma & Premoli Silva 1986). Alternatively, it is possible that Oligocene diversity is underestimated in our compilation because no synoptic atlases for this epoch currently exist. That said, we note that the Oligocene is a low point in other published diversity curves (e.g., Tappan & Loeblich 1988), and that the downturn in origination rate starts prior to the Oligocene and is therefore reflected by synoptic atlases compiled for the Eocene (Pearson et al. 2006).

Origination rates steadily increase over the late Oligocene and earliest Miocene, but only Zone N4, just after the Oligocene–Miocene boundary, has an origination rate above the confidence bounds (**Figure 2b**); extinction remains low throughout this interval (**Figure 2c**). A prominent increase in foraminiferal  $\delta^{18}\text{O}$  records (Mi-1 event), signaling a short-lived but appreciable expansion of Antarctic ice sheets and abrupt cooling, occurs near the beginning of Zone N4 (Zachos

#### Figure 4

Cenozoic summary. Cenozoic species diversity (*purple line*) and spindle diagrams for select genera. The height of each spindle scales to the number of species in that genus per time interval. Vertical dark gray bars delimit the timing of various climatological and oceanographic events that occurred within time intervals highlighted by lighter gray vertical bars. Intervals with significant origination (*light blue*) and extinction (*red*) are indicated by rectangles along the abscissa. Persistent polar ice is noted along the top of the Cenozoic timescale. Abbreviations: EECO, Early Eocene Climate Optimum; MMCO, Mid-Miocene Climate Optimum; MPCO, Mid-Pliocene Climate Optimum; MPT, Mid-Pleistocene Transition; Oi-1, early Oligocene oxygen isotope event 1; P, Pleistocene; PETM, Paleocene–Eocene Thermal Maximum; SE, significant extinction; SO, significant origination. The Oi-1 and the MPCO have been expanded to include multiple zones because of their coincidence at, or near, boundaries between successive biozones.

et al. 2001, Billups & Schrag 2002). This glaciation was associated with an orbital configuration and  $p\text{CO}_2$  levels similar to those of the antecedent Oi-1 event (Pagani et al. 1999, Liebrand et al. 2011). Zone N4 is also coincident with a major turnover in radiolarians (Kamikuri et al. 2005) and regional extinctions in coral (Budd 2000). Spatial patterns of deep-sea sedimentation in the Pacific Ocean basin reportedly change during Zone N4 (Keller & Barron 1983). This shift in deep-sea sedimentation entails a decline in carbonate mass accumulation rates (Lyle 2003), though a similar decrease in carbonate sedimentation is not evident in a more recent compilation for the equatorial Pacific region (Pälike et al. 2012).

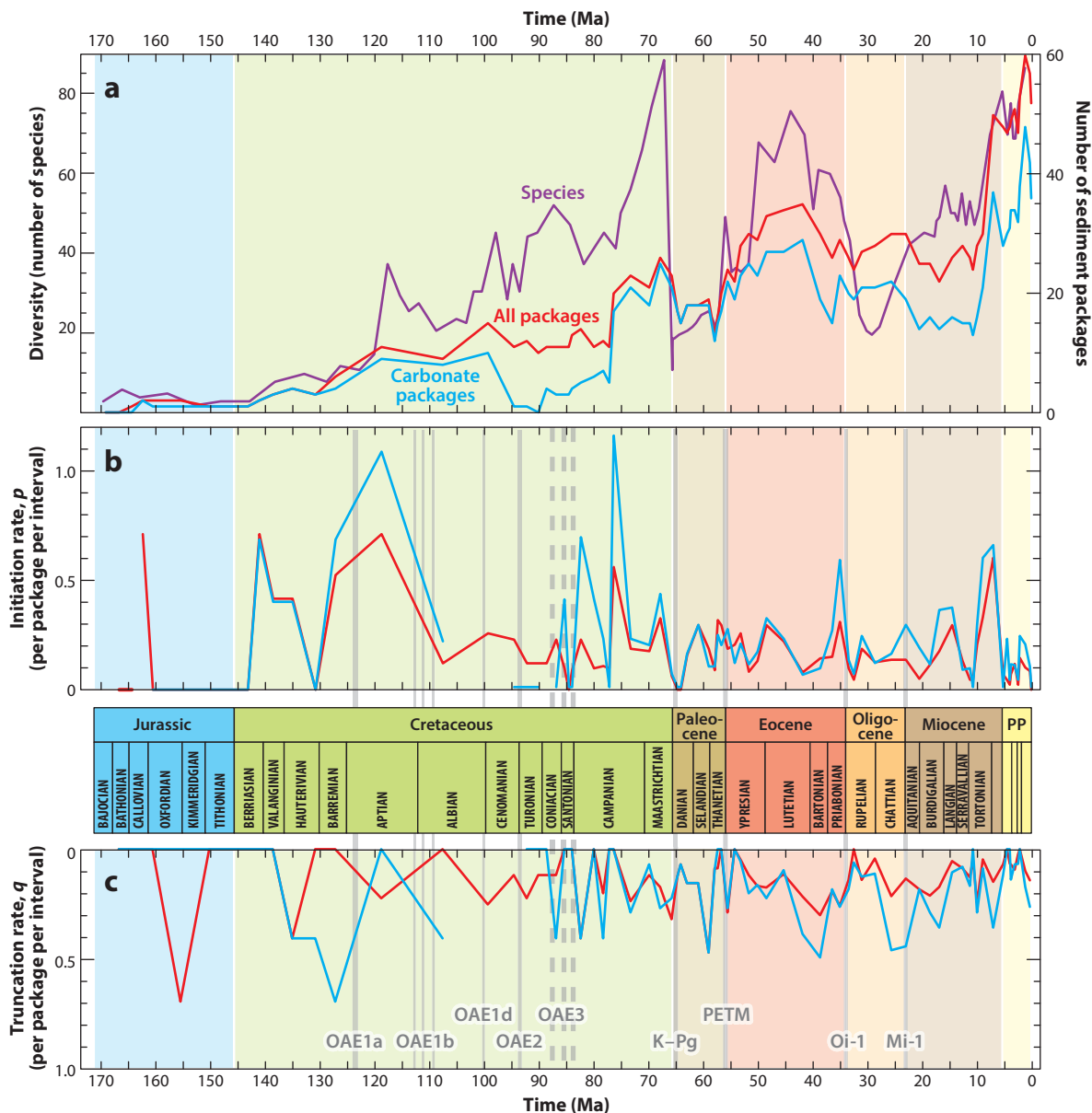
The planktic foraminifera undergo substantial evolutionary change over the course of the Neogene, but none of the time intervals postdating Zone N4 register significantly high rates. Studies have indicated notable macroevolutionary activity near the Pliocene–Pleistocene boundary (e.g., Berggren 1969, Wei & Kennett 1986, Stanley et al. 1988), roughly synchronous with substantial fluctuations in ostracode diversity driven by changes in ocean circulation and ice-sheet dynamics (Benson et al. 1984). Similar ocean–climate forcings have been invoked as driving macroevolutionary rate increases among Plio–Pleistocene planktic foraminifera (Wei & Kennett 1986). Our curves for species origination and extinction rates reflect this change, but the values do not exceed the upper bound of the confidence intervals produced by species range randomization. One possible explanation for this is that the transitions are detectable primarily through their more qualitative effects on fossil assemblages. Another possibility is that the Neogene radiation occurs in the context of the diversification of many major lineages, and macroevolutionary rates during the latest Neogene may therefore be held in check by a type of diversity dependency (Ezard et al. 2011).

#### 4.4. Relationship to Macrostratigraphic Quantities

It has long been recognized that many of the same environmental factors that can cause perturbations to the evolution of planktic foraminifera also likely affect the spatial and temporal distribution of deep-sea sedimentation, either by shifting the position of the calcite compensation depth; by rerouting, slowing, or intensifying ocean currents; or by affecting the location and quantity of biogenic sediment production (e.g., van Andel 1975, Moore et al. 1978, Keller et al. 1987). Thus, there are a priori reasons to expect that patterns of sedimentation and macroevolutionary patterns of planktic foraminifera should exhibit some amount of covariation. That is, there may be a common cause that exerts a complex but consistent control on both the stratigraphic record and true biological turnover (Peters 2005, 2008).

Macrostratigraphy is an analytical approach to quantifying spatial and temporal patterns of sedimentation that is sensitive to both the total areal extent of sediment and, more importantly, the spatially integrated temporal continuity thereof (Peters 2006). Hiatuses therefore serve a critical role in macrostratigraphy by defining sediment package boundaries at each geographic sampling location. Expansions in hiatuses cause widespread truncations in sedimentation (i.e., increases in package truncation rates), and geographic contractions in the extent of hiatuses are caused by widespread initiation of sedimentation (i.e., increases in package initiation rates). Tabulations of the times of initiation and truncation of sediment packages for multiple geographic locations arrayed across a target region constitute the fundamental data of macrostratigraphy. The same survivorship-based turnover rates and diversity metrics used in macroevolutionary analyses (Foote 2000) can then be used to characterize the quantity and temporal persistence of sedimentation.

The macrostratigraphic record in the Atlantic Ocean basin is summarized in **Figure 5**. Rates of package initiation and truncation (**Figure 5b,c**) are poorly constrained in the Jurassic and Early Cretaceous due to the small number of available offshore drilling sites that penetrate rocks of that



**Figure 5**

Macrostratigraphic results derived from 73 offshore drilling sites in the Atlantic Ocean basin. (a) Total number of sediment packages (red line) and carbonate-rich packages (light blue line; includes pure carbonate sediments, such as chalk, and siliceous and siliciclastic sediments that are calcareous). Species-level diversity from **Figure 2a** (purple line) is shown for comparison. (b) Rates of package initiation,  $p$ . (c) Rates of package truncation,  $q$ . All rates are calculated using the same survivorship-based rate metrics used for calculating rates of species turnover. Note that data are plotted at the midpoints of calcareous nannoplankton zones. Abbreviations: K-Pg, Cretaceous–Paleogene boundary; Mi-1, early Miocene oxygen isotope event 1; OAE, oceanic anoxic event; Oi-1, early Oligocene oxygen isotope event 1; PETM, Paleocene–Eocene Thermal Maximum; PP, Plio-Pleistocene.

age. This is not a sampling artifact, but it instead reflects the fact that the Atlantic only began opening in the latest Triassic or Jurassic and remained very narrow throughout this interval. From the Campanian onward, rates are reasonably well constrained and many of the fluctuations observed correspond to events discussed in Sections 4.2 and 4.3. The notable exception is the K–Pg event. Although there are some sediment packages that truncate in the latest Cretaceous, resulting in a very small positive excursion in truncation rate (**Figure 5c**), many more packages do not. Thus, the end-Cretaceous does not appear unusual from the perspective of macrostratigraphy. This is perhaps not unexpected given the anomalous nature of the K–Pg event and the nature of the environmental changes caused by bolide impact. Most other internally driven changes in environment, such as the Eocene–Oligocene global cooling, do correspond to macrostratigraphic rate changes. Some macrostratigraphic rate excursions are also observed that are not discussed above, but these generally correspond to noted changes in ocean circulation. The most notable of these is the late Miocene shift toward more modern-like patterns of thermohaline circulation through the gradual rerouting and/or increased production of proto–North Atlantic Deep Water (Thomas & Via 2007), which resulted in a large increase in package initiation in the Atlantic.

A recent analysis (Peters et al. 2013) compared the macrostratigraphic data in **Figure 5** to the macroevolutionary history of planktic foraminifera (**Figure 2**) and demonstrated that there are quantitative similarities that transcend the expectations of sampling bias. However, that analysis focused only on comparisons between analogous turnover quantities (i.e., species extinction rates were compared only with sediment package truncation rates and species origination rates were compared only with sediment initiation rates). Here, we expand on this analysis and include all pairwise comparisons between macroevolutionary and macrostratigraphic quantities. We also separate the sedimentary data into all sediments and carbonate-rich sediments only, for the purpose of calculating macrostratigraphic rates (**Figure 5**; **Table 2**).

Our expanded comparison of macrostratigraphic and macroevolutionary results suggests that previous work, which has only compared quantitatively identical rate terms (e.g., extinction to truncation), may mask underlying relationships between macrostratigraphy and macroevolutionary patterns. For example, species-level origination is more strongly correlated with the total number of sediment packages than it is with the analogous macrostratigraphic quantity of package initiation, but the same is not true for extinction (**Table 2**). Indeed, the discrepancy between the strength of the extinction-truncation correlation and the strength of the origination-initiation correlation is reduced when origination is compared with all macrostratigraphic quantities, not just package initiation (**Table 2**). Thus, it is possible that rates of taxonomic origination are also

**Table 2** Correlations between macrostratigraphic and species-level macroevolutionary quantities

|                          |            | Extinction   |                | Origination  |               | Diversity    |                 |
|--------------------------|------------|--------------|----------------|--------------|---------------|--------------|-----------------|
|                          |            | $\rho$       | $p$ -value     | $\rho$       | $p$ -value    | $\rho$       | $p$ -value      |
| All sediments            | Truncation | <b>0.491</b> | <b>0.00002</b> | 0.397        | 0.0008        | 0.420        | 0.0004          |
|                          | Initiation | 0.176        | 0.151          | 0.250        | 0.040         | 0.264        | 0.029           |
|                          | Packages   | 0.333        | 0.005          | <b>0.427</b> | <b>0.0003</b> | <b>0.526</b> | <b>0.000004</b> |
| Carbonate-only sediments | Truncation | 0.280        | 0.022          | 0.291        | 0.016         | 0.176        | 0.154           |
|                          | Initiation | 0.206        | 0.092          | 0.281        | 0.020         | 0.304        | 0.012           |
|                          | Packages   | <b>0.335</b> | <b>0.005</b>   | <b>0.420</b> | <b>0.0004</b> | <b>0.421</b> | <b>0.0004</b>   |

Data are binned here into 69 calcareous nannoplankton zones (from NN20 to CC2, as in Peters et al. 2013). Spearman rank-order correlations and  $p$ -values for time series that have been detrended by taking first differences are shown. The strongest correlations in each macroevolutionary quantity are highlighted in bold.



linked to physical environmental changes, as suggested for extinction by Peters et al. (2013), but in ways that are different from the mechanisms that link extinction to the environmental changes that are recorded by its macrostratigraphic analog, sediment package truncation. Given that both macrostratigraphic quantities and macroevolutionary rates subsume many complexities in both the physical and biological systems, this is perhaps not surprising.

## 5. FUTURE RESEARCH AVENUES

The fossil record of the planktic foraminifera provides a fertile testing ground for exploring many aspects of biotic evolution and its links to changes in the global ocean-climate system. As planktic foraminifera are marine calcifiers, the growth and chemistries of their tests are strongly influenced by the carbonate saturation state of the ocean; hence, a better understanding of this group and the factors that have governed its evolutionary history will provide useful constraints on the consequences of carbon emissions and ocean acidification for marine ecosystems. Although the present-day rate of carbon input is probably unprecedented (Zeebe & Zachos 2013), the study of past carbon cycle perturbations, such as the PETM (~56 Ma) and the Cretaceous OAEs, will continue to provide much-needed insight into our possible future (Hönsch et al. 2012).

Confirmation, through the use of molecular phylogenetics, of the long-held suspicion that certain microperforate groups of planktic foraminifera are tychoipelagic is also altering our perception of foraminiferal evolution (Leckie 2009). This line of research has shown that the planktic foraminifera are a polyphyletic group with their benthic progenitors repeatedly colonizing the epipelagic realm (e.g., Darling et al. 1997). This may prove especially important for understanding the recovery of planktic foraminifera in the aftermath of catastrophes like the end-Cretaceous impact event (e.g., Darling et al. 2009).

The Oligocene epoch is the most understudied time interval of the Cenozoic era, but morphological variation within the planktic foraminifera clearly decreases during the Oligocene (e.g., Cifelli 1969). The roles of convergent evolution and extinction in driving this diversity decline need to be more clearly tested. The Oligocene also represents a critical transition between the Paleogene-to-Neogene diversifications, but the timing of the diversity nadir and the number of Oligocene species, as well as the duration of the recovery following the E–O boundary crisis, need to be better constrained. It is evident that a number of taxonomic, biostratigraphic, and phylogenetic issues need to be resolved for this time interval before we can fully understand the Paleogene-to-Neogene transition.

We have discussed possible connections between the sedimentological record of physical environmental change and the macroevolutionary history of planktic foraminifera. Indeed, many extinction events, like those at the Aptian–Albian (OAE1b) and Santonian–Campanian (Santonian turnover) boundaries, occur during intervals that are recognized as having widespread hiatuses, which constitute the critical breaks that define macrostratigraphic packages. Although originations are less consistently linked to their analogous macrostratigraphic quantity of package initiation, origination rates do covary with macrostratigraphic quantities. The hypothesis of common cause needs to be investigated at the level of individual events, where specific physical environmental changes can be more directly linked to large-scale patterns of sedimentation as well as to global patterns of biotic evolution.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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# Contents

|   |     |
|---|-----|
| A Conversation with James J. Morgan<br><i>James J. Morgan and Dianne K. Newman</i> .....  | 1   |
| Global Monsoon Dynamics and Climate Change<br><i>An Zhibeng, Wu Guoxiong, Li Jianping, Sun Youbin, Liu Yimin, Zhou Weijian,<br/>Cai Yanjun, Duan Anmin, Li Li, Mao Jiangyu, Cheng Hai, Shi Zhengguo,<br/>Tan Liangcheng, Yan Hong, Ao Hong, Chang Hong, and Feng Juan</i> ..... | 29  |
| Conservation Paleobiology: Leveraging Knowledge of the Past<br>to Inform Conservation and Restoration<br><i>Gregory P. Dietl, Susan M. Kidwell, Mark Brenner, David A. Burney,<br/>Karl W. Flessa, Stephen T. Jackson, and Paul L. Koch</i> .....                               | 79  |
| Jadeitites and Plate Tectonics<br><i>George E. Harlow, Tatsuki Tsujimori, and Sorena S. Sorensen</i> .....  | 105 |
| Macroevolutionary History of the Planktic Foraminifera<br><i>Andrew J. Fraass, D. Clay Kelly, and Shanan E. Peters</i> .....  | 139 |
| Continental Lower Crust<br><i>Bradley R. Hacker, Peter B. Kelemen, and Mark D. Behn</i> .....   | 167 |
| Oceanic Forcing of Ice-Sheet Retreat: West Antarctica and More<br><i>Richard B. Alley, Sridhar Anandakrishnan, Knut Christianson, Huw J. Horgan,<br/>Atsu Muto, Byron R. Parizek, David Pollard, and Ryan T. Walker</i> .....   | 207 |
| From Geodetic Imaging of Seismic and Aseismic Fault Slip<br>to Dynamic Modeling of the Seismic Cycle<br><i>Jean-Philippe Avouac</i> .....   | 233 |
| The Pyrogenic Carbon Cycle<br><i>Michael I. Bird, Jonathan G. Wynn, Gustavo Saiz, Christopher M. Wurster,<br/>and Anna McBeath</i> .....  | 273 |
| The Architecture, Chemistry, and Evolution of Continental<br>Magmatic Arcs<br><i>Mibai N. Ducea, Jason B. Saleeby, and George Bergantz</i> .....  | 299 |
| Paleosols as Indicators of Paleoenvironment and Paleoclimate<br><i>Neil J. Tabor and Timothy S. Myers</i> .....   | 333 |

|   |     |
|---|-----|
| Role of Arc Processes in the Formation of Continental Crust<br><i>Oliver Jagoutz and Peter B. Kelemen</i> .....   | 363 |
| Environment and Climate of Early Human Evolution<br><i>Naomi E. Levin</i> .....   | 405 |
| Magma Fragmentation<br><i>Helge M. Gonnermann</i> .....   | 431 |
| Atmospheric Escape from Solar System Terrestrial<br>Planets and Exoplanets<br><i>Feng Tian</i> .....  | 459 |
| A Tale of Amalgamation of Three Permo-Triassic Collage Systems in<br>Central Asia: Oroclines, Sutures, and Terminal Accretion<br><i>Wenjiao Xiao, Brian F. Windley, Shu Sun, Jiliang Li, Baochun Huang,<br/>Chunming Han, Chao Yuan, Min Sun, and Hanlin Chen</i> ..... | 477 |
| Atmospheric Dynamics of Hot Exoplanets<br><i>Kevin Heng and Adam P. Showman</i> .....   | 509 |
| Transient Creep and Strain Energy Dissipation: An Experimental<br>Perspective<br><i>Ulrich Faul and Ian Jackson</i> .....   | 541 |
| Rapid Plate Motion Variations Through Geological Time:<br>Observations Serving Geodynamic Interpretation<br><i>Giampiero Iaffaldano and Hans-Peter Bunge</i> .....  | 571 |
| Rethinking the Ancient Sulfur Cycle<br><i>David A. Fike, Alexander S. Bradley, and Catherine V. Rose</i> .....  | 593 |
| <b>Indexes</b>  |     |
| Cumulative Index of Contributing Authors, Volumes 34–43 .....   | 623 |
| Cumulative Index of Article Titles, Volumes 34–43 .....   | 628 |

## Errata

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