Invited Review Article

Turnover and stability in the deep sea: Benthic foraminifera as tracers of Paleogene global change

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A B S T R A C T

Benthic foraminifera are the most common meiofaunal unicellular deep-sea biota, forming skeletons used as proxies for past climate change. We aim to increase understanding of past non-analog oceans and ecosystems by evaluating deep-sea benthic foraminiferal responses to global environmental changes over latest Cretaceous through Oligocene times (67–23 million years ago). Earth suffered an asteroid impact at the end of the Cretaceous (~instantaneous; 66 Ma), episodes of rapid global warming during the Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma) and other hyperthermals (millennial timescales), followed by gradual, but punctuated cooling (timescales of hundred thousands of years) from a world without polar ice sheets to a world with a large Antarctic ice sheet. Here we present the first compilation of quantitative data on deep-sea foraminifera at sites in all the world's oceans, aiming to build a first unique, uniform database that allows comparison of deep-sea faunal turnover across the uppermost Cretaceous through Paleogene. We document variability in space and time of benthic foraminiferal diversity: lack of extinction at the asteroid impact even though other marine and terrestrial groups suffered mass extinction; major extinction at the PETM followed by recovery and diversification; and gradual but fundamental turnover during gradual cooling and increase in polar ice volume (possibly linked to changes in the oceanic carbon cycle). High latitude cooling from ~45 Ma on, i.e., after the end of the Early Eocene Climate Optimum (53.2–49.2 Ma), may have made the middle Eocene a critical period of several millions of years of faunal turnover and establishment of latitudinal diversity gradients. This compilation thus illuminates the penetration of global change at very different rates into the largest and one of the most stable habitats on Earth, the deep sea with its highly diverse biota.

1. Introduction

The deep sea is the largest habitat on Earth (Verity et al. 2002), and its particular geological, physical, geochemical and biological processes make it a unique and still largely unknown environment with a highly diverse, though little-known ecosystem (e.g., Ramirez-Llodra et al. 2010; Gooday et al. 2020). Present temperatures are around 1 °C, there is eternal darkness, and in most areas very little food because only ~1–3% of organic matter from surface primary productivity makes it to the deep seafloor in open ocean settings (e.g. Meyer-Reil and Köster 1991; Lutz et al. 2002). Frigid, dark, and energy-deprived, the deep sea appears hostile to us, but the environment is stable and supports one of the highest levels of biodiversity on Earth (Snelgrove and Smith 2002; Rex and Etter 2010). Benthic foraminifera are the most common group of eukaryote, meiofaunal unicellular organisms in the extreme environment where deep-sea biota live (e.g., Gooday et al. 1992; Gooday et al., 2020; Zeppilli et al. 2018), are excellent proxies for environmental conditions (e.g., Murray 2006; Jorissen et al. 2007), and provide the best fossil record of deep-sea Cenozoic organisms (e.g., Schmiedl 2019).

The relation between foraminiferal test morphology and

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microhabitat (infaunal, living within the sediment; and epifaunal, living in the uppermost cm or on the seafloor) is not fully understood, especially for the non-analog oceans of the past (e.g., Thomas 2007; Hayward et al. 2012), but is commonly used to infer some combination of oxygenation and trophic conditions at the seafloor (e.g., Jorissen et al. 2007), with dominance of infaunal taxa associated with high food supply and/or low oxygen availability.

Possibly due to the long-term stability of the deep sea, morphological species have slow turnover rates (appearances and extinctions) and thus long durations (Ramirez-Llodra et al. 2010; LeCroq et al. 2009), with deep-sea benthic foraminiferal average species lives estimated at ~50 Myrs, compared to planktic foraminifera (~11 Myrs) or shallow-water benthic foraminifera (~5–6 Myrs) (Hayward et al. 2012). Propagules make deep-sea benthic foraminifera highly effective dispersers (Alve and Goldstein 2010), and they display genetic uniformity over large distances, in contrast to planktic and shallow-water benthics (Pawlowski et al. 2007; LeCroq et al. 2009). Many morphospecies have a close to cosmopolitan distribution, but lack of reliable taxonomy obscures recognition of biogeographical patterns (e.g., Murray 2007; Arreguín-Rodríguez et al. 2018).

The paleoclimate of the Cenozoic has been reconstructed to a very large extent using geochemical data on deep-sea benthic foraminiferal tests (see refs. in Barnet et al., 2019; Schmiedl 2019; Westerhold et al. 2020). Deep-sea temperatures generally reflect high-latitude surface temperatures even during warm climates, because these coldest waters had the highest density over most of the Cenozoic (e.g., Huber and Thomas 2008). Potential exceptions are relatively short intervals of very warm climates (hyperthermals), when more saline warm waters could reach sufficiently high density. The geochemical signal in deep-sea benthic foraminiferal tests thus reflects changes in high-latitude surface temperatures, which vary more in temperature than the planetary average (polar amplification; Pierrehumbert 2010).

The early Cenozoic was a 'greenhouse' world without polar ice sheets, and fundamentally different ecosystem structures (e.g., Norris et al. 2013). The early Eocene (especially the Early Eocene Climate Optimum, EECO, 53.26–49.14 Ma; Zachos et al. 2008; Westerhold et al. 2018, 2020) was the warmest interval of the past 67 My, with mean annual surface air temperatures over 10 °C warmer than during the preindustrial period (e.g., Cramwinckel et al. 2018), deep sea temperatures ca. 10–12 °C (~1 °C in the modern oceans; Zachos et al. 2008; Cramer et al., 2009, 2011; Westerhold et al. 2020), and an Arctic without sea ice, with surface water temperatures reaching up to 20 °C (e.g., Sluijs et al. 2008).

Metabolic rates of deep-sea biota may have been about twice as high in this warm world as in modern oceans, because such rates roughly double with a temperature increase of ~10 °C (e.g., Gillooly et al. 2001). Floral, faunal, geochemical and modeling data suggest that Greenhouse World surface productivity may have been lower than today's productivity (Winguth et al. 2012; Norris et al. 2013). In a warmer ocean, however, the contribution of particulate organic matter to the deep-sea floor biota by dark inorganic fixation (Molari et al. 2013; Gooday, 2020) may have been larger than in the present cold oceans (Thomas 2007).

Many of the more common Paleogene deep-sea benthic foraminiferal taxa (Hayward et al. 2012; Arreguín-Rodríguez et al. 2018) are extinct, with their morphology non-existent in the modern oceans, suggesting that Greenhouse deep-sea biota were non-analog to living faunas (Thomas and Gooday 1996; Thomas 2007), which makes their interpretation in environmental terms difficult. Global cooling in the middle and late Eocene, especially at high latitudes, eventually led to the establishment of continental ice sheets in Antarctica in the early Oligocene (33.6 Ma) (e.g., Zachos et al. 2008; Cramer et al., 2009; Westerhold et al. 2018), and gradual as well as stepped transition into modern deep-sea benthic foraminiferal assemblages (e.g., Thomas 2007).

Geochemical proxies suggest that the oceanic carbon cycle and possibly the microbial loop functioned differently in the Greenhouse world than in that of today. Vertical gradients in planktic foraminiferal carbon isotope values are consistent with more efficient remineralization, thus recycling and reduced burial of organic carbon (John et al. 2014). Under such conditions, oceans might be less oxygenated, as confirmed by $\delta^{15}N$ of foraminifera shell-bound organic matter (Kast et al. 2019), suggesting widespread denitrification on the shelves and high rates of N_2 fixation. Oceanic Nitrogen isotope values changed unidirectionally during early-middle Eocene oceanic cooling, as did Tl-isotope values in ferromagnese crusts (Nielsen et al. 2009), and Sulfur isotopes in foraminiferal calcite (Rennie et al. 2018) and barite (Yao et al. 2020). The S isotope change is not well understood, but indicates increased pyrite burial (Yao et al. 2020). We thus do not yet fully understand the combined proxy records, but they indicate that the oceanic Nitrogen and Sulfur cycles (thus probably overall oceanic microbial life) changed profoundly during oceanic cooling in the late early to middle Eocene, and organic matter remineralization may have been more important at shallower depths than today in the Greenhouse world (John et al. 2014; Boscolo-Galazzo et al. 2018). Climate-dependent variability in remineralization may have occurred through warm intervals in the middle Eocene, such as the Middle Eocene Climate Optimum (Boscolo-Galazzo et al., 2014) and the Late Lutetian Thermal Maximum (Rivero-Cuesta et al., 2020), and the oceanic reservoirs of dissolved and particulate organic matter in a warm world thus may have differed importantly from those of today.

Most compilations of deep-sea benthic foraminiferal data have focused on individual, relatively short events across the Paleogene. Integrated studies on the long-term evolution of benthic foraminifera are scarce, and generally use few sites (Miller et al. 1992; Thomas 1992, 2007; Thomas and Gooday 1996), or limited sets of taxa (Hayward et al. 2012), mainly due to taxonomic problems (Arreguín-Rodríguez et al. 2018). Because of the taxonomic problems, the longer-term discussions tend to include taxonomy by few (Thomas and Gooday 1996) or one author (Kaiho 1994; Thomas 2007).

Here, we present the first compilation of data on deep-sea foraminifera as proxies for global climate change across a 44 Myr interval from the Upper Cretaceous through the Oligocene (67 to 23 Ma), at sites in all the world's oceans (Fig. 1; and Supplementary Tables S1, S2). We illuminate Earth's long-term climate evolution and its effect on deep-sea biota, as well as the penetration of global change into one of the most stable habitats on Earth, the deep sea.

2. Material and methods

We compiled a unique, uniform database of published and unpublished quantitative studies on smaller benthic foraminifera that allows comparison of the faunal turnover across the uppermost Cretaceous and Paleogene. Numerous studies on small benthic foraminifera are available in the literature, but the information cannot easily be compiled because of major differences in taxonomic concepts (Arreguín-Rodríguez et al. 2018). Detailed analysis of available studies included examination of quantitative data and taxonomic concepts used for the identification of benthic foraminifera, the studied size fraction, as well as paleodepth and availability of age information for each sample, Numerous sites that were not readily comparable because of the aforementioned criteria were not used in our analysis, and a database was built with a selection of 25 locations mostly on the western hemisphere (Fig. 1). In order to avoid the loss of information on overall small species which commonly dominate after major extinction events (e.g., the PETM), only studies that use the >63 μm or >100 μm size fraction were selected. The study localities include 25 bathyal (>600 m) ocean drilling sites and land sections (Fig. 2), grouped into six main paleogeographic areas: Pacific Ocean, Southern Ocean, Tethys Ocean, and three areas within the Atlantic Ocean: the Gulf of Mexico, the Bays of Biscay and Loya, and other Atlantic sites. Benthic assemblages are strongly dominated by agglutinated Flysch-type faunas (Kaminski and Gradstein 2005) in the Bays of Biscay and Loya (NE Atlantic), and contain
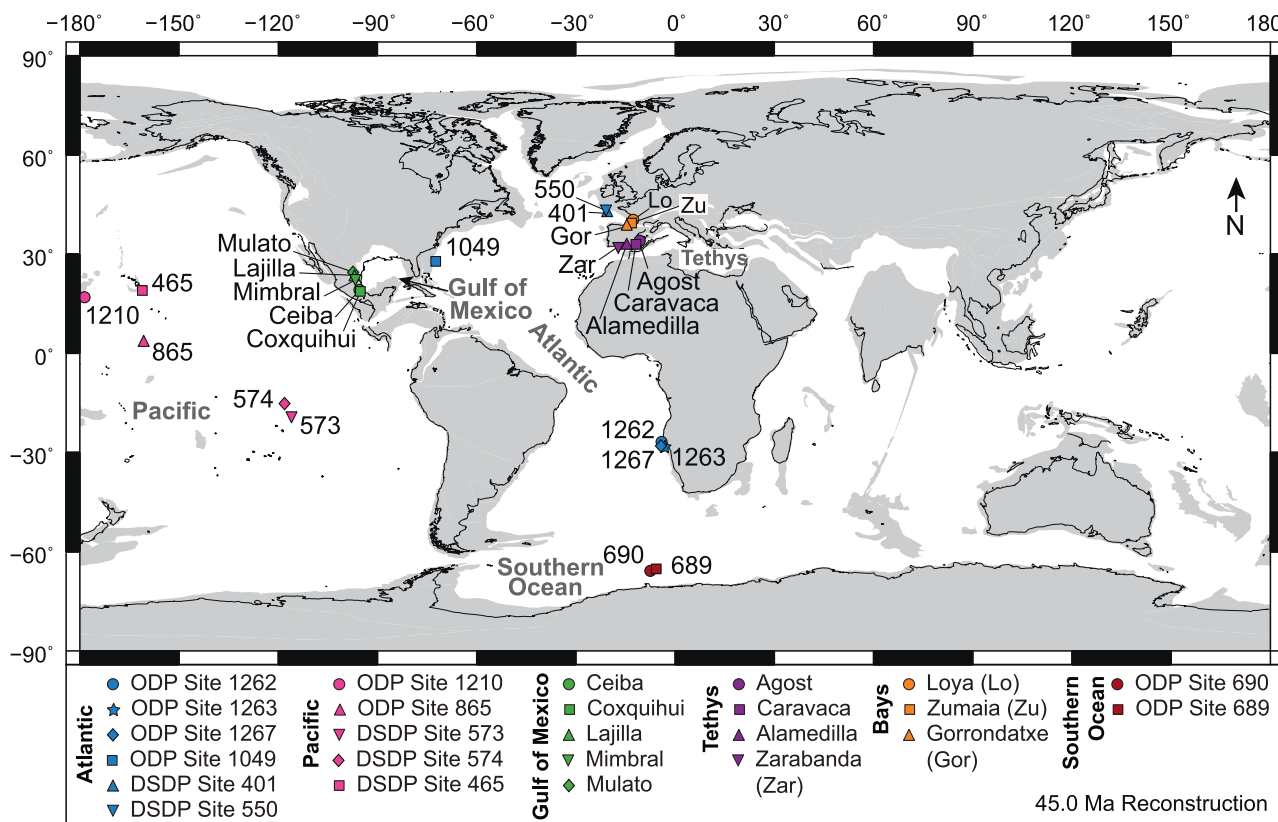
Fig. 1. Location of the study ocean drilling sites and land based sections. Palaeogeographic reconstruction (45 Ma) from Hay et al. (1999).
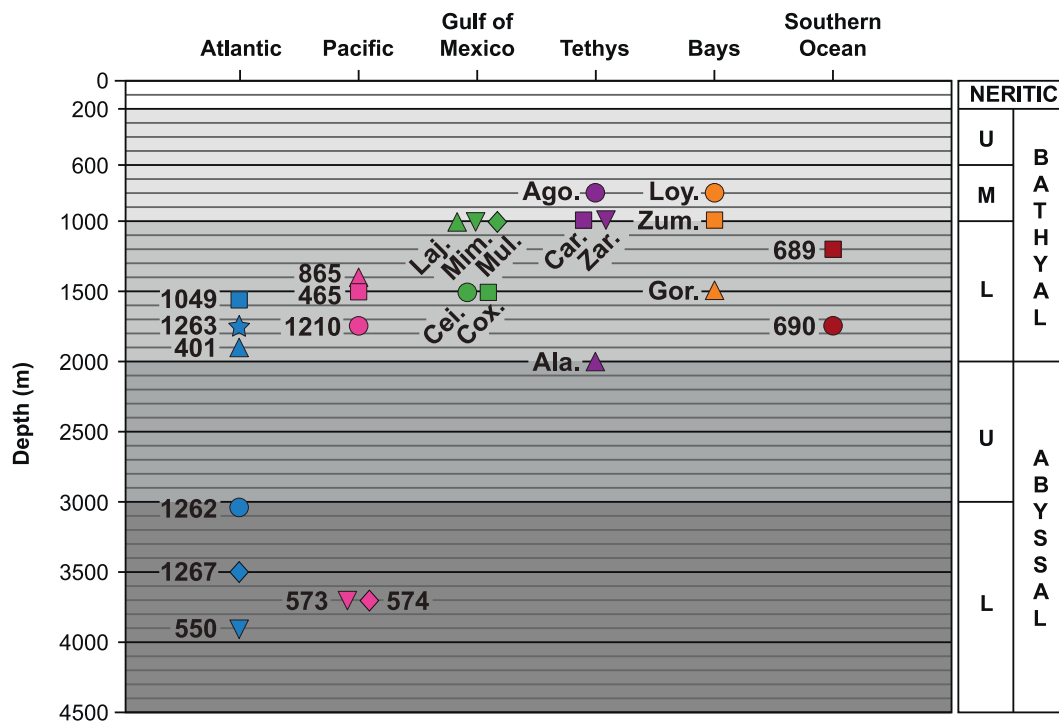

Fig. 2. Paleobathymetry of deep-sea sites and land sections. The markers indicate the mean value of the paleodepth range, see Supplementary Table S1 for detailed data. Abbreviations: Laj. = Lajilla, Mim. = Mimbral, Mul. = Mulato, Cei. = Ceiba, Cox. = Coxquihui, Ago. = Agost, Car. = Caravaca, Zar. = Zarabanda, Ala. = Alamedilla, Loy. = Loya, Zum. = Zumaia, Gor. = Gorrondatxe, U = upper, M = middle, L = lower.

abundant agglutinated taxa in the Gulf of Mexico (Supplementary Table S2). These regions thus have substantially distinct assemblages than other Atlantic sites, so that we included them as separate areas (Fig. 3). All databases include age information for each sample, with age models most commonly based on biostratigraphy (calcareous nannoplankton or planktic foraminiferal biozones) and/or orbitally-based. We used the numerical ages in Gradstein et al. (2012) for the Eocene and Oligocene, and the updated age model of Barnet et al. (2019) for the Maastrichtian to early Eocene (Supplementary Fig. S1). The Paleogene magneto-biochronologic scale was updated by graphically correlating it with new age models and adding other biozones (Arreguín-Rodríguez et al., 2020). The biostratigraphic position of hyperthermal events (West-erhold et al. 2018) is shown in Supplementary Table S3 and Supplementary Fig. S1, and the stratigraphic range represented in each locality is shown in Supplementary Fig. S2.

With the exception of some widely known species, the compilation of benthic foraminiferal data is hampered by taxonomic inconsistency among different authors. Here we revised the taxonomic concepts used in each dataset and the photographs included in each publication, when available. Following a taxonomic review by Arreguín-Rodríguez et al. (2018), we grouped published quantitative data of species with similar morphologies, some of which have been commonly identified under different names, especially for the informal groups defined in the former publication. All species that are very abundant (> 15%) in at least one sample from a given locality (Supplementary Tables S1 and S2) were included in the general database, and their evolution through time is documented in Figs. 4 and 5. In order to test the robustness of the quantitative data for each dataset (i.e., the representativeness of the data), the number of specimens and the number of species identified in each sample were correlated, and the R2 value was calculated for each locality (Supplementary Table S4), with values close to 1 pointing to a strong correlation between number of specimens and species, and values
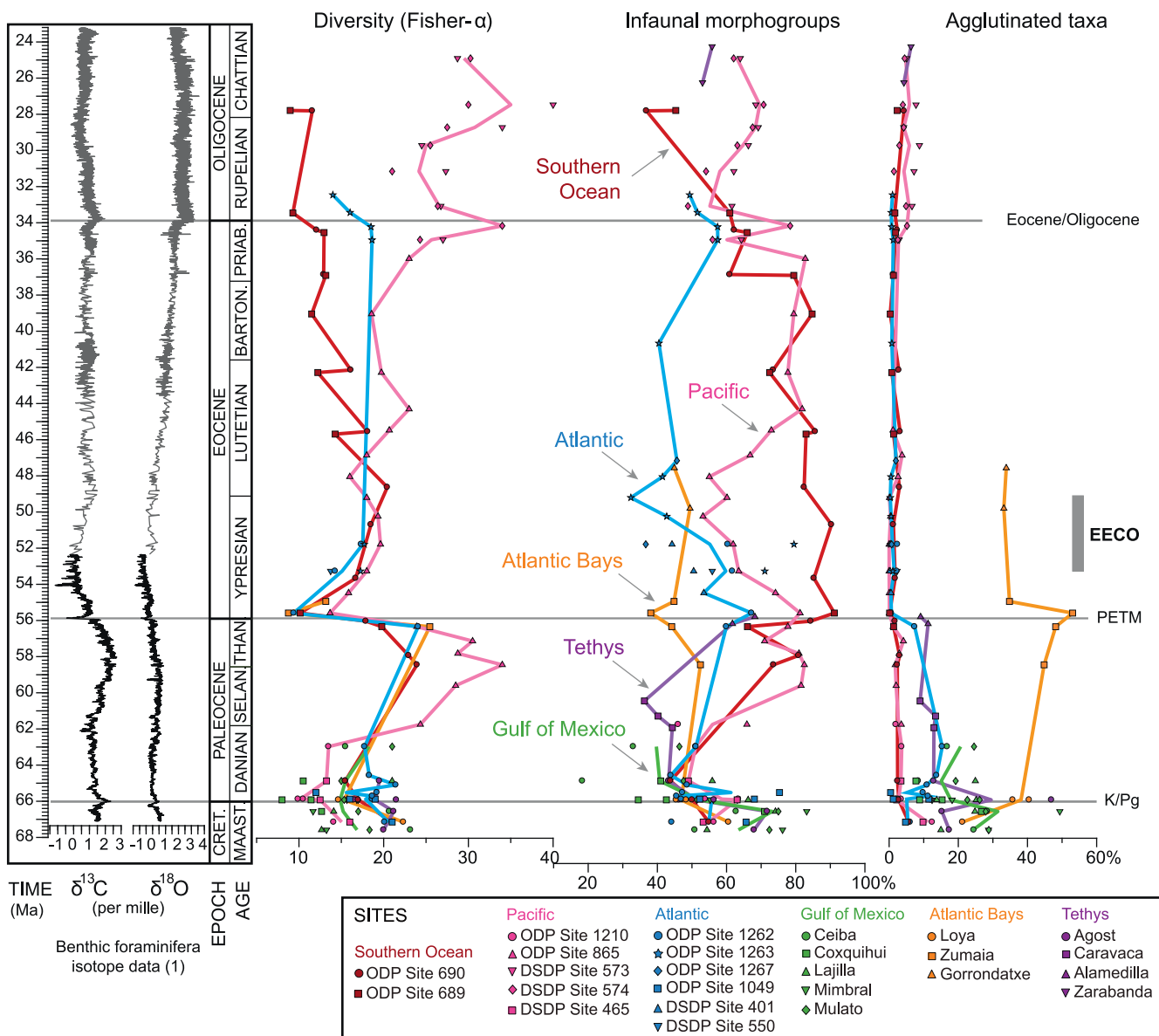

Fig. 3. Benthic foraminiferal diversity and relative abundance of infaunal and agglutinated taxa across the uppermost Cretaceous and Paleogene. The trend lines correspond to the average values for each region in each biozone. (1) Benthic foraminifera δ¹³C and δ¹⁸O curves include datasets by Zachos et al. (2008, grey line) and a compilation made by Barnet et al. (2019, black line), plotted against timescale using age models from Gradstein et al. (2012, for a 53 – 23 Ma time frame) and Barnet et al. (2019, for a 67–52 Ma interval). EECO: Early Eocene Climatic Optimum; PETM: Paleocene-Eocene Thermal Maximum; K/Pg, Cretaceous/Paleogene; Cret. Cretaceous; Maast., Maastrichtian; Selan., Selandian; Than., Thanetian; Barton., Bartonian; Priab., Priabonian.
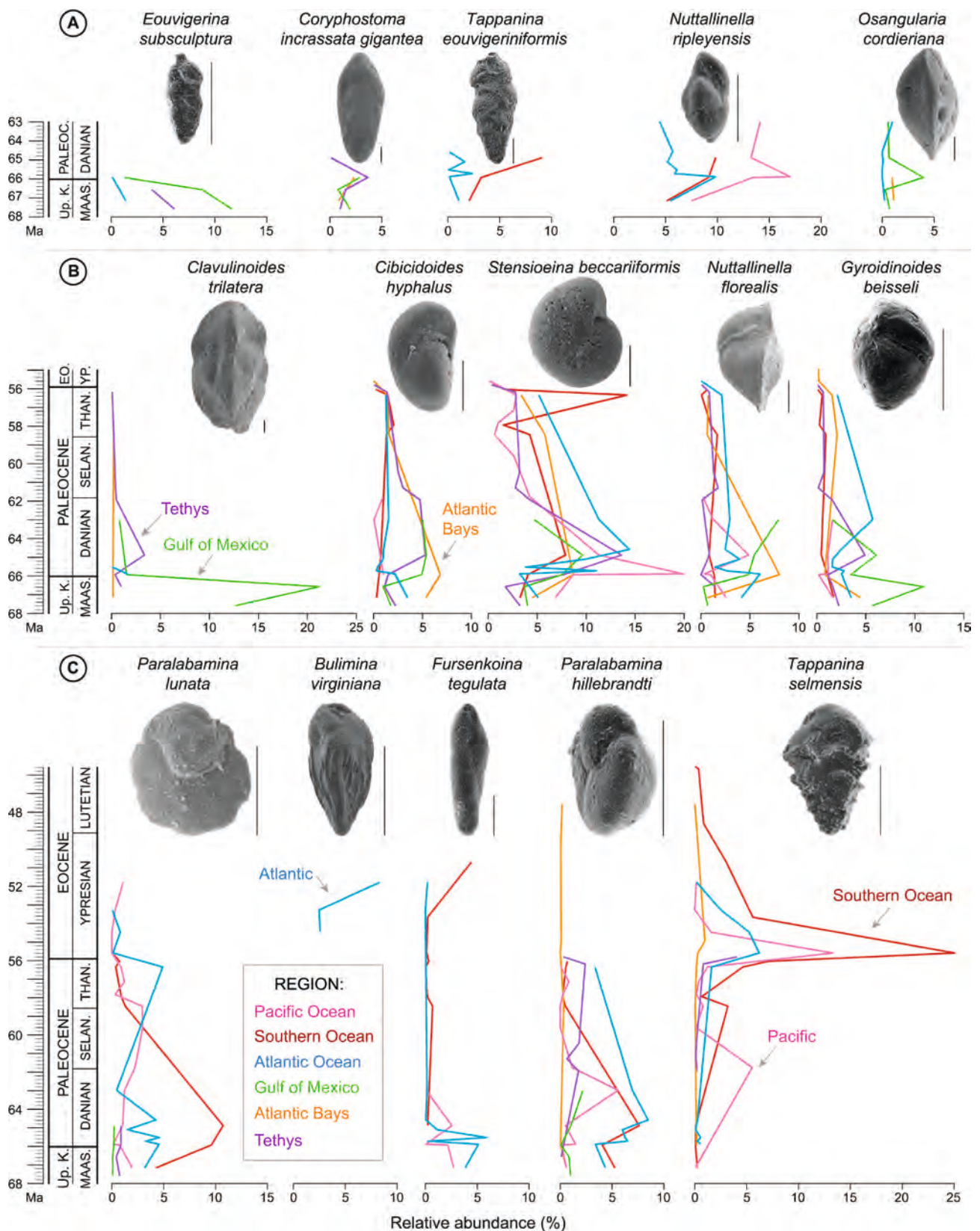
Fig. 4. Benthic foraminiferal species that make up >15% in at least one sample from a given locality (Supplementary Table S2) across the uppermost Cretaceous and Paleogene, plotted against timescale using age models from Gradstein et al. (2012, for a 53 – 23 Ma time frame) and Barnet et al. (2019, for a 65–53 Ma interval). The trend lines correspond to the average values for each region in each biozone. The photographs' scale bars equal 100 μm. Abbreviations: Up. K., Upper Cretaceous; Maas., Maastrichtian; Paleoc., Paleocene; Selan., Selandian; Than., Thanetian; Yp., Ypresian.

close to 0 indicating no correlation (i.e., species well represented in the samples; Thomas 1985). This test was necessary to evaluate the validity of data for samples with a smaller number of specimens (<300). Samples that were not representative were excluded from this analysis. In general terms, samples with R2 values <0.5 were considered representative, except for those across the Mid Paleocene Biotic Event (MPBE) at Zumaia, which display a slightly higher R2 value (0.5641). In this case, no samples were excluded from the general database because the high value of R2 is given by a sample with a very high number of counted specimens (>800), and not by a poorly represented sample.

In order to minimize taxonomic bias (use of different taxonomic concepts by different authors) in our compilation, we calculated the abundance of selected suprageneric groups (Fig. 6) and informal groups (as defined by Arreguín-Rodríguez et al. 2018; Fig. 7) that show significant patterns over time (Supplementary Table S2). Among suprageneric groups, the buliminids sensu *lato* (*s.l.*) group was calculated following Alegret and Thomas (2013), including biserial and triserial elongate genera of the superfamilies Buliminacea, Bolivinacea, Loxostomatacea, Turrilinacea, Fursenkoinacea, Pleurostomellacea and Stilostomellacea (Sen Gupta 1999).

The relative abundance of infaunal (vs. epifaunal)-habitat related morphogroups was calculated (Fig. 3, Supplementary Table S2) following Jones and Charnock (1985), Corliss (1985, 1991), Corliss and Chen (1988) and Murray et al. (2011). The term infaunal is here used in the broad sense, including benthic foraminifera that live in the top 1 cm of the sediment (shallow infauna; Jorissen et al. 2007). This relative abundance of infaunal taxa can be used as a proxy for a combination of oxygenation and trophic conditions at the seafloor (e.g., Jorissen et al., 1995, 2007). Caution must be used in this evaluation, because assignments to such morphogroups are correct for living foraminifera only in about 75% of cases (Buzas et al. 1993).

The average value of the percentage of species, groups of species, and diversity (Fisher-α index; Murray 2006; Fig. 3) was calculated per biozone to facilitate correlation among different localities, and a Matlab application was developed for the analysis and representation of this dataset (for a full description of methods, see Arreguín-Rodríguez et al., 2020). This methodology was developed to facilitate the analysis of long-term trends of taxonomic groups throughout the Paleogene. The trend lines represented in Figs. 3 to 9 correspond to the average values for each region in each biozone. Note that, although all the species that make up >15% in at least one sample from a given locality were included in the general database, the average value within a single biozone does not necessarily exceed 15% (Figs. 4, 5). The raw data, including samples per biozone, the relative abundance of species that make up >15% of the assemblages at each locality, selected suprageneric groups and informal groups, calcareous and agglutinated taxa, infaunal and epifaunal morphogroups, and Fisher-α index; their average values, minimum, maximum and standard deviation are included in Supplementary Tables S5 to S40. In addition, unpublished foraminiferal counts for Site 689 are included in Supplementary Table S37.

Using these methods, we document the response of benthic foraminifera to events of different rates and magnitude over the time interval between ~67–23 Ma. The impact of an asteroid at the K/Pg boundary occurred at a time scale considerably shorter than deep-sea circulation, but the PETM, though a relatively fast event on geological time scales, was slower, occurring on the time scale of deep ocean circulation (thousands of years; Lord et al. 2016). Cooling of the oceans from the middle Eocene on occurred on much longer time scales, of hundreds of thousands of years (Zachos et al. 2008; Cramer et al., 2009). In order to use benthic foraminifera as tracers of global change, the most significant trends were compared with the evolution of phytoplankton groups and with climatic events across the Paleogene (Figs. 8 and 9).

3. Results and discussion

3.1. General assemblage composition

Our review of studies of benthic foraminifera published to date showed that the only 25 locations that met our selection criteria for quality and comparability are located on the western hemisphere. Comparable studies are needed from the eastern hemisphere, and quantitative data made publicly available. Ocean drilling cores recently recovered by the International Ocean Discovery Program e.g. in the Tasman Sea (Expedition 371; Sutherland et al., 2019) and off SW Australia (Expedition 369; Hobbs et al., 2019) can be expected to contribute to fill, at least in part, this geographical gap, and ongoing and future studies on benthic foraminifera will likely provide key information on these areas.

Our compilation shows that bathyal-abyssal assemblages are strongly dominated by calcareous taxa at all study sites apart from the NE Atlantic Bays (Fig. 3), which contain abundant trochamminids (Fig. 6) and other agglutinated, Flysch-type taxa (Kaminski and Gradstein 2005). The relative abundance of morphogroups varies through time among different paleogeographic areas, but the percentage of infaunal morphogroups (Fig. 3) is higher than 30% at all study sites except for one Danian biozone from the La Ceiba section (Gulf of Mexico). This abundance exceeds 50% of the assemblages at most sites from the Pacific Ocean, the Atlantic Ocean and the Southern Ocean, especially during the Paleocene and early Eocene Greenhouse Earth. Infaunal buliminids *s.l.* (e.g., *Eouvigerina subsculptura, Coryphostoma incrassata gigantea, Fursenkoina tegulata, Tappanina eouvigeriniformis, Tappanina selmensis, Aragonia aragonensis*; Figs. 4, 5) generally made up a large portion of the assemblages during the Paleocene and early Eocene, gradually decreasing across the late Eocene and Oligocene (Fig. 6). This pattern is also observed in informal groups such as the fusiform buliminids, costate buliminids, *Bolivinoides* cf. *decoratus* group, *Bulimina simplex* group, *Bolivina huneri* group, or *Bulimina elongata* group (Fig. 7). A similar trend is seen in infaunal groups such as the uniserial lagenids, polymorphinids, or *Lenticulina* (shallow infauna), whereas stilostomellids significantly increased in abundance in the Pacific and Southern Ocean (and pleurostomellids in the Pacific Ocean) across the Eocene, followed by a decrease in the Oligocene.

Among epifaunal morphogroups, many species that were abundant during the Paleocene went extinct at the Paleocene/Eocene boundary (e. g., *Stensioeina beccariiformis, Cibicidoides hyphalus, Nuttallinella florealis*) or decreased in abundance towards the Eocene (*Paralabamina hillebrandti, Paralabamina lunata, Gyroidinoides beisseli*). *Nuttallides truempyi* was most common during the Paleocene and early to middle Eocene, gradually decreasing in abundance until its extinction at or close to the Eocene/Oligocene boundary (e.g., Thomas 1985; Miller et al. 1992). In contrast, other epifaunal species increased in abundance towards the late Eocene and Oligocene, including *Epistominella vitrea, Epistominella exigua, Gyroidinoides mediceus* (Figs. 4, 5), and notably the *Nuttallides umbonifera* informal group (Fig. 7).

3.2. Faunal turnover across Paleogene events

Benthic foraminifera show a decrease in diversity during the latest Cretaceous (Fig. 3), but there is no evidence for elevated extinction rates (Hull et al. 2020). This decrease is followed by a sudden drop in diversity across the K/Pg boundary (Fig. 3), but without significant extinction (Thomas 1990; Kaiho 1994; Culver 2003; Alegret et al. 2012), in contrast to planktic foraminifera and many other species that suffered a mass extinction. The global decline in diversity probably resulted from local disappearance of taxa that survived in refugia ('Lazarus effect') (e.
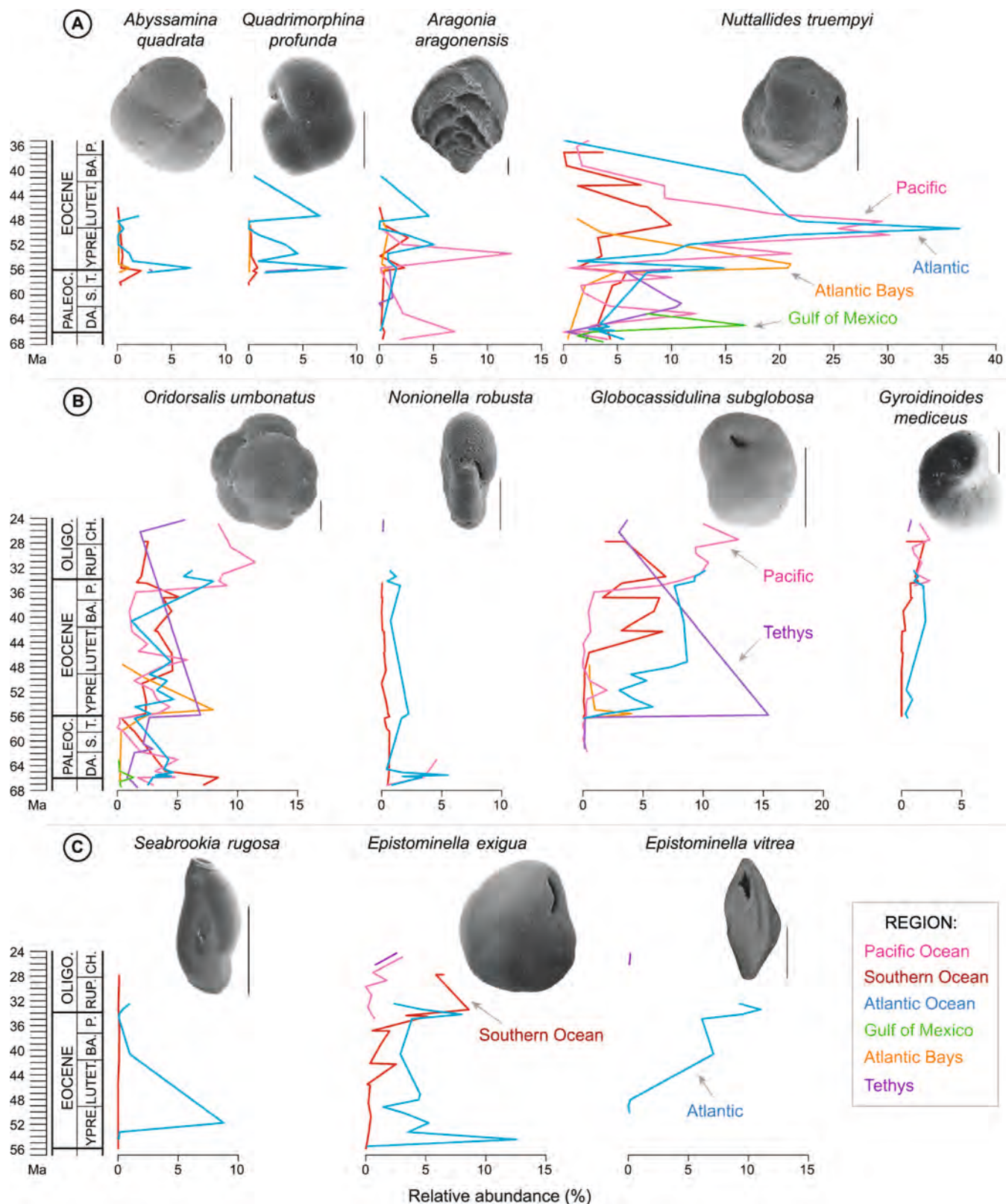
Fig. 5. Benthic foraminiferal species that make up >15% in at least one sample from a given locality (Supplementary Table S2) across the uppermost Cretaceous and Paleogene, plotted against timescale using age models from Gradstein et al. (2012, for a 53 – 23 Ma time frame) and Barnet et al. (2019, for a 65–53 Ma interval). The trend lines correspond to the average values for each region in each biozone. The photographs' scale bars equal 100 μm. Abbreviations: Paleoc., Paleocene; Da., Danian; S., Selandian; T., Thanetian; Ypre., Ypresian; Lutet., Lutetian, Ba., Bartonian; P., Priabonian.; Oligo., Oligocene; Rup., Rupelian; Ch., Chattian.
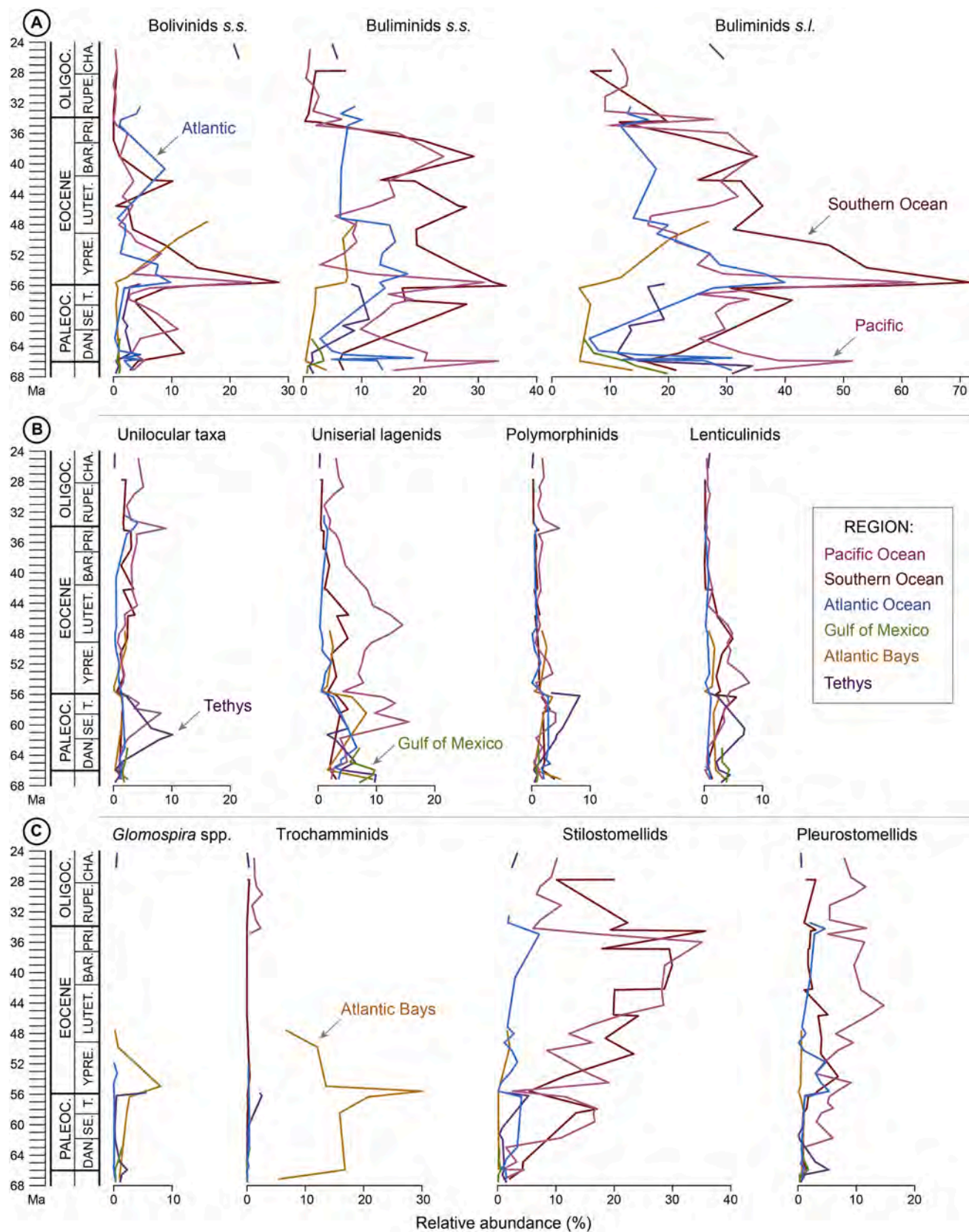
Fig. 6. Benthic foraminiferal suprageneric groups across the uppermost Cretaceous and Paleogene, plotted against timescale using age models from Gradstein et al. (2012; for a 53 – 23 Ma time frame) and Barnet et al. (2019; for a 65–53 Ma interval). The trend lines correspond to the average values for each region in each biozone. Abbreviations: Paleoc., Paleocene; Dan., Danian; Se., Selandian; T., Thanetian; Ypre., Ypresian; Lutet., Lutetian, Bar., Bartonian; Pri., Priabonian.; Oligoc., Oligocene; Rupe., Rupelian; Cha., Chattian.

Fig. 7. Benthic foraminiferal informal groups (defined by Arreguín-Rodríguez et al. 2018) across the uppermost Cretaceous and Paleogene, plotted against timescale using age models from Gradstein et al. (2012; for a 53 – 23 Ma time frame) and Barnet et al. (2019; for a 65–53 Ma interval). The trend lines correspond to the average values for each region in each biozone. Abbreviations: Paleoc., Paleocene; Da., Danian; S., Selandian; T., Thanetian; Ypr., Ypresian; Lute., Lutetian, B., Bartonian; P., Priabonian.; Olig., Oligocene; Rup., Rupelian; Ch., Chattian.
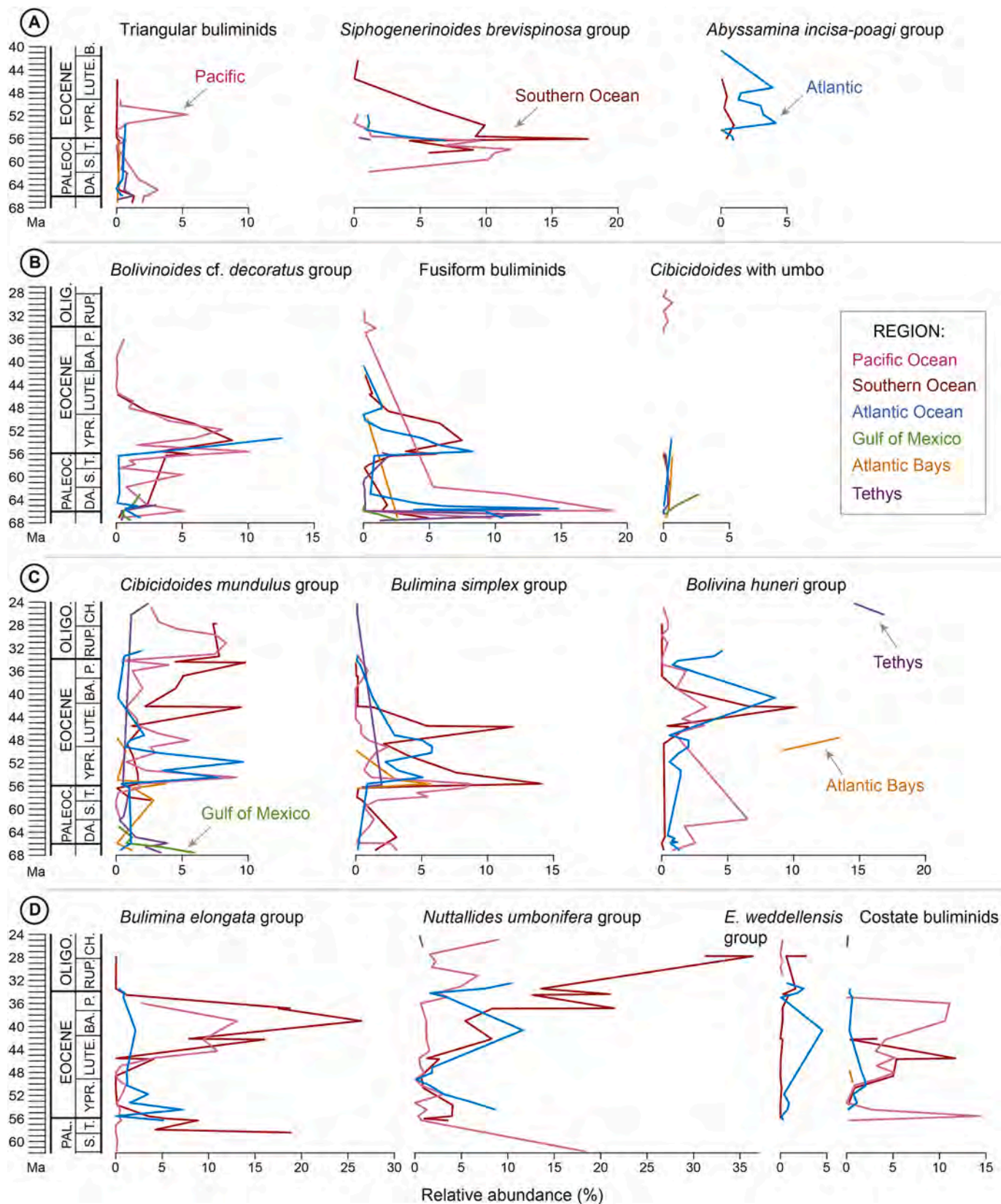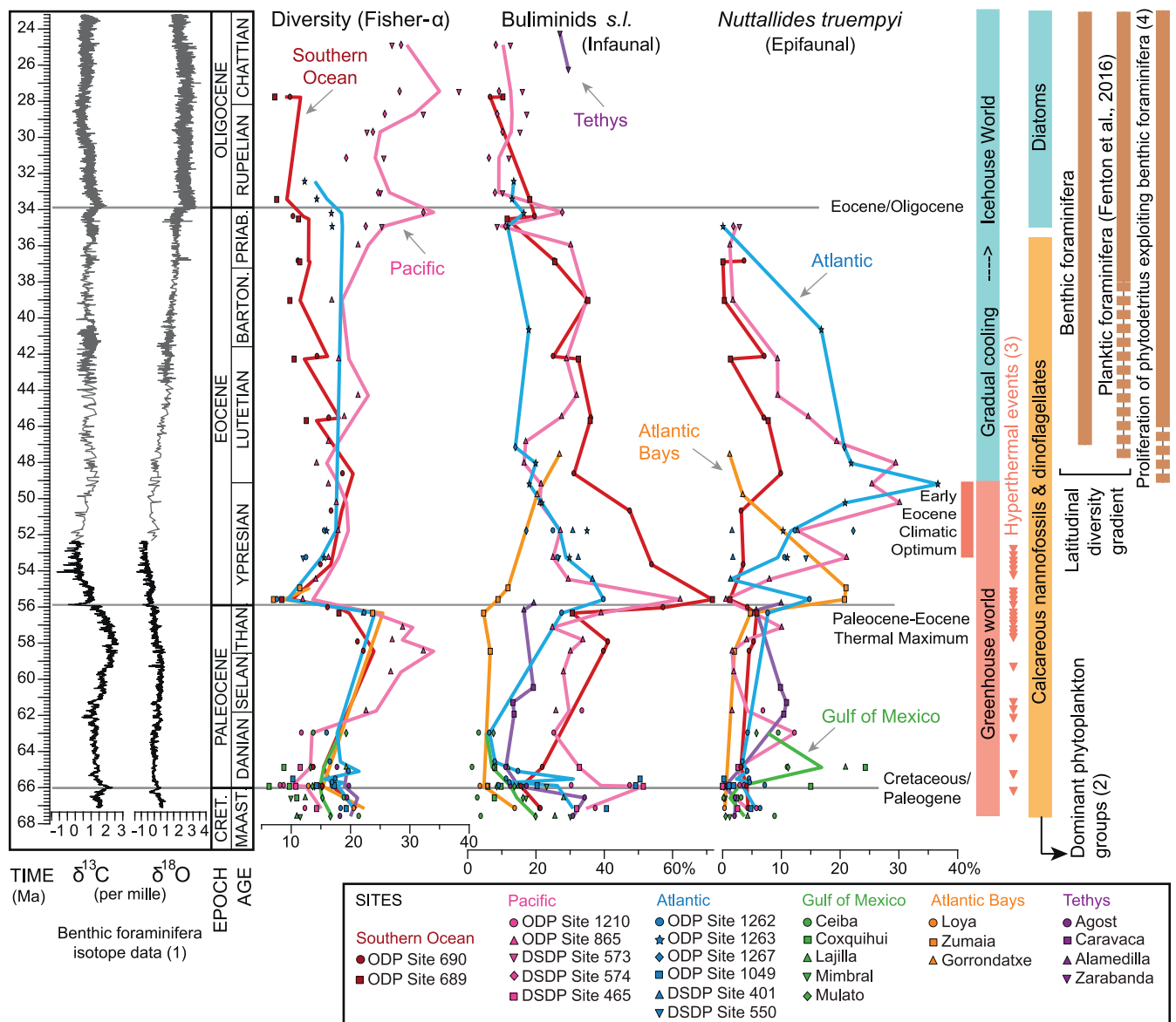
Fig. 8. Benthic foraminiferal diversity and percentages of buliminids *s.l.* and *N. truempyi* across the uppermost Cretaceous and Paleogene. The trend lines correspond to the average values for each region in each biozone. (1) As in Fig. 3. (2) Modified from Hayward et al. (2012). (3) Biostratigraphic position of events in Supplementary Table S3. (4) Ortiz and Thomas 2015. Abbreviations: Cret. Cretaceous; Maast. Maastrichtian; Selan. Selandian; Than. Thanetian; Barton. Bartonian; Priab. Priabonian.

g., Thomas 1990; Alegret et al. 2012). The post-impact scenario in the deep-sea was geographically heterogeneous, with assemblages dominated by infaunal buliminids indicative of high food supply to the sea-floor in the Pacific Ocean, mixed infaunal and epifaunal morphogroups indicative of mesotrophic conditions in the Southern Ocean, and dominance of either infaunal or epifaunal taxa at various Atlantic and Tethyan sites (Alegret et al. 2012, 2015; Giusberti et al. 2016) (Fig. 3). These geographic differences have been related to trophic heterogeneity of the oceans after the K/Pg impact, with regional plankton blooms accounting for enhanced export productivity, whereas other areas show less change or a moderate decrease in export productivity (e.g., Hull and Norris 2011; Alegret et al. 2012; Lowery et al. 2018; Sepulveda et al. 2019; Henehan et al. 2019; Bralower et al. 2020). Locally or regionally, assemblages might have been affected by changes in ocean carbonate saturation associated with the extinction of planktonic calcifyers (Alegret and Thomas 2013).

Following the K/Pg, the late Danian (~62 Ma) stands out as a critical

time when assemblages in the Pacific Ocean, which had been characterized by the lowest diversity (Fig. 3), became more diverse and remained so at least until the end of the Oligocene (i.e., for ~40 myr). The Pacific data are from a seamount setting, potentially affected by trophic focusing (ODP Site 865), thus a local increase in diversity may not have been typical for the Pacific Ocean overall. Globally, diversity recovered rapidly to above latest Cretaceous levels, in part due to the proliferation of infaunal buliminid species in the Southern Ocean, and stilostomellid species (extinct uniserial forms with a complex aperture; Hayward et al. 2012) in the Pacific and Southern Oceans (Fig. 6).

The most extreme drop in global diversity corresponds to the Benthic Extinction Event at the start of the PETM, a period of rapid and exceptional global warming (e.g., Thomas and Shackleton 1996; Thomas 1998; Dunkley-Jones et al. 2013) and the largest Mesozoic-Cenozoic deep-sea benthic foraminiferal extinction (e.g., Tjalsma and Lohmann 1983; Thomas 1989, 1990, 1998, 2007; Katz and Miller 1991; Kennett and Stott 1991; Kaiho 1994; Alegret et al., 2009, 2018). Extinction rates
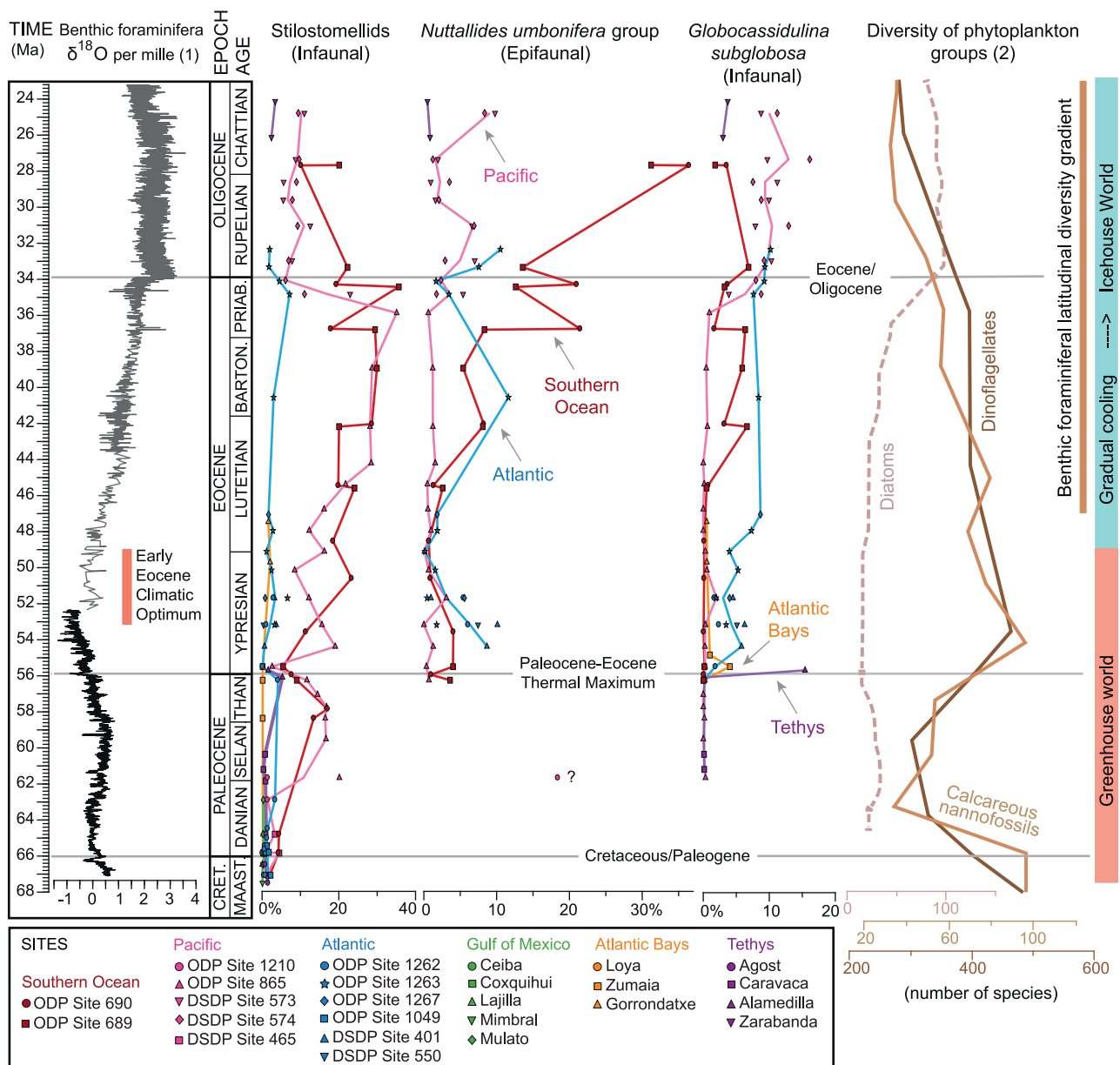
Fig. 9. Relative abundance of benthic foraminiferal taxa, and diversity of phytoplankton species, including diatoms (Spencer-Cervato 1999), calcareous nannofossils (Bown et al. 2004) and dinoflagellates (Stover et al. 1996). (1) As in Fig. 3. Abbreviations as in Fig. 8.

in the deep sea ranged from 29% of the species in the Southern Ocean (Hayek et al. 2019) to 54% in the Northeast Atlantic Ocean (Alegret et al. 2018). Such high rates of extinction are extremely rare in the deep oceans, because they indicate a lack of refugia in the very large deep-sea habitat, even for the efficient-dispersive deep-sea benthic foraminifera (Alve and Goldstein 2010).

Our selected sites can be divided into two groups: truly pelagic, generally oligotrophic open ocean settings, and sites near continental margins, more nutrient-rich due to coastal upwelling along continental margins and more runoff from land due to the intensification of the hydrological cycle during hyperthermals (Giusberti et al. 2016; Dunkley Jones et al. 2018). Post-extinction, low-diversity assemblages dominated by buliminids *s.l.* in open-ocean parts of the North Atlantic, some Pacific sites (e.g., seamount Site 865) and the Southern Ocean (Fig. 6) point to enhanced export productivity and/or low-oxygen conditions at the seafloor (e.g., Thomas 1998, 2007). In contrast, oligotrophic taxa such as *Nuttallides truempyi* (Fig. 5) and abyssaminid species (Fig. 7) dominated the post-extinction assemblages in the South Atlantic (Walvis

Ridge sites; Thomas 1998; Arreguín-Rodríguez et al. 2018) and deeper Pacific sites (Arreguín-Rodríguez et al. 2018). Opportunistic aggluti-nated taxa (including the so-called *Glomospira* acme; Arreguín-Rodrí-guez et al. 2013) bloomed and increased in absolute abundance after the P/E boundary in the NE Atlantic and the Tethys Ocean (Fig. 6).

After the PETM, diversity moderately increased, reaching close to latest Cretaceous values in the Southern Ocean and in the Atlantic Ocean, slightly higher values in the Pacific Ocean (Fig. 3). Diversity remained relatively constant across the lower half of the Eocene, punctuated by short-lived declines - but no extinctions- across later hyperthermal events (e.g., Jennions et al. 2015; Thomas et al. 2018). These low-diversity assemblages commonly after later hyperthermals were dominated by the same taxa as were dominant directly after the PETM, but the temporary effects on the assemblages during these events cannot be resolved within the time resolution of this compilation (see 'material and methods', and Supplementary Table S3). The proliferation of the oligotrophic species *Nuttallides truempyi* (Miller et al. 1992; Thomas 1998) during the early-middle Eocene in all oceans except the

Southern Ocean contributed to the low diversity values (Fig. 8), and points to a higher food supply to the seafloor in the Southern Ocean as compared to other ocean basins during the early Eocene. This species has been argued to be CaCO$_3$ corrosion-resistant, similar to its extant descendant *Nuttallides umbonifera* (Thomas 1998), but the dominance of calcareous taxa (>90% of the assemblages; Supplementary Table S2) in all ocean basins except the Bay of Biscay rules out increased CaCO$_3$-corrosivity of bottom waters as the main cause of its proliferation.

Significant assemblage changes started in the middle Eocene (Lutetian) at ~47 Ma, associated with the beginning of cooling and glaciation at high latitudes and in the deep sea (Bralower et al. 1995; Moran et al. 2006; Eldrett et al. 2007): 1) diversity trends decoupled in the Pacific and in the Southern Ocean (Thomas and Gooday 1996), gradually decreasing in the Southern Ocean (where *Nuttallides umbonifera* became progressively more abundant) and increasing in the Pacific Ocean; 2) the relative abundance of *Nuttallides truempyi* gradually decreased in the Pacific and Atlantic Oceans and in the Southern Ocean (Miller et al. 1992); 3) the percentage of *Nuttallides umbonifera,* the descendant of *N. truempyi* (and to a minor extent, the percentage of *Globocassidulina subglobosa)* increased in the Southern Ocean and in the South Atlantic. *G. subglobosa* was a phytodetritus exploiting species (Corliss et al. 2009), and *N. umbonifera* is common to abundant in CaCO$_3$-corrosive (Bremer and Lohmann 1982) and/or food-poor, deep waters (e.g., Thomas 1998; Ortiz and Thomas 2015). These two species were a minor component of the assemblages in the only Pacific site available for this time interval (Site 865), but they were common at other Pacific sites across the latest Eocene and Oligocene (Figs. 5B, 7D).

Stilostomellids did not suffer severe extinction at the PETM and gradually became more abundant across the Eocene, dominating the assemblages in the Pacific and in the Southern Ocean. This group may have had a shallow infaunal life style (Hayward et al. 2012; Mancin et al. 2013), suspension feeding in the water column by extending their pseudopods through the complex aperture (e.g., Mancin et al. 2013). However, we speculate that some of these forms may have used extended pseudopods to feed on dissolved organic matter, as observed in some modern agglutinated dendritic forms (e.g., Lipps 1983; see also Arreguín-Rodríguez et al., 2016). They thus may have benefitted from active bottom currents. Their long-term increase in abundance across a 27 My-long interval might indicate enhanced regional current activity in the Southern Ocean and in the Pacific Ocean, although their apparent dominance in the Pacific reflects their abundance at the local seamount-top environment of ODP Site 865 (Supplementary Table S2). Their global abundance started to decrease in the late Eocene, correlated with a shift from nannoplankton- and dinoflagellate-dominated assemblages to diatom-dominated assemblages (Fig. 9).

Benthic assemblages declined moderately in diversity across the Eocene/Oligocene boundary, coinciding with the extinction of *Nuttallides truempyi* (after its long-term decline for more than 10 Myr; Fig. 8), the decreased abundance of buliminids *s.l.* and stilostomellids, the proliferation of the *Nuttallides umbonifera* group in the Southern Ocean and of *Globocassidulina subglobosa* mostly in the Pacific Ocean. Such a limited decrease in diversity (Corliss 1981; Corliss et al., 1984; Thomas 1992) contrasts with significant extinctions and assemblage turnover among other groups such as warm and surface-dwelling planktic foraminifera (e.g., Wade and Pearson 2008; Ezard et al. 2011).

3.3. Benthic foraminifera as tracers of global change

Benthic foraminiferal assemblage turnover was intimately linked to global events and the evolution of climate and the oceans from 67 to 23 Ma. The timing of the latest Cretaceous decline in diversity cannot be resolved within the resolution of the present study, but it may have been coeval with the ~2 °C volcanogenic warming followed by cooling to pre-event temperatures in the Cretaceous part of magnetochron C29r (Hull et al. 2020).

The asteroid impact at the K/Pg boundary was a geologically instantaneous event, but did not lead to significant extinctions among deep-sea biota, in contrast to many other groups that underwent severe extinction (~75% of species; Schulte et al. 2010; Hull et al. 2020), and this decoupling between the deep-sea benthic and surface extinctions was noted by several authors (Thomas 1990, 2007; Kaiho 1994; Culver 2003). The decline in diversity of benthic foraminifera at the K/Pg boundary due to the temporary disappearance of Lazarus taxa in refugia was a global signature (Culver 2003; Alegret et al. 2012), but its magnitude was small compared to changes in diversity across other time periods (Fig. 3). The impact occurred at a time scale shorter than deep-sea circulation, and rapid surface ocean acidification may have strongly contributed to ecological collapse in surface waters (Henehan et al. 2019), but may not have penetrated to the deep sea (Alegret et al. 2012; Lord et al. 2016). Earth system modeling supports a partial reduction in global marine primary productivity, with locally increased productivity through blooms of non-calcifying phytoplankton (e.g., Sepulveda et al. 2019; Bralower et al. 2020). This scenario is consistent with regional differences in export productivity as inferred from benthic foraminiferal assemblages, and possibly linked to the availability of locally abundant nutrients due to phytoplankton extinctions elsewhere (Henehan et al. 2019). Recovery of evolution-driven marine biodiversity (e.g., Birch et al. 2016) and carbon cycling in the oceans was much slower (over 1 Myr after the impact; Henehan et al. 2019).

The PETM was a slower, but geologically speaking fast event, with duration of its initiation debated, but probably on the order of 1–2 millennia (e.g., Zeebe et al. 2014), on the time scale of deep ocean circulation (Lord et al. 2016). It strongly affected deep-sea benthic foraminifera, causing their largest extinction in the Mesozoic-Cenozoic. The metazoan ostracods, however, did not have a similarly extreme extinction (Steineck and Thomas 1996; Webb et al. 2009; Yamaguchi and Norris 2012). Global extinctions are rare in the deep oceans, and when occasionally recorded, indicate a lack of refugia in the very large deep-sea habitat even for the efficient-dispersive benthic foraminifera (Alve and Goldstein 2010). Site location may have been a key factor controlling assemblage composition after the extinction event (Arreguín-Rodríguez et al. 2018), due to the possible expansion of the trophic resource continuum (Hallock 1987; Thomas 1998; Winguth et al. 2012), with buliminids and *N. truempyi* indicating high or low export productivity at some open-ocean sites, respectively. The proliferation of opportunistic agglutinated taxa after the P/E boundary, including the *Glomospira* acme in the NE Atlantic and the Tethys Ocean, has been related to enhanced terrestrial input (Alegret et al., 2009, 2018; Arreguín-Rodríguez et al. 2013) triggered by a more vigorous hydrological cycle (Giusberti et al. 2016).

Warming ~20–30 kyr before the main extinction event and before the onset of the negative excursion in δ^{13}C that marks the Paleocene/Eocene boundary (Secord et al., 2010; Giusberti et al. 2016) was coeval with the beginning of extinctions in the latest Paleocene (Alegret et al., 2009, 2018). Accelerated metabolic rates through the deep-sea warming, and reduced export productivity due to increased remineralization of organic matter in the water column at higher temperatures (Ma et al. 2014), may have led to starvation and extinction in the deep-sea (Alegret et al., 2009, 2010), as also argued for smaller Eocene hyperthermal events (Boscolo-Galazzo et al. 2014, 2018; Jennions et al. 2015; Thomas et al. 2018).

Other factors might have contributed to the stress leading to the extinction of deep-sea benthic foraminifera (Hayek et al. 2019), and low oxygen conditions have been mentioned as such an additional factor. During the PETM, low-oxygen conditions were widespread as Oxygen Minimum Zones expanded not only in marginal basins but also in open ocean (Chun et al. 2010; Pälike et al., 2014; Zhou et al. 2014, 2016). We think it is less likely that oxygen deficiency was the main cause of extinction: quite a few species of the protistan benthic foraminifera survive or even thrive under low oxygen conditions (e.g., Koho and Piña-Ochoa, 2012; Heinz and Geslin 2012; Orsi et al., 2020), although the assemblage composition may well have been affected (e.g., Thomas 1998).

Ocean acidification, in contrast, may have been a significant factor in the extinction of the protistan foraminifera (e.g., Thomas, 1998, 2007), with less effect for the more metabolically complex metazoan ostracods (Melzner et al. 2009). The acidification of large regions of the deep-sea (Zachos et al., 2005; Lord et al. 2016) caused by emissions of carbon-compounds on millennial time scales (e.g. Zeebe et al. 2014) may have been a causal factor in the decoupling of surface extinction (almost instantaneous emission) and deep-sea extinctions (Thomas 1990; Kaiho 1994).

The severe extinction of pelagic calcifiers combined with lack of deep-sea calcifier extinction at the K/Pg contrasts strongly with the severe benthic extinction at the PETM with minor effects in surface calcifiers. The magnitude of surface pH at the K/Pg (Henehan et al., 2016) was similar to that during the PETM (Penman et al. 2016; Gutjahr et al., 2017). This observation has been used to argue that acidification at the K/Pg was not the main cause of biotic effects (Lowery et al. 2020) despite the pattern of extreme extinction of calcifiers. We argue that the difference in duration, thus rate of acidification during these two events (close to instantaneous during the K/Pg, millennia during the PETM) may have caused the difference in biotic effects of acidification events of similar magnitude (Hönisch et al., 2012; Lord et al. 2016).

The proliferation of *N. truempyi* during the early-middle Eocene in all oceans except the Southern Ocean is consistent with increased ocean stratification and ocean circulation changes during polar cooling (Cramer et al. 2011; Ortiz and Thomas 2015). Benthic foraminifera point to a higher food supply to the seafloor in the Southern Ocean, similar to what we see in modern high latitude settings where productivity is highly seasonal and driven by phytoplankton blooms (Martin 2003), potentially resulting in a more efficient transfer of food particles to the seafloor (Berger and Wefer 1990; Henson et al. 2012).

The question remains why Cretaceous to Eocene faunas in the open ocean resemble present faunas at relatively high levels of food supply (e. g., Thomas 2007), as characterized by abundant buliminids and infaunal uniserial taxa with highly complex apertures, when it has generally been argued that surface productivity in a Greenhouse World was lower than today's productivity (Norris et al. 2013). Autotrophic picoplankton accounts for possibly up to 50% of modern marine productivity, and dominates in warm oligotrophic conditions (Agusti et al. 2019). Its global contribution may have been higher during a high-pCO$_2$, warm world (Ramirez-Llodra et al. 2010), but we do not know the role of non-fossilizing picoplankton in the food supply in the non-analog, Cenozoic Greenhouse World, where eukaryote diatoms were much less abundant than in todays' oceans (Falkowski et al. 2004). Alternatively or additionally, in a warmer ocean, deep-sea particulate organic matter may have been, to a larger extent than in today's oceans (Molari et al. 2013, Gooday et al., 2020), provided by dark inorganic fixation. Uncertainties regarding the processes of transfer of organic matter to the seafloor and on its local production by Archaea and Bacteria hamper comparison with the present day oceans (see speculations in Thomas 2007). In oceans with higher remineralization of organic carbon (e.g., Boscolo-Galazzo et al. 2018), due to a high portion of productivity by pico-plankton in oligotrophic waters and to high metabolic rates, at least part of the food supply to benthic foraminifera may have been in the form of dissolved organic matter, as in a few living forms (Lipps 1983). We must realize that under such conditions bentho-pelagic coupling may have functioned differently from that in todays' oceans.

The middle Eocene (Lutetian) at ~47 Ma stands out as a critical time when the latitudinal diversity gradient (low diversity at high latitudes e. g., Southern Ocean; and higher diversity in the Pacific Ocean) was established among benthic foraminifera, as in the plankton (Fenton et al. 2016), which experienced significant speciation (Ezard et al., 2011). This contrasts with the Maastrichtian–early Eocene benthic assemblages, which had similar diversity at high and low latitudes. The latitudinal diversity gradient (and decrease in high-latitude diversity), previously dated back to the transition from a "greenhouse" to an "icehouse" world (Thomas and Gooday 1996), has been linked to higher

seasonality in productivity (Thomas and Gooday 1996; Culver and Buzas 2000; Corliss et al. 2009) at a time when high latitude surface waters cooled and sea ice started to form or expand, coeval with an increase in relative abundance of phytodetritus exploiting taxa (PET) from the middle Eocene to the Oligocene (Thomas and Gooday 1996; Ortiz and Thomas 2015). Such taxa include *Globocassidulina subglobosa* (Suhr et al. 2003; Fenero et al. 2010), documented to respond to seasonal pulses of fresh phytodetritus (Gooday 1988) and preferentially feeding on diatoms today (Suhr et al. 2003).

Cooling from the late early Eocene on, though interrupted by hyperthermal events including the Middle Eocene Climate Optimum (Boscolo-Galazzo et al. 2014) and the Late Lutetian Thermal Maximum (Rivero-Cuesta et al., 2020), led to major changes in phytoplankton diversity (Bown et al. 2004; Falkowski et al. 2004) and in the oceans' microbial systems (nitrogen, Kast et al. 2019; sulfur, Rennie et al. 2018, and Yao et al. 2020), increased seasonality at high latitudes (Thomas and Gooday 1996; Fenero et al. 2010), and potentially changes in the rate of remineralization (John et al. 2014; Boscolo-Galazzo et al. 2018), ocean oxygenation and the size of the dissolved organic oceanic reservoir, leading to significant long-term reorganization of benthic assemblages. The upper depth limit of *N. umbonifera* rose from the Eocene to the Oligocene (Van Morkhoven et al. 1986) while the CCD deepened (Merico et al. 2008), suggesting more oligotrophic conditions (assemblages dominated by *N. umbonifera*, which replaced *N. truempyi*) and more seasonal food supply (increased abundance of Phytodetritus Exploiting Taxa). In addition, low diversity at high latitudes likely reflects a complex response to the increased abundance of diatoms (Lazarus et al. 2014) among the autotrophic plankton (Fig. 8), including the establishment of the modern bentho-pelagic coupling. Slower metabolic rates induced by cooling may have reduced the food requirements of benthic foraminifera, at a time of long-term changes in pelagic ecosystems, more vigorous thermohaline circulation, increased turbulence of high latitude surface waters (and pulsed nutrient supply), resource competition with the main phytoplankton groups (dinoflagellates and calcareous nannoplankton) and increased physical weathering at the time of glaciation in Antarctica (Falkowski et al. 2004).

4. Conclusions

Deep-sea benthic foraminifera are intimately linked to the long-term climatic evolution of the Cenozoic, and reflect the nature and pace of global environmental change. Rapid events such as an asteroid impact may be devastating to life in surface environments, but the effects (even with severe extinction of phytoplankton) are attenuated before they reach the deep-sea environments. In contrast, events on time scales of deep-sea circulation (millennia) may severely affect deep-sea biota, but probably only if they reach a 'tipping point', which was reached during the PETM but apparently not during subsequent hyperthermals.

Neither the K/Pg nor the PETM (despite its severe extinctions) significantly changed the overall structure of the deep-sea benthic assemblages, however. Such a fundamental change happened during the gradual Cenozoic cooling, which resulted in long-term, lasting changes in the oceanic carbon cycle, including the microbial loop, and the establishment of 'modern' bentho-pelagic coupling. We speculate that this fundamental change in benthic assemblages may have been linked to major changes in functional types of dominant phytoplankton. The proliferation of dinoflagellates after the mass extinction of calcareous plankton at the K/Pg boundary was not critical to benthic foraminifera, but their replacement by diatoms during the Eocene-Oligocene transition did have a profound effect. Further studies are needed to evaluate the close link between the long-term evolution of benthic assemblages and changes in functional types of dominant phytoplankton. Our review of currently available, comparable studies on deep-sea benthic foraminifera provides insight into the origin of oceanic bentho-pelagic coupling and latitudinal diversity gradients, and throws new light into

the potential intimate link of their long-term evolution to global climate change and the evolution of pelagic oceanic ecosystems.

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