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Cenozoic record of elongate, cylindrical, deep-sea benthic foraminifera in the North Atlantic and equatorial Pacific Oceans

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A B S T R A C T

In the late Pliocene–middle Pleistocene a group of 95 species of elongate, cylindrical, deep-sea (lower bathyal–abyssal) benthic foraminifera became extinct. This Extinction Group (Ext. Gp), belonging to three families (all the Stilostomellidae and Pleurostomellidae, some of the Nodosariidae), was a major component (20–70%) of deep-sea foraminiferal assemblages in the middle Cenozoic and subsequently declined in abundance and species richness before finally disappearing almost completely during the mid-Pleistocene Climatic Transition (MPT). So what caused these declines and extinction?

In this study 127 Ext. Gp species are identified from eight Cenozoic bathyal and abyssal sequences in the North Atlantic and equatorial Pacific Oceans. Most species are long-ranging with 80% originating in the Eocene or earlier. The greatest abundance and diversity of the Ext. Gp was in the warm oceanic conditions of the middle Eocene–early Oligocene. The group was subjected to significant changes in the composition of the faunal dominants and slightly enhanced species turnover during and soon after the rapid Eocene–Oligocene cooling event. Declines in the relative abundance and flux of the Ext. Gp, together with enhanced species loss, occurred during middle–late Miocene cooling, particularly at abyssal sites. The overall number of Ext. Gp species present began declining earlier at mid abyssal depths (in middle Miocene) than at upper abyssal (in late Pliocene–early Pleistocene) and then lower bathyal depths (in MPT). By far the most significant Ext. Gp declines in abundance and species loss occurred during the more severe glacial stages of the late Pliocene–middle Pleistocene.

Clearly, the decline and extinction of this group of deep-sea foraminifera was related to the function of their specialized apertures and the stepwise cooling of global climate and deep water. We infer that the apertural modifications may be related to the method of food collection or processing, and that the extinctions may have resulted from the decline or loss of their specific phytoplankton or prokaryote food source, that was more directly impacted than the foraminifera by the cooling temperatures.

1. Introduction

1.1. Cenozoic deep-sea foraminiferal species turnovers

During the Cenozoic, deep-sea benthic foraminifera are reported to have had relatively slow background species turnover of ~2%Myr^{-1} (Boltovskoy, 1987; McKinney, 1987; Kucera and Schönfeld, 2007), equating to average species durations of ~50 Myr. These species turnovers mostly occurred during four periods of significant global climate change (Fig. 1) and involved species originations and extinctions and also changes in the major components of the deep-sea assemblages.

The first turnover was during the Paleocene–Eocene Thermal Maximum event (PETM, ~55 Ma: Thomas, 1992a), when ~30–35% of deep-sea species disappeared (Tjalsma and Lohmann, 1983; Thomas, 1998, 2007) at a time of rapid expansion of warm, oxygen-depleted, corrosive bottom waters (Katz et al., 1999). Typical highly diverse late Cretaceous–Paleocene foraminiferal assemblages, with common *Stensioeina beccariiformis*, were replaced by late Paleogene Greenhouse World faunas, dominated by *Nuttallides truempyi* and a variety of buliminids (e.g., Tjalsma and Lohmann, 1983; Thomas, 1990, 2007; Kaiho et al., 1996; Takeda and Kaiho, 2007; Alegret et al., 2009).

The second turnover, during late Eocene–early Oligocene cooling, was more gradual, had fewer species originations and extinctions, but resulted in significant faunal assemblage changes (e.g. Thomas et al., 2000). Greenhouse World dominants like *Nuttallides truempyi* and many

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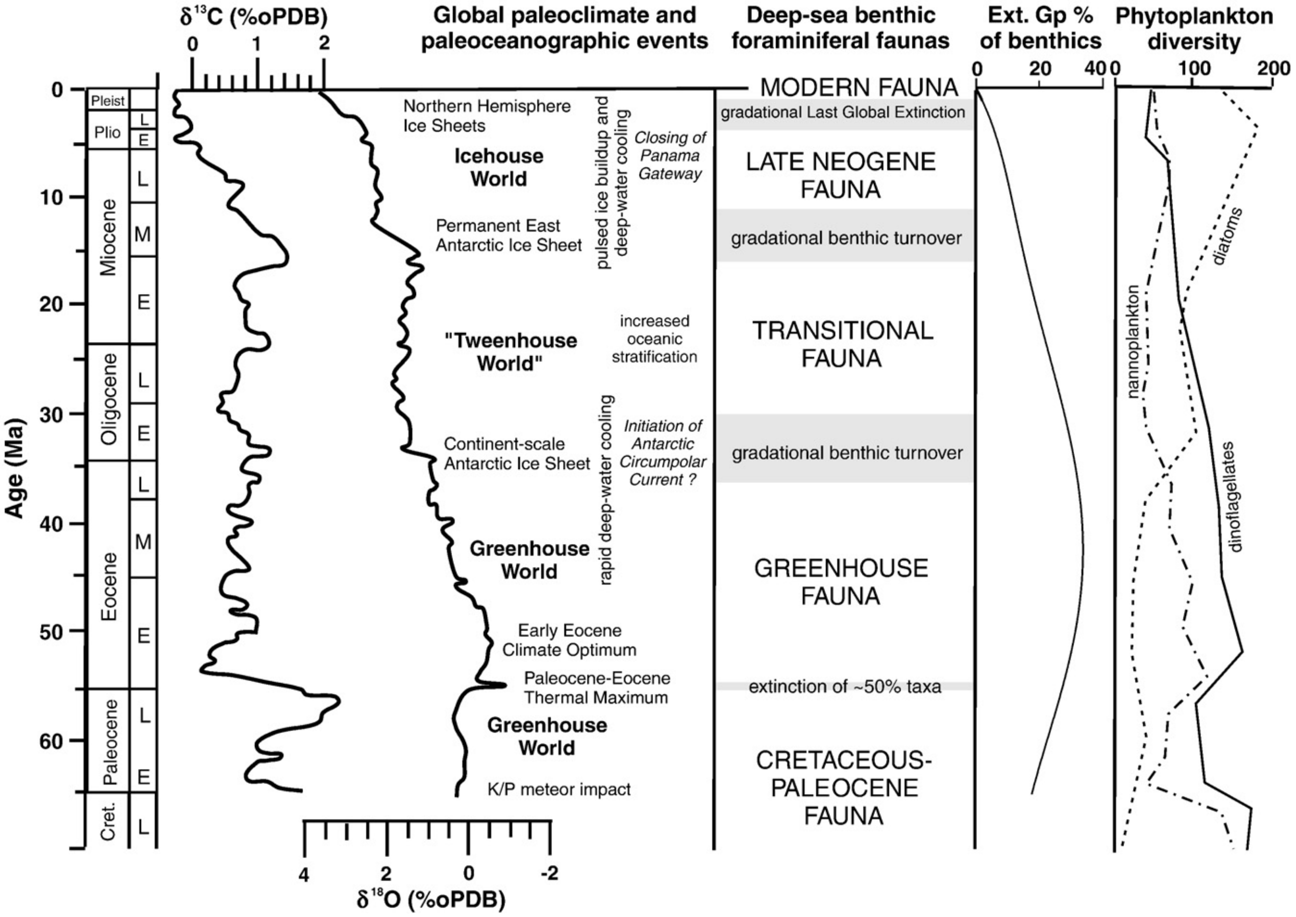

Fig. 1. Equatorial Pacific Ocean compilation of benthic foraminiferal carbon and oxygen isotopic data (from Cramer et al., in press) through the Cenozoic together with inferred timing of major global paleoclimatic and paleoceanographic events, deep-sea benthic foraminiferal faunas and turnovers (modified after Thomas, 2007), mean trendline for relative abundance of Extinction Group benthic foraminifera as percentage of total deep-sea benthic foraminifera (data from Thomas, 2007 and this study), and global species richness (number of species) of diatoms, nannoplankton and dinoflagellates (from Bown et al., 2004; Stover et al., 1996; and Spencer-Cervato, 1999).

large buliminids disappeared and were replaced by faunas transitional in composition between those of the warm late Paleogene and the late Neogene Icehouse World (e.g. Thomas, 1992a, b). This period experienced the largest deep-water cooling (~8 °C) of the Cenozoic (e.g., Zachos et al., 2001; Liu et al., 2009) and led to major changes in oceanic phytoplankton composition and productivity (e.g., Aubry, 1992; Baldauf, 1992; Falkowski et al., 2004a, b; Bown, 2005). Deep-water cooling may have been associated with increased ventilation and carbonate-corrosiveness (e.g., Wright and Miller, 1996; Thomas, 2007), but the nature of deep-sea circulation and meridional overturning in the Greenhouse World is still poorly known and may have been fundamentally different from the modern patterns (e.g., Emanuel 2002; Thomas et al., 2006). From the early Oligocene on, low-latitude faunas became dominated by opportunistic, seasonal phytodetritus-feeding-species such as *Epistominella exigua* and later *Alabaminella weddellensis* (Nomura, 1995; Thomas et al., 2000; Gooday, 2003). High latitude deep-water became dominated by *Nuttallides umbonifera*, characteristic of cold, carbonate-corrosive, oligotrophic, southern-sourced water (e.g., Bremer and Lohmann, 1982; Schröder-Adams, 1991; Thomas, 1992b; Jorissen et al., 2007), although this species' exact ecology is not well known.

The third turnover, during middle Miocene cooling, had effects on the deep-sea foraminiferal faunas similar to those of the second turnover (e.g., Woodruff, 1985; Thomas, 1986a, b, 1987). At this time there was further strengthening of the circulation of cool, well-oxygenated bottom water and increasing primary productivity and seasonality of phytoplankton blooms in the oceans, coupled with global cooling due to formation and growth of East Antarctic ice sheets (e.g., Thomas and Vincent, 1987; Thomas, 2007). Through the middle Miocene and into the early late Miocene (15–8 Ma) the transitional faunas were transformed into those characteristic of late Neogene times with the evolution of *Cibicides wuellerstorfi* and further increases in seasonal phytodetritus-feeding-species at bathyal depths, increased dominance of *Nuttallides umbonifera* at abyssal depths, and the descent of miliolid genera such as *Pyrgo* into the deep sea (e.g., Woodruff, 1985; Kurihara and Kennett, 1986; Schröder-Adams, 1991; Thomas, 1992a; Hayward et al., 2004; Smart et al., 2007).

The fourth turnover or Last Global Extinction (LGE) of deep-sea benthic foraminifera ("*Stilostomella* Extinction" of Weinholz and Lutze, 1989; Schönfeld, 1996) resulted in the extinction of ~20% of lower bathyal–abyssal foraminiferal diversity. It occurred in the late Pliocene to middle Pleistocene (~2.6–0.55 Ma) during increasingly cold glacial periods that accompanied growth of polar sea ice sheets and further increases in primary productivity at lower latitudes (Hayward et al., 2007). Late Neogene assemblages were replaced by faunas characteristic of modern oceans, with the loss of elongate, cylindrical species and decline in the abundance of reticulate-ornamented bolivinids, *Rectuvigerina*, *Vulvulina*, *Trifarina bradyi*, *Bulimina exilis*, and *Uvigerina hispida*. These were replaced by increasingly dominant *Cassidulina carinata*, *Bulimina marginata* var. *aculeata*, *Nonionella*, *Trifarina angulosa*, *Alabaminella weddellensis* and *Uvigerina peregrina* (e.g., Kurihara and Kennett, 1986; Mackensen et al., 1992; Nomura, 1995; Yasada, 1997; Hayward, 2002; Hayward et al., 2004). No deep-water species originations are known from this period.

1.2. The Last Global Extinction (LGE)

During the LGE ~ 20% (19 genera, 95 species) of cosmopolitan, deep-sea (500–4000 m), benthic foraminiferal species (excluding unilocular taxa), belonging to three families, became extinct. During the late Pliocene–middle Pleistocene (3.0–0.12 Ma), a whole family (Stilostomellidae, 30 species) was wiped out and a second (Pleurostomellidae, 29 species) was decimated with just one species possibly surviving to the Present (Hayward et al., 2007). Most of these extinctions (76 species) occurred during the mid-Pleistocene Climate Transition (MPT, 1.2–0.55 Ma). Unlike the PETM deep-sea extinction event (MacLeod et al., 2000), this LGE preferentially impacted species with specific morphologies (elongate, cylindrical, often uniserial tests) and apertural types (e.g., small rounded, dentate, cribrate, or lunate).

We have recently standardized the previously chaotic taxonomy of the Extinction Group of taxa (Ext. Gp), so as to consistently document the global architecture of its populations through the late Pliocene–Recent decline in 23 deep-sea core sites (Hayward, 2001, 2002; Hayward et al., 2006, 2007, 2009; Kawagata et al., 2005, 2006, 2007; O'Neill et al., 2007). These publications show that the Ext. Gp suffered widespread, pulsed declines in abundance and diversity during the more severe glacial stages, with partial interglacial recoveries. The decline started in the late Pliocene in deeper depths bathed in southern-sourced deep-water masses, such as Antarctic Bottom Water (AABW) and Circumpolar Deep Water (CPDW) and extended into the shallower Antarctic Intermediate Water (AAIW) and North Atlantic Deep Water (NADW) during the MPT, with the latest declines in sites furthest down-current from high-latitude source areas of intermediate water (Hayward et al., 2007).

1.3. Rationale for the study

The purpose of this study is to investigate what caused the Last Global Extinction of foraminifera in the deep sea during increasingly cold glacial periods of the late Pliocene to mid-Pleistocene Climate Transition. To do this we address the following questions:

1. Does the Cenozoic history of the Ext. Gp provide clues as to why it became extinct?
2. Was the Ext. Gp composed of taxa with a long history of frequent turnovers?
3. Was the Ext. Gp impacted by other periods of major, rapid global climate change (i.e., Paleocene–Eocene Thermal Maximum, the Eocene–Oligocene cooling and the middle Miocene cooling)?
4. Were the Ext. Gp taxa some of the last remnants of the Greenhouse World deep-sea biota?

We chose to study four deep-sea core sites with long Cenozoic records and well-preserved benthic foraminiferal faunas — two from the North Atlantic and two from the equatorial Pacific. To these we have added records from the late Pliocene–Pleistocene previously documented by us from five further sites — three from the North Atlantic and two from the equatorial Pacific.

1.4. Study sites

DSDP Site 317 (11° 00′S, 162° 16′W, upper abyssal present water depth) and KR9912-PC4 (12° 48′S, 162° 10′W, upper abyssal) are located on the Manihiki Plateau in the equatorial Pacific Ocean (Fig. 2). KR9912-PC4 is a 14 m-long piston core that sampled the upper Pliocene–Recent. At Site 317 (Fig. 3) samples were taken from a near continuous, 400 m-thick sequence of middle Eocene to Recent foraminiferal–nannofossil ooze and chalk (Schlanger et al., 1976) (Table 1). The age model for Site 317 is the original nannofossil-based model of Schlanger et al. (1976), whereas the age model for KR9912-PC4 (Fig. 4) is an unpublished astronomically-tuned model using planktic oxygen isotopes (Kawagata, pers. obs.). Total benthic foraminiferal faunas of Site 317 have been described by Boltovskoy and Watanabe (1994). Schönfeld (1995) described the total benthic faunas from the upper Pliocene–Recent in a piston core (SO67 34KL) adjacent to Site 317 and documented the disappearance of stilostomellids and pleurostomellids during the MPT in it. As the two sites are situated close together and at similar depths we have combined their records.

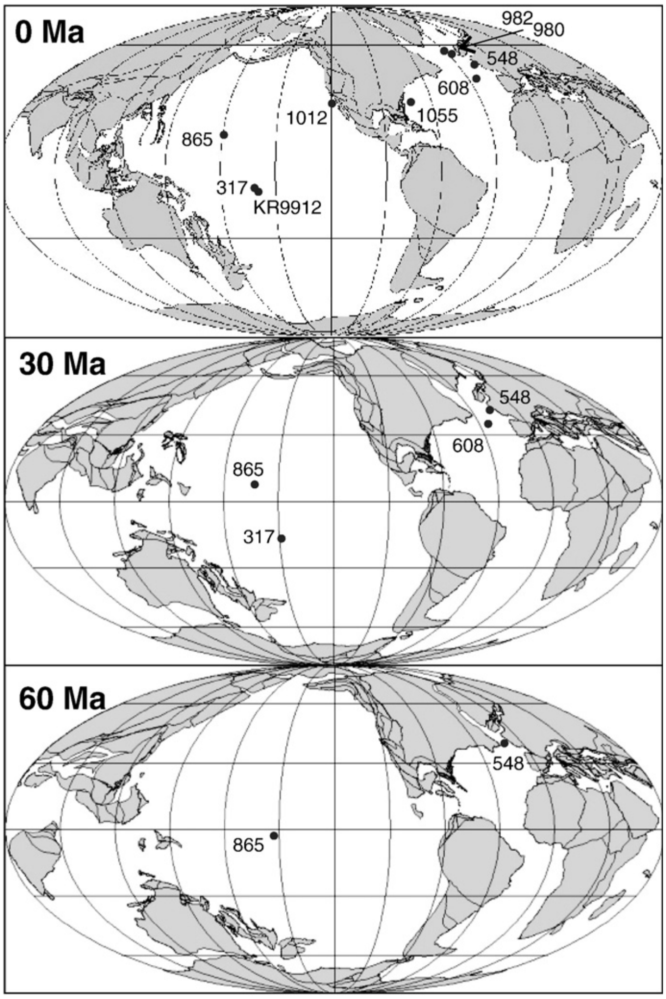

Fig. 2. Back-tracked location of ODP study sites in the Paleocene (60 Ma), Oligocene (30 Ma) and modern (0 Ma). Tectonic reconstructions are from Schettino and Scotese (2005) (http://www.serg.unicam.it/Intro-Reconstr.html).

DSDP Site 548 (48° 55′N, 12° 10′W, lower bathyal) is located on the continental slope of the Northeast Atlantic, south-west of Ireland (Fig. 2). Samples were taken from an essentially complete Paleocene–middle Pleistocene sequence with a few short hiatuses (Fig. 5). The age model is based on the original biostratigraphic model of de Graciansky et al. (1985). A previous work on the total benthic foraminiferal faunas of this site has been undertaken by Caralp (1985), Poag and Low (1985), and Boltovsky et al. (1992).

DSDP Site 608 (42° 50′N, 23° 05′W, mid abyssal) lies between the mid-Atlantic Ridge and the Iberian Peninsula in the northeastern Atlantic (Fig. 2). For this study we used samples processed by Thomas (1987) from a 450 m-thick essentially complete upper Oligocene–Recent sequence (Fig. 6). The age model is based on the paleomagnetic and biostratigraphic syntheses of Baldauf et al. (1987). The total benthic foraminiferal faunas have been studied by Thomas (1986a, b, 1987).

ODP Site 865 (18° 26′N, 179° 33′W, lower bathyal) is located on the summit of Alison Guyot near the centre of the equatorial North Pacific Ocean (Fig. 2). Samples were taken from an essentially complete 130 m-thick lower Paleocene to lower Miocene sequence of foraminiferal–nannofossil ooze (Fig. 7). The age model is based on

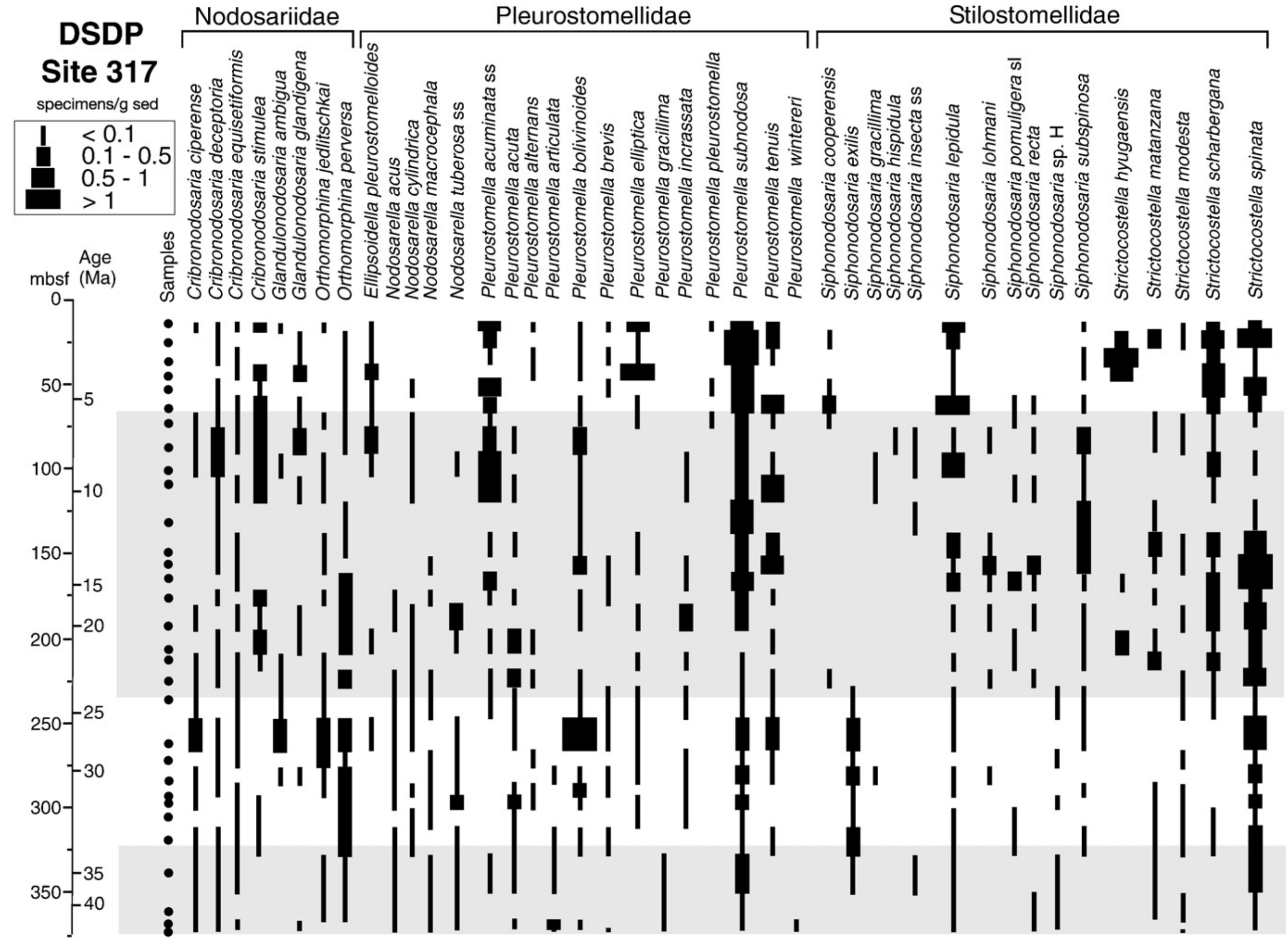

Fig. 3. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in DSDP Site 317. Eocene and Miocene shaded.

the nannofossil biostratigraphy of Bralower and Mutterlose (1995). A detailed study of the benthic foraminiferal extinction across the Paleocene–Eocene Thermal Maximum at this site has been undertaken at this site by Thomas (1998).

ODP Sites 980 and 982 (55–57°N, 14–15°, lower bathyal and upper abyssal) are located in the North Atlantic Gateway (Fig. 2). In this study we use the published results of Kawagata et al. (2005) who documented the demise of the Ext. Gp through the latest Pliocene–middle Pleistocene. As Sites 548 and 980 occur at similar water depths in the northern North Atlantic, we have combined their records.

ODP Site 1012 (31° 17′N, 118° 23′W, lower bathyal) is located in the Northeast Pacific Ocean (Fig. 2). Studied samples come from the

Table 1
Location of the North Atlantic and equatorial Pacific Ocean deep-sea study sites and the number, age range and source of samples.

Core site	Location latitude, longitude	Present depth	No. of samples	Age of samples	No. Ext. Gp spp.	Sample sources
DSDP 317	Equat. Pacific Ocean 11° 00′S, 162° 16′W	2598 m	33	m Eoc-l Plio	67	ODP store
KR9912-PC4	Equat. Pacific Ocean 12° 48′S, 162 10′W	2326 m	102	l Plio-m Pleist	39	Unpub. Kawagata study
DSDP 548	NE Atlantic Ocean 48° 55′N, 12°10′W	1250 m	33	l Paleo-m Pleist	74	ODP store
DSDP 608	N Atlantic Ocean 42° 50′N, 23° 05′W	3534 m	15 15	l Oligo-l Mio l Oligo-Rec	58	ODP store from Thomas (1987)
ODP 865	N Pacific Ocean 18° 26′N, 179° 33′W	1518 m	29	e Paleo-e Mio	73	
ODP 980	N Atlantic Ocean 55° 29′N, 14° 42′W	1145 m	38	e-m Pleist	49	Kawagata et al. (2005)
ODP 982	N Atlantic Ocean 57° 31′N, 15° 52′W	2168 m	46	l Plio-m Pleist	43	Kawagata et al. (2005)
ODP 1012	NE Pacific Ocean 31° 17′N, 118° 23′W	1772 m	28	e-m Pleist	34	ODP store
ODP 1055	NW Atlantic Ocean 32° 47′N, 76° 17′W	1798 m	13	e-m Pleist	45	ODP store
Total number of samples			352			

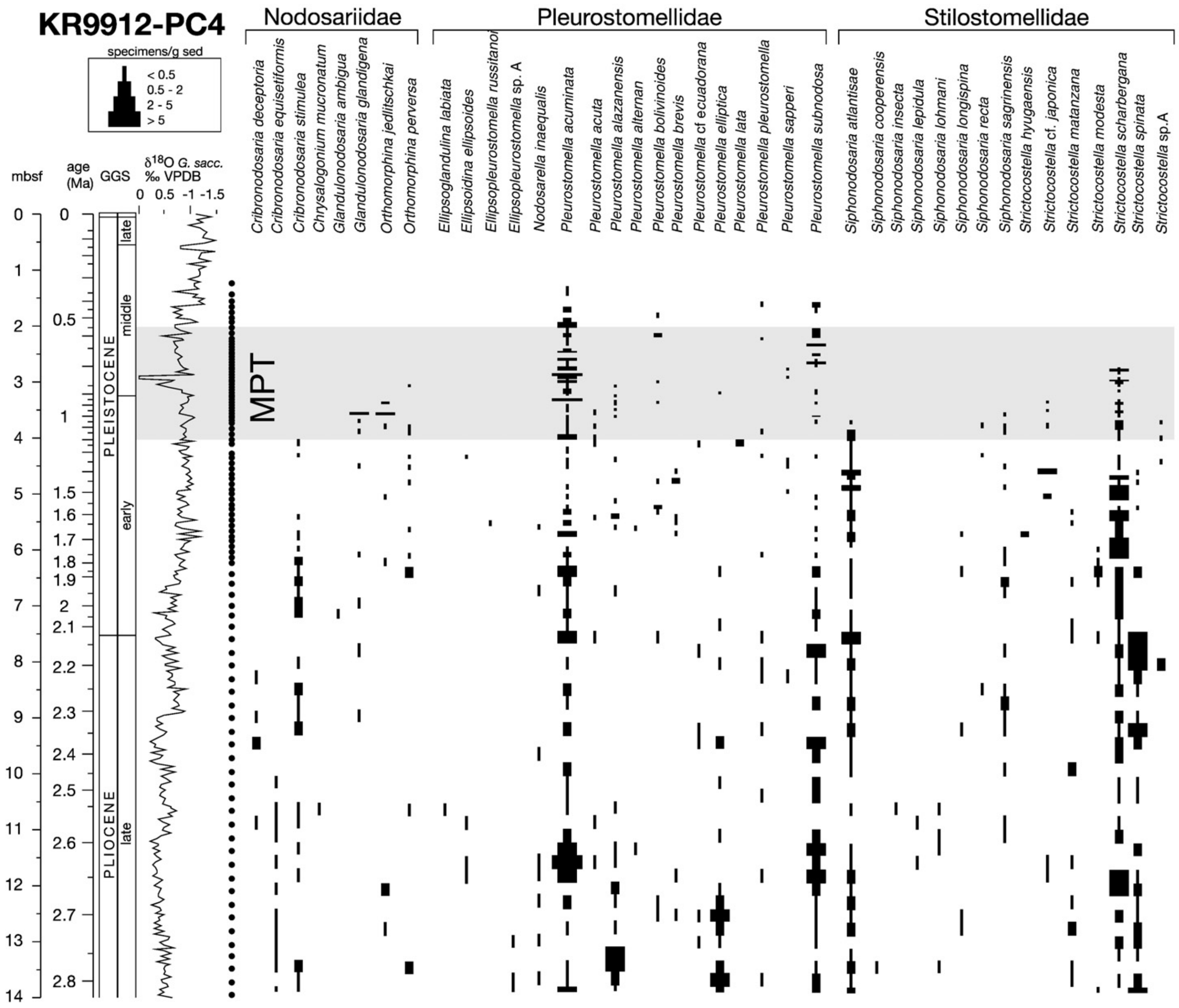

Fig. 4. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in KR9912-PC4. Mid-Pleistocene Climate Transition (MPT) shaded.

lower–middle Pleistocene sequence (Fig. 8). The age model is the same as that used by Lisiecki and Raymo (2005).

ODP Site 1055 (32° 47′N, 76° 17′W, lower bathyal) is located on the Carolina Slope in the North-west Atlantic Ocean. Studied samples are from the lower–middle Pleistocene section (Fig. 9). We use the astronomically-tuned age model of Grützner et al. (2002) for the section <0.9 Ma; below that, age was calculated using the calcareous nannofossil datum for the top of large *Gephyrocapsa* = 1.24 Ma (Keigwin et al. 1998).

The age models of all sites have been recalibrated to the latest International Commission on Stratigraphy's time scale (Gradstein et al., 2004), with the base Quaternary taken at 1.8 Ma, and divisions between the early, middle and late Pleistocene defined at 0.78 and 0.126 Ma.

2. Methods

2.1. Sample processing

Core sites were selected for their long Cenozoic carbonate-rich records from lower bathyal–mid abyssal depths (1000–4000 m) with common Ext. Gp specimens. Samples were selected to span as much of the Cenozoic as possible at each studied site (Table 1). Approximately 20 cm^3 of dry sediment was weighed, washed gently with water over a 63 μm sieve, and the retained sand fraction was dried.

2.2. Census counts

Each sample was dry-sieved, and three size fractions (>300 μm, 150–300 μm, and 63–150 μm) were picked and separately counted. In every sample 100% of the >300 μm fraction was searched, and dependent upon the quantity of sand fraction in the other size fractions, the amount searched was 50–100% of the 150–300 μm fraction and 5–50% of the 63–150 μm fraction. Census counts were subsequently multiplied up to the number of specimens in the total sample. For most samples from Site 608 we used Thomas's (1987) quantitatively picked slides of ~300 benthic foraminifera (>63 μm) to obtain an initial census of reidentified Ext. Gp specimens and their relative abundance as a percentage of the total benthic foraminiferal faunas. These were supplemented by additional picks, especially of the coarser fractions (as above), and all data multiplied up and combined to provide standardized absolute abundance data.

The benthic foraminiferal census counts were selective and designed to target just Ext. Gp (Table 2) specimens, which are quite distinctive with

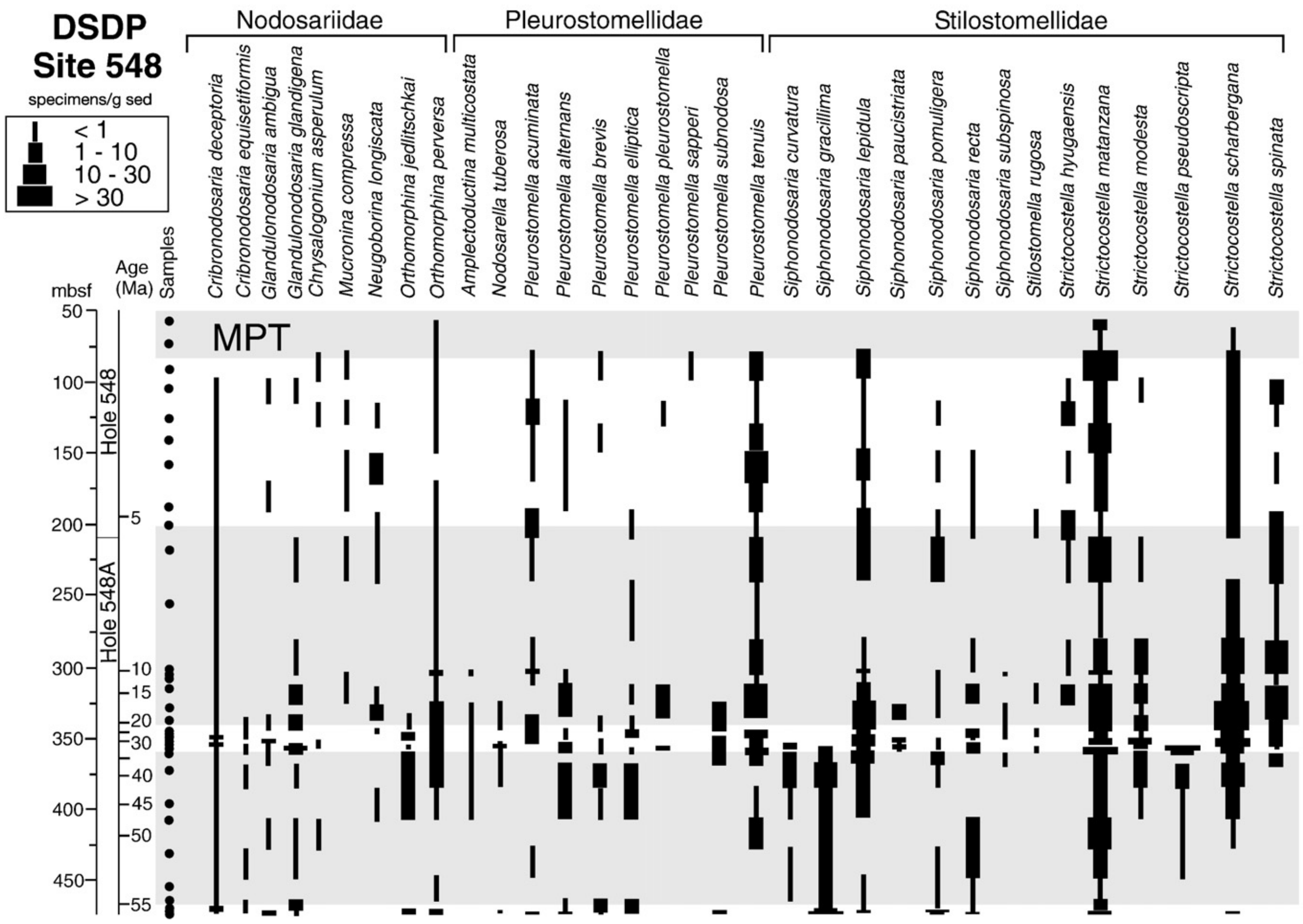

Fig. 5. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in DSDP Site 548. Eocene, Miocene and mid-Pleistocene Climate Transition shaded.

their generally elongate tests. All Ext. Gp specimens encountered were picked from each split fraction and mounted on gummed slides for more detailed identification (Appendix A) and counting (Appendices B–H). Census counts were converted into absolute abundances (specimens g^{-1} sediment) and flux rates (flux = specimens cm^{-2} kyr^{-1}) using sample dry bulk density, weights, and calculated sedimentation rates (cm kyr^{-1}). The majority of the Ext. Gp comprises large species with their populations largely found in the >150 µm size fractions (Hayward et al., 2006) that were more comprehensively examined than the finest fraction, where specimens of only 5–10 Ext. Gp species were present. The total number of benthic foraminifera and extant uniserial nodosariids in a split of unsieved sample was also counted and used in calculations of the relative abundance of the Ext. Gp and total uniserial nodosariids as percentages of benthic foraminifera.

Previous higher resolution Ext. Gp census results from the upper Pliocene and Pleistocene of Sites 980 and 982 (Kawagata et al., 2005) obtained by the same methodology and using our revised taxonomy have been re-used in this studies' analyses. To keep our data consistent, all identifications were made by the Geomarine Research-based authors using our revised taxonomy.

2.3. Computer methods

The faunal data consist of census counts (0–500 specimens per sample) of 127 Ext. Gp foraminiferal species from 352 samples (Appendices B–H). For cluster analysis only the 200 samples with >8 Ext. Gp species present were used. The data matrix was standardized by converting counts to percentages of total Ext. Gp specimens in each sample. Unconstrained and stratigraphically-constrained Q-mode cluster analysis dendrogram classifications were produced using chord dissimilarity coefficient on square-root transformed data (Sneath and Sokal, 1973). Detrended canonical correspondence analysis (DCCA; Kovach, 1993) was used to summarise the Ext. Gp faunal distribution and assist in its interpretation with respect to stratigraphy, bathymetry and biogeography. Ordinations of the samples and species were plotted on the first two detrended correspondence analysis axes. The direction and length of the time, water depth, latitude and longitude vectors (arrows) indicate the direction and strength of their correlation with the faunas. The analyses were carried out using the MVSP statistical package (Kovach, 1993).

2.4. Specimen archiving

Picked slides of Ext. Gp specimens used for census counts are housed in the collections of the GNS Science, Lower Hutt, New Zealand.

3. Cenozoic history and architecture of the Extinction Group

The stratigraphic range and absolute abundance of the more common Ext. Gp species are shown for each of the study sites in Figs. 3–9.

3.1. Species richness

A total of 127 Ext. Gp taxa are identified from the Cenozoic of the North Atlantic and equatorial Pacific Oceans (Appendix A). Ninety percent of the 110 Ext. Gp species known globally from the Pliocene–Pleistocene are recorded from the North Atlantic and equatorial Pacific Oceans. Most of those not recorded are classified in the subfamily

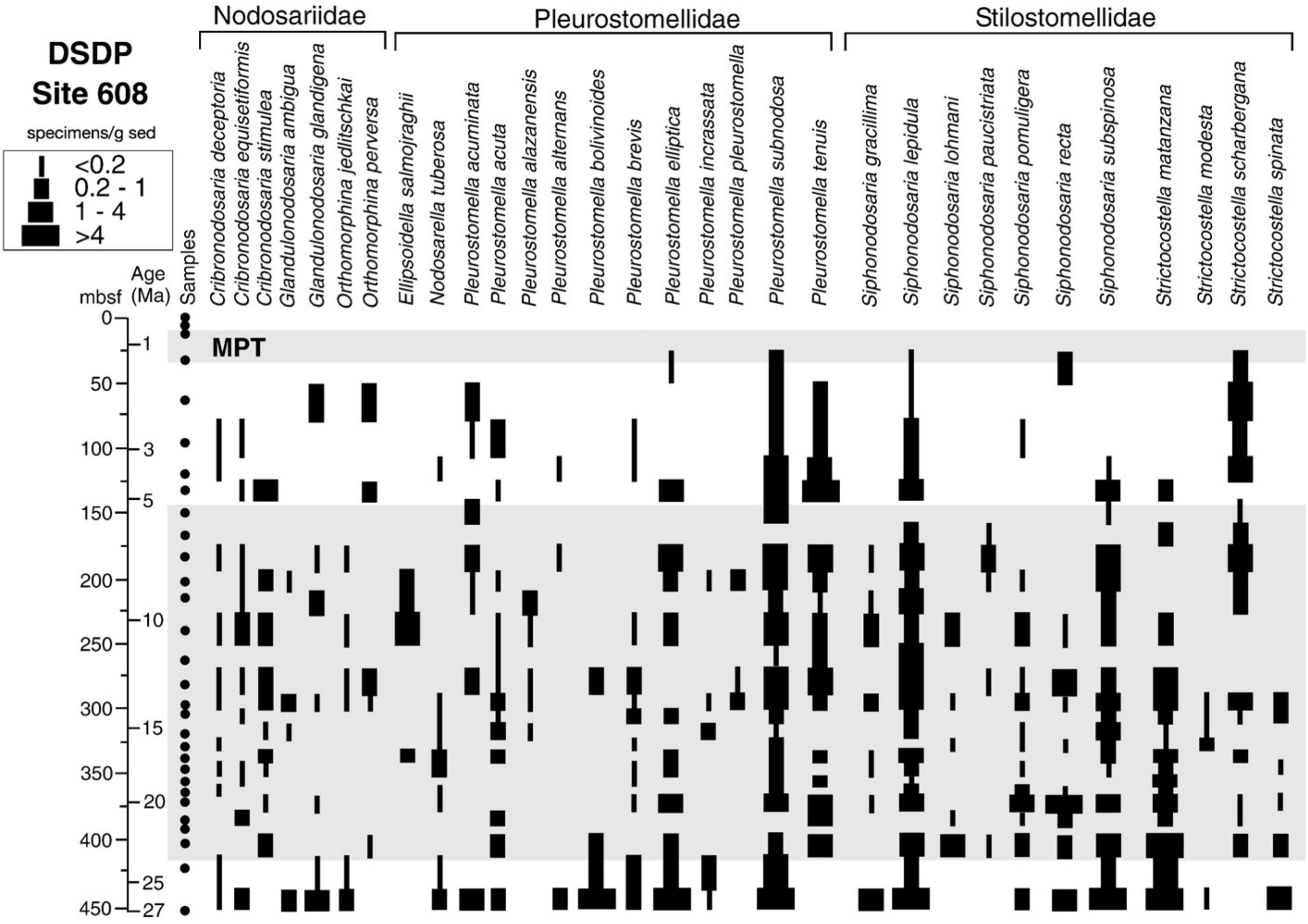

Fig. 6. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in DSDP Site 608. Miocene and mid-Pleistocene Climate Transition shaded.

Plectofrondiculariinae, known to be more prevalent in shallower water (outer shelf-mid bathyal) than our sites.

Not unexpectedly, sites where studies were limited to the Pliocene–Recent interval had the lowest Ext. Gp species richness (34–49 spp.) with apparently fewer species present at that time in the Pacific (34–39 spp.) than the North Atlantic sites (43–49 spp.) (Table 1). At the three sites where most of the Paleogene and Neogene intervals were studied (Sites 317, 548, and 865), total species richness was similar (67–74 spp.) in both oceans. Overall the two regions in this study had similar Ext. Gp species richness (North Atlantic = 103 spp., equatorial Pacific = 105 spp.) with 25 species not in common (Appendix I). This compares with 113 species recorded through the same interval from a similar study in the Indian Ocean (Hayward et al., 2010) with an additional 12 rare species not yet recorded beyond the Indian Ocean.

The greatest species richness in individual samples occurred in the Oligocene in Sites 317, 548 and 608 and in the late Eocene–Oligocene in Site 865 (Fig. 10). In terms of overall number of species at a site (where each species is considered to have been continuously present from its FO to LO, and where absence from samples in between was due to its rareness), numbers increased during the Paleocene and Eocene reaching a peak species richness in the mid-late Eocene at Site 865 and in the early Oligocene at Sites 317 and 548 (Fig. 10). Overall species number began to decline earliest (during the late Eocene) in the equatorial North Pacific (865), but this may be an artifact of the few post-Eocene samples (3) studied at this site (Fig. 7). A slow decline in the other Pacific site (317) began in the early Oligocene but with the major loss of species in the Pleistocene. In the North Atlantic abyssal site (608), overall species number declined progressively from the middle Miocene through to the Pleistocene, whereas at the bathyal site (548) there was no significant decline through the Miocene or Pliocene, but a dramatic disappearance in the MPT (Fig. 10).

3.2. Species turnover

To investigate the timing of species turnovers at individual sites we have calculated the number of first occurrences (FOs) and last occurrences (LOs) in 1 Myr and 5 Myr intervals (Fig. 11). The numerous FOs near the base of the studied sections at each site are clearly an artifact of the sampling, as is the late early Miocene peak of LOs in Site 865 at the top of the section studied in that site. When these artifacts are ignored, it is possible to identify a period of enhanced FOs in the early Oligocene at Sites 317 and 548, and perhaps in the late middle Miocene at Site 548 (Fig. 11).

There was also a peak of LOs in the early Oligocene at all three sites that sampled this interval (317, 548, and 865), with the interval of enhanced LOs starting in the late Eocene in Pacific Site 865 (Fig. 11). After the early Oligocene there was a low level of scattered LOs from the late Oligocene to early Pliocene at these sites. In the deepest site (608) however, there were three peaks of LOs each more significant than the previous (in the middle Miocene, late Miocene, and late Pliocene–early Pleistocene). The most significant period of species turnover at all sites that sampled up to the Recent was the LOs during the late Pliocene through to the MPT (Figs. 4–6, 8, 9, and 11). These are the local records of the Last Global Extinction when our Ext. Gp

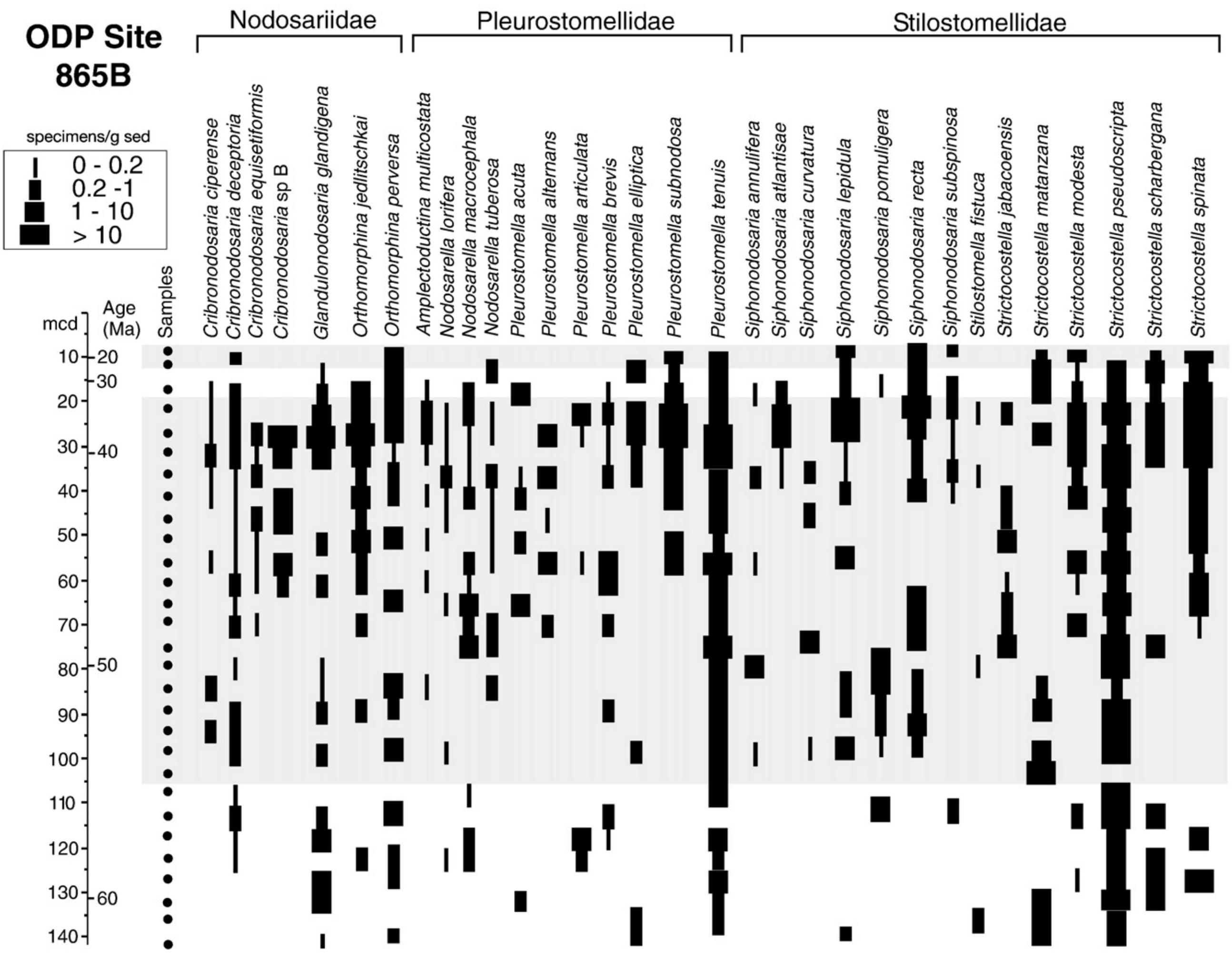

Fig. 7. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 865. Eocene and Miocene shaded.

disappeared world-wide (Hayward et al. 2007). The peak of LOs occurred earlier (late Pliocene) in deeper water (608) and later (during the Pleistocene) in shallower sites (KR9912-PC4, 548, 980, 982, 1012, and 1055; Kawagata et al., 2005; Hayward et al. 2007). The latest record of any of the Ext. Gp species occurred between 0.7 and 0.65 Ma in all sites except Sites 1055 and KR9912, where there are sporadic rare records above this.

3.3. Flux, absolute and relative abundance

The peak absolute abundance (specimens g^{-1} sediment) and flux (specimens cm^{-2} kyr^{-1}) of the Ext. Gp were in the Oligocene in both North Atlantic sites (548 and 608), but in the late Eocene in the bathyal Pacific site (865) and the middle Miocene and Plio-Pleistocene in the abyssal Pacific site (317) (Fig. 12). The relative abundance (number of Ext. Gp specimens as a percentage of the total benthic foraminifera) is equally inconsistent. Once again the earliest peak of relative abundance was in the bathyal Pacific site (865), but in this instance in the early Eocene (Fig. 12). There were three equal peaks of relative abundance in abyssal Pacific Site 317 (Oligocene, middle Miocene, and Pliocene) and also (less pronounced) in the bathyal North Atlantic Site 548 (early Eocene, Oligocene, and Plio-Pleistocene). Abyssal North Atlantic Site 608 underwent a stepped decline in relative abundance of the Ext. Gp (in the early Miocene, middle Miocene, and late Pliocene), whereas there was a single significant period of decline in Sites 317 and 548 in the Pleistocene (Fig. 12).

3.4. Species duration

We use species duration as the length of time between the first and last stratigraphic occurrences of a species. This gives an indication of the rate of Ext. Gp species turnover. All the species recorded as having species durations of less than 0.5 Myr (Fig. 13) are extremely rare, often with only single recorded occurrences in this study. We consider these durations to be unreliable because of the rarity of the species. The same could be true for most of the species with durations of 0.5–4 Myr and some of those with 5–9 Myr durations. Apart from these short-ranged records, the peaks of species durations in the North Atlantic were in the 50–59 and 20–29 Myr categories, and in the North Atlantic at 60–69 and 30–39 Myr (Fig. 13). The mean species duration for all the recorded Ext. Gp species in the North Atlantic was 23 Myr and in the equatorial Pacific 27 Myr. The sampled interval in the North Atlantic in this study precluded any species durations >60 Myr and this would account for the slightly shorter species duration in that region.

3.5. Faunal composition

We recognize 11 Ext. Gp associations (plus two divided into two sub-associations each) on the chord cluster analysis dendrogram of all

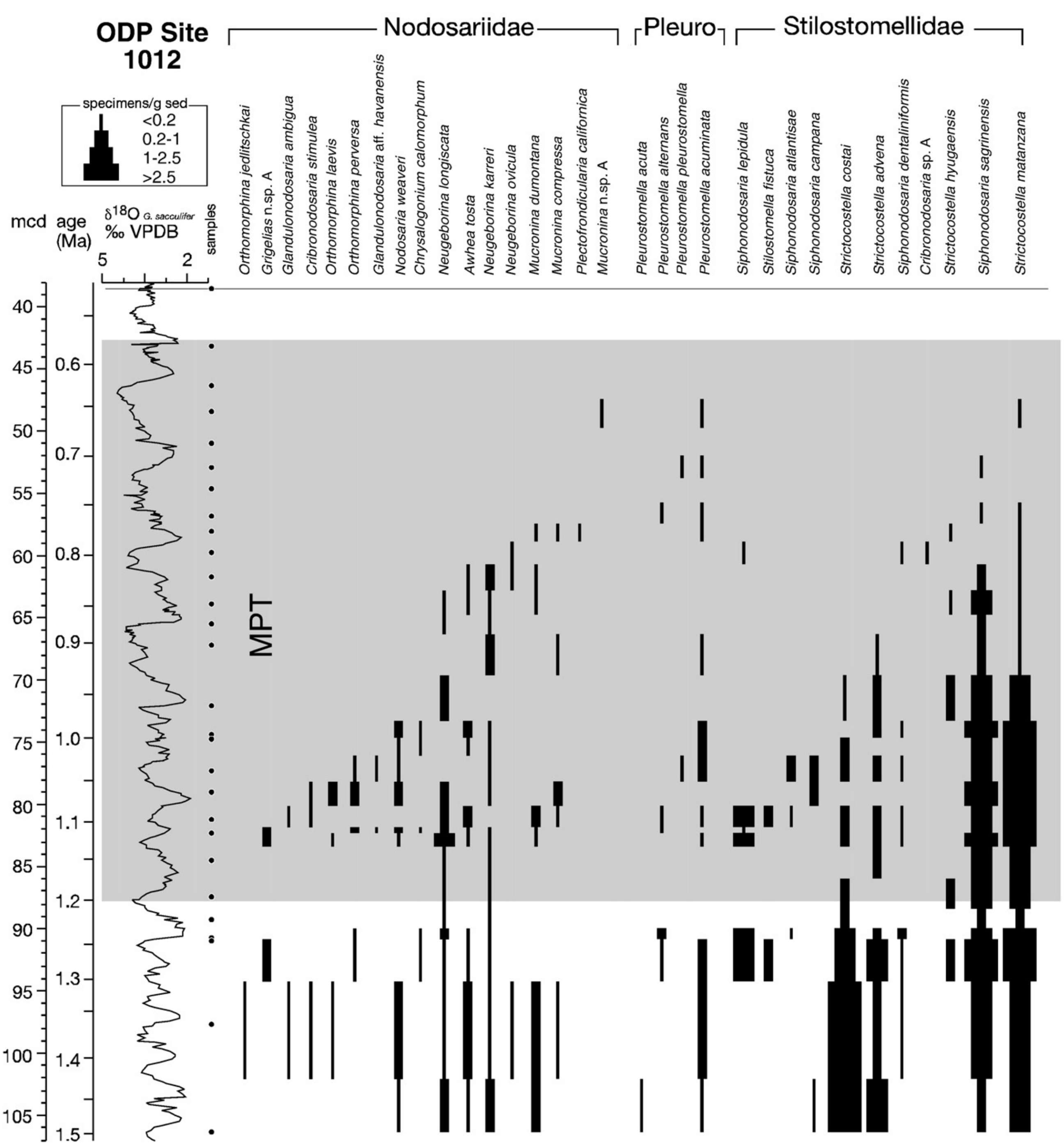

Fig. 8. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 1012. Mid-Pleistocene Climate Transition (MPT) shaded.

samples with more than 8 Ext. Gp species (Supplementary On-line Fig. 1, Appendix J). These associations were all dominated by various combinations of species of *Strictocostella*, *Siphonodosaria* and *Pleurostomella*, particularly *S. matanzana*, *S. spinata*, *S. scharbergana*, *S. lepidula*, *P. tenuis* and *P. subnodosa* (Fig. 14, Table 3).

Nearly all these dominant species were long-lived throughout the Cenozoic (Figs. 3, and 5–7) and common at abyssal and lower bathyal depths in both the North Atlantic and equatorial Pacific Oceans. Thus, while the variable relative abundances of these dominant species contribute to the clustering, the large group of less common species also play a significant role in helping to discriminate between the recognized associations.

The vectors on the DCCA ordination of the faunal data indicate that factors that varied with geographic location, time and depth all influenced the composition of these Ext. Gp faunas (Fig. 15). The associations have been numbered in approximately stratigraphic order with the lower diversity Paleocene–middle Eocene associations (1–3) passing upward into higher diversity late Eocene (2b and 4a) and Oligocene–Miocene (2b and 4b–8), and finally lower diversity Pliocene–Pleistocene (9–11) associations (Fig. 16).

On the DCCA ordination there is not a simple age-related arrangement of the associations (from 1 to 11 in Fig. 15) as would occur if species evolution was the major driver of faunal association changes. There is however, a general age-related trend from a group of Paleocene–Eocene

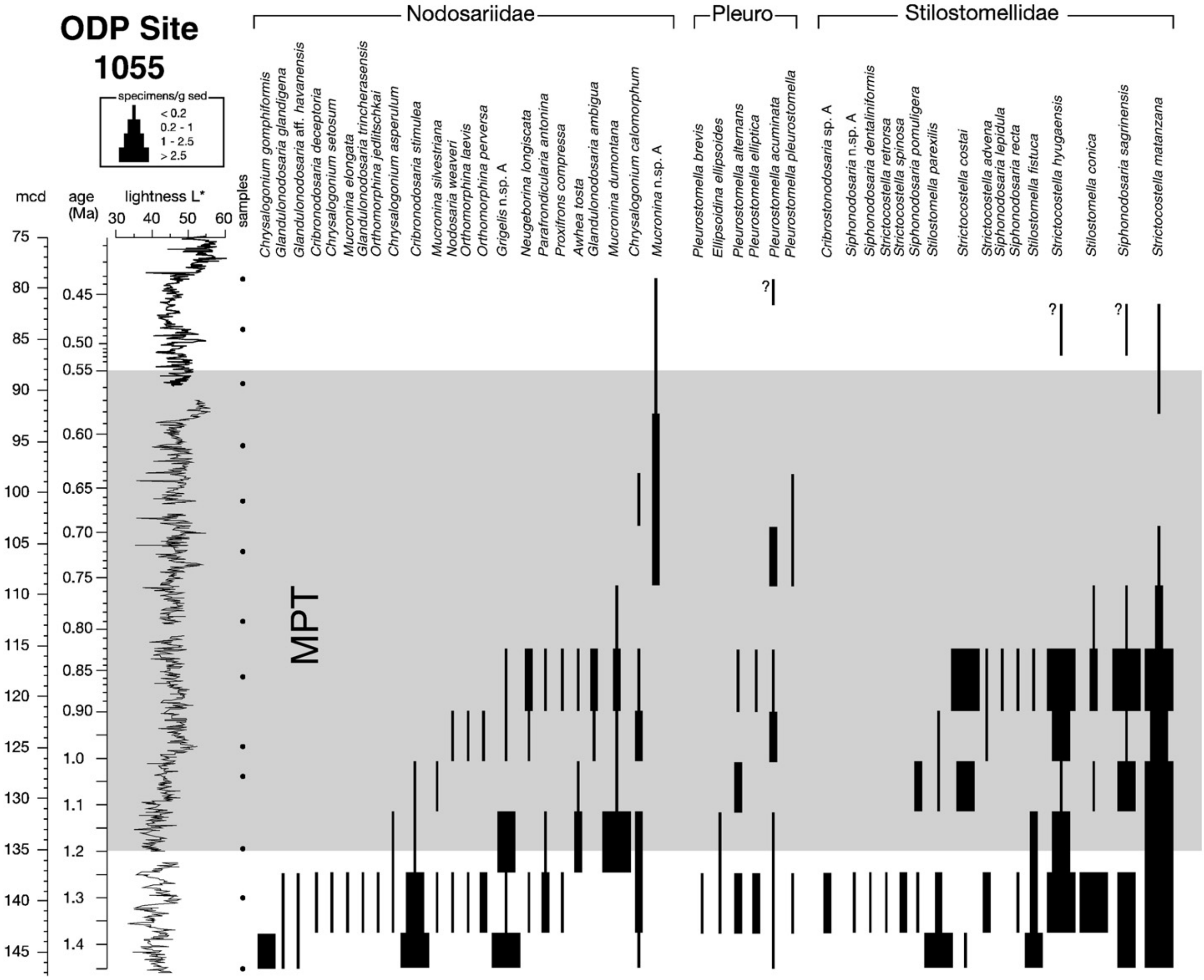

Fig. 9. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 1055. Mid-Pleistocene Climate Transition (MPT) shaded.

associations (1–4a) on the top left, to a group of Oligocene–Pliocene associations (4b–9) in the middle and the two youngest, Pleistocene associations (10–11) on the far right. This trend corresponds with a change in the composition of many of the second-ranked common species, with species plotting on the far left of the ordination (Fig. 15) being common in the Paleogene (e.g. *Amplectoductina multicostata*, *Nodosarella acus*, *N. macrocephala*, *N. tuberosa*, *Pleurostomella articulata*, *P. gracillima*, *Siphonodosaria curvatura*, *S. exilis*, *S. gracillima*) and species on the right being common in the Neogene (e.g. *Awhea tosta*, *Mucronina dumontana*, *Neugeborina ovicula*, *Pleurostomella sapperi*, *Siphonodosaria lepidula*, *Strictocostella advena*, *S. hyugaensis*, *S. scharbergana*).

Table 2
Taxonomic composition of foraminifera in the Extinction Group, the focus of this study.

Nodosariidae	Pleurostomellidae	Stilostomellidae
Awhea	*Amplectoductina*	*Siphonodosaria*
Chrysalogonium	*Ellipsoglandulina*	*Stilostomella*
Cribronodosaria	*Ellipsoidella*	*Strictocostella*
Glandulonodosaria	*Ellipsoidina*	
Grigelis (in part)	*Ellipsopleurostomella*	
Mucronina	*Nodosarella*	
Neugeborina	*Pleurostomella*	
Nodosaria acutecosta, *N. weaveri*		
Orthomorphina		
Plectofrondicularia		

On the DCCA ordination the abyssal-restricted associations (4, 5, and 7–9) plot on the lower left (Fig. 15) with their associated species (mostly Pleurostomellidae) that are more common in the deeper water (e.g. *Chrysalogonium stimuleum*, *Cribronodosaria ciperoense*, *C. deceptoria*, *Nodosarella acus*, *Pleurostomella alazanensis*, *P. articulata*, *P. bolivinoides*, *P. elliptica*, *P. gracillima*, *P. incrassata*, *P. subnodosa* and *P. tenuis*). Stilostomellid taxa (e.g. *Siphonodosaria*, *Strictocostella*) have wider bathymetric distributions and were usually the dominant and more common species at bathyal depths.

The timings of major changes in the overall composition of the Ext. Gp faunas can be determined using constrained cluster analysis of the relative abundance of the species in each of the four longest studied sequences (Fig. 17). The arrows on these diagrams indicate the intervals when the largest faunal changes occurred. It is clear that faunal changes occurred at differing times at each of the four sites and they share little in common in terms of the timings, except that the largest changes at the three sites that spanned the Paleogene (317, 548, and 865) was in the middle Eocene, 45–38 Ma (highest levels of clustering, Fig. 17). Other significant times of Paleogene change occurred at the PETM (865), in the

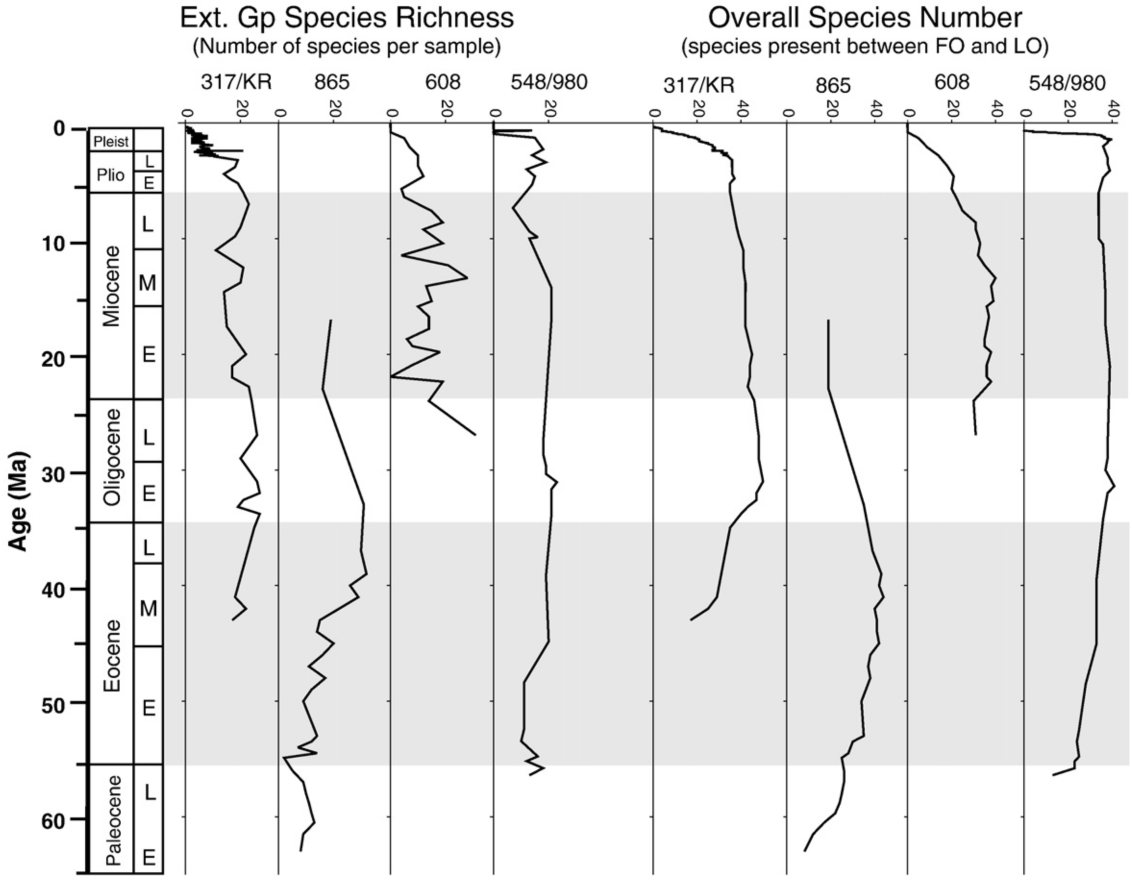

Fig. 10. Stratigraphic records of the number of Ext. Gp species (species richness) recorded in each sample and total number of Ext. Gp species inferred to have been present (assuming continuous presence between first occurrence (FO) and last occurrence (LO) of each species) through the studied intervals at each site. Eocene and Miocene shaded.

early Eocene (865) and Oligocene (548, 865). Significant faunal change in the Neogene occurred in the early Miocene (317), early middle Miocene (608), and near the Pliocene–Pleistocene boundary (317 and 548).

4. Global stratigraphic record of the relative abundance of the Extinction Group

Previous studies in the Indian and Southern Oceans (Thomas and Gooday, 1996; Thomas 2007; Hayward et al., 2010) have shown that the Ext. Gp's maximum relative abundance increased from the Paleocene, through the Eocene to a maximum (50–70%) in the late Eocene–earliest Oligocene, followed by a gradational decline through the Oligocene and Neogene until its disappearance in the middle Pleistocene (Fig. 18). The pattern was somewhat different in the present study with maximum relative abundance of the Ext. Gp in the equatorial Pacific already high (>40%) in the Paleocene increasing to a peak (65%) in the middle Eocene declining slightly to Oligocene, Miocene and Pliocene peaks each of ~50%, before the major decline and disappearance in the Pleistocene (Fig. 18). Paleogene data from the North Atlantic is restricted to that from Site 548 where maximum Ext. Gp relative abundance is low (<15%) throughout the Paleocene and most of the Eocene increasing from the late Eocene to an earliest Miocene peak (50%) before declining gradually through the Neogene with a rapid Pleistocene collapse (Fig. 18).

The running average trendlines for Ext. Gp relative abundance follow a similar pattern to the maximum relative abundance in the Indian and Southern Oceans (Fig. 18). In the North Atlantic the average relative abundance of the Ext. Gp peaks in the latest Eocene followed by a dramatic decline in the early Oligocene, followed by a recovery in the late Oligocene then a steady decline through to the Pleistocene. The equatorial Pacific running average trendline indicates a sudden decline and equally rapid recovery in relative abundance across the PETM and a middle Eocene peak. This is followed by two further lower peaks of relative abundance in the early Miocene and middle Pliocene separated by lower abundances in the Oligocene and middle–late Miocene (Fig. 18).

Within the families that comprise the Ext. Gp, the Stilostomellidae was the largest component and its relative abundance patterns were the same as the Ext. Gp as a whole. The other two component families had different patterns. The Pleurostomellidae, which were more abundant at abyssal depths (also shown by Katz et al., 2003), exhibited different patterns of relative abundance in each ocean with low peaks of abundance in the Eocene in the Southern Ocean, in the early Oligocene and early Miocene in the Indian, N Atlantic and Pacific, and also in the Pliocene in the equatorial Pacific. There was a general decline in average relative abundance of the uniserial Nodosariidae from a Paleocene–Eocene maximum of 10–20% of benthic foraminifera to <8% in the Neogene (Fig. 18), except in the North Atlantic where the sparse data indicates low relative abundances through the Paleocene–middle Eocene.

5. Global Extinction Group species turnovers

Times of Ext. Gp species turnover can be identified by peak occurrences of first and last occurrence datums. In the North Atlantic and equatorial Pacific peak first occurrences were in the Paleocene (Fig. 19), partly because these were the oldest samples studied. A comparison with our global data set indicates that this peak of earliest appearances

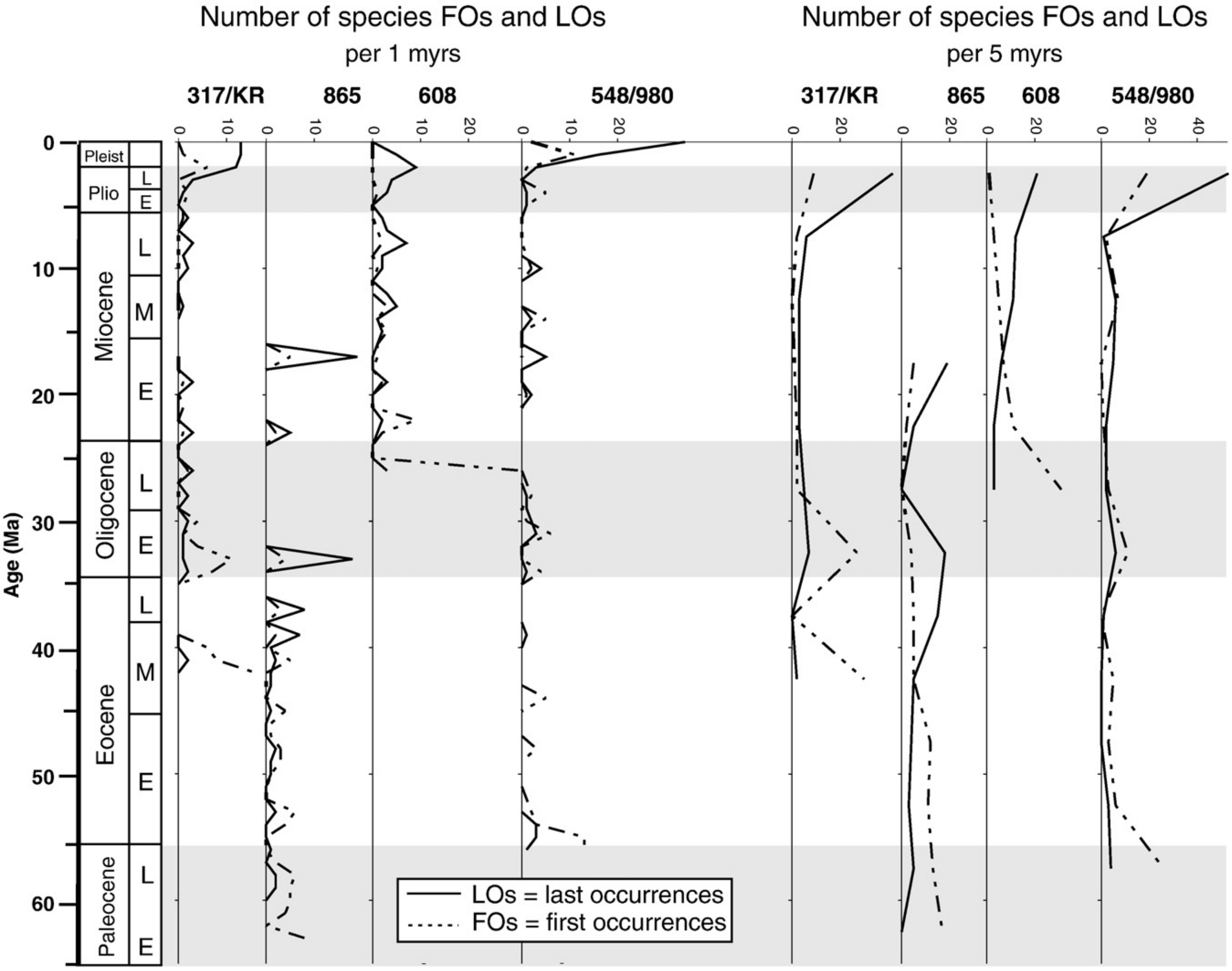

Fig. 11. Stratigraphic records of the number of first occurrences (FOs) and last occurrences (LOs) per 1 Myr and per 5 Myr of Ext. Gp species through the studied intervals at each site.

was likely spread between the Cretaceous and Paleocene. In the equatorial Pacific there was a second peak of first occurrences in the Eocene. The later Oligocene peak in the North Atlantic probably reflects the small number of samples studied from the Eocene in this region. Our global data set indicates that this second peak of appearances was most pronounced in the middle and late Eocene. The number of Neogene first occurrences was low with a small middle–late Miocene peak in the North Atlantic (Fig. 19). Our global data set indicates that only one species first appeared in the Pleistocene, and therefore we infer that our small peak of first occurrences at this time in the North Atlantic and equatorial Pacific was of rare species encountered because of the large number of Pleistocene samples examined from a wide range of water depths.

In the North Atlantic, equatorial Pacific and globally there was an Oligocene peak of last occurrences and extinctions followed by a dip in the early Miocene (Fig. 19). There was also an increased number of last occurrences in the middle–late Miocene and Pliocene, with by far the greatest extinction turnover occurring in the early and middle Pleistocene (60% of Ext Gp species disappeared).

The North Atlantic and equatorial Pacific patterns of first occurrence were similar to, but not as pronounced as, the overall global pattern for all Ext. Gp species (Fig. 19a, b). Our data and the more limited data of Boltovskoy (1987) both indicate that >80% of Ext. Gp species first appeared in the Cretaceous–Eocene (Greenhouse World) and that ~10% originated in the Neogene. This can be compared with modern deep-sea benthic foraminifera, where ~30% originated in the Cretaceous–Eocene and ~50% in the Neogene (Fig. 19c, d).

6. Timing of Extinction Group changes

6.1. Paleocene–Eocene Thermal Maximum, PETM

The PETM appears to have had no net impact on the Ext. Gp benthic foraminifera in the one sequence studied across it in the North Atlantic (548). In the equatorial Pacific sequence studied (865) however there was a small change in the overall faunal composition (Fig. 17) from Assoc. 2 to Assoc. 1, and a sharp decline in species richness and relative abundance followed by a rapid recovery to Paleocene levels (Figs. 10 and 18). No species of the Ext. Gp taxa had its LO through this period although some taxa had low relative abundances during the PETM. These results are consistent with our previous study in Site 744 in the southern Indian Ocean (Hayward et al., 2010) where the Ext. Gp did not suffer significant extinction during the PETM.

Thus it would appear that the Ext. Gp of deep-sea benthic foraminifera was little affected by the rapid expansion of warm, possibly oxygen-depleted, carbonate-corrosive bottom waters that occurred during the short PETM event (Katz et al., 1999). This contrasts with the reported 30–35% loss of total deep-sea benthic foraminiferal diversity and major changes in dominant faunal assemblage composition (e.g., Kaiho et al., 1996; Thomas, 1998).

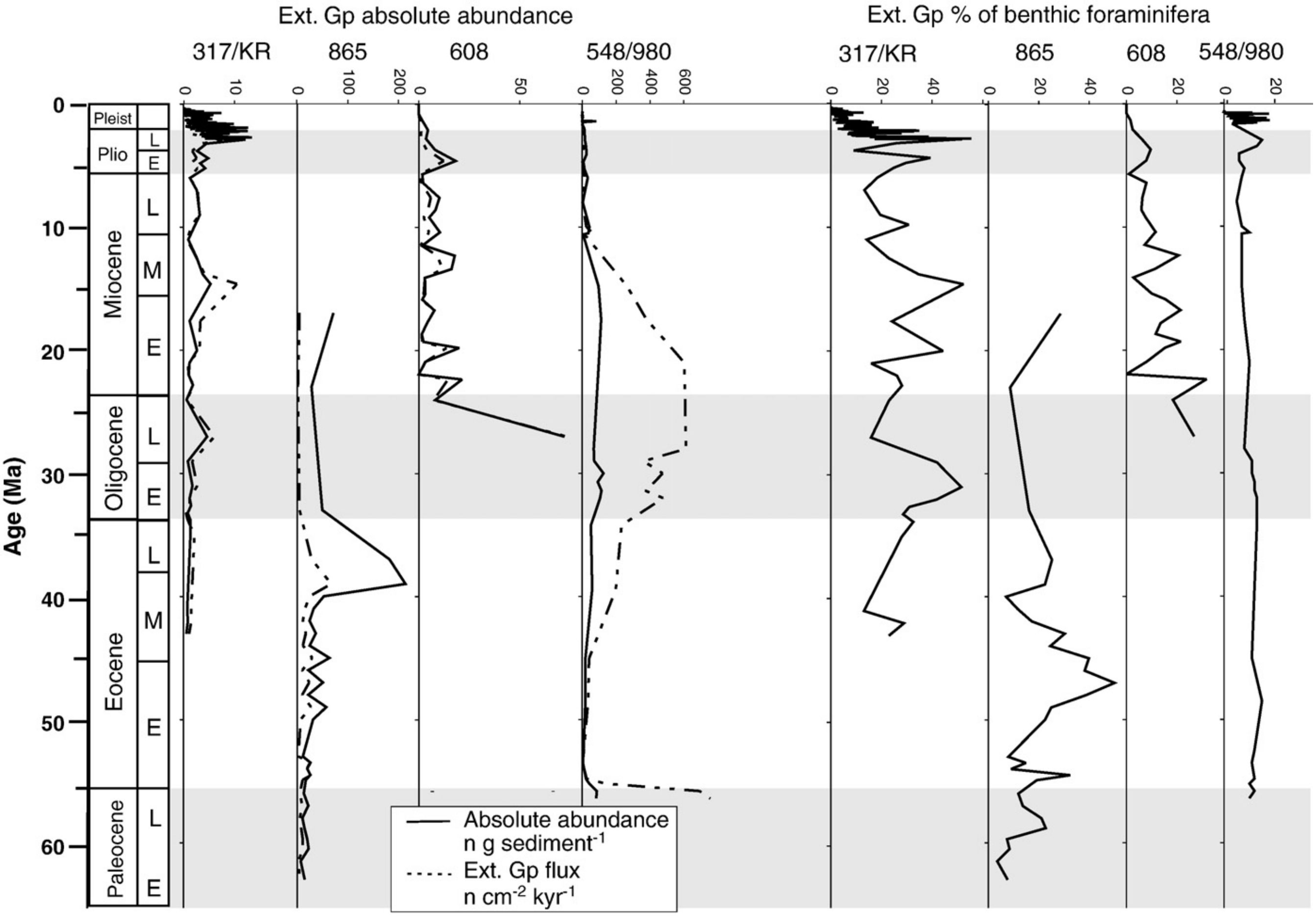

Fig. 12. Stratigraphic records of the absolute abundance (specimens g sediment^{-1}), accumulation rate (specimens cm^{-2} kyr^{-1}) and relative abundance (% of total benthic foraminifera) of the Extinction Group through the Cenozoic at the main study sites.

6.2. Early Eocene climate optimum

There were no significant changes in the composition, species richness or flux of the Ext. Gp through this period. A number of Ext. Gp species may have originated at this time and the group reached its greatest relative abundance as a percentage of the total benthic fauna in the equatorial Pacific study site (865, Fig. 12).

6.3. Middle–late Eocene gradual cooling

This period hosted the peak relative abundances of the Ext. Gp in the North Atlantic, Southern Ocean and globally (Fig. 18). Across this interval there was a significant change in the Ext. Gp faunal composition in the North Atlantic bathyal study site (548) from Assoc. 3 to Assoc. 6 (Figs. 16 and 17), but no enhanced species turnover (Fig. 19). At bathyal depths in the equatorial Pacific (865) the Ext. Gp enjoyed peak absolute abundance, flux, species richness and overall species number during this period (Figs. 10 and 12) and it also witnessed an increase in last occurrences that was to peak in the earliest Oligocene (Figs. 11 and 19). Globally this interval had enhanced Ext. Gp species originations, which could be reflected in the increasing overall species number at abyssal depths in the equatorial Pacific (317, Figs. 10 and 19), but not in our two bathyal sites (548 and 865). During the early middle Eocene there was a slight shift in overall faunal composition in Site 865 from Assocs. 2a to 2b (Figs. 16 and 17).

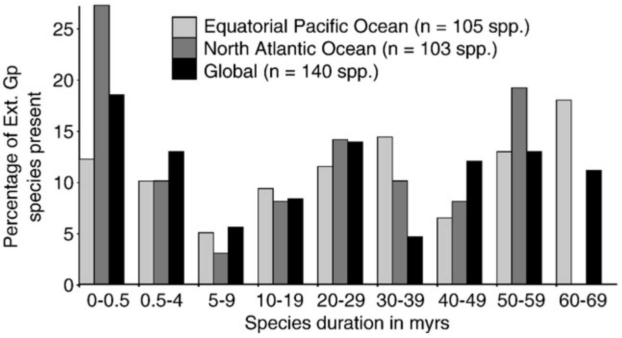

Fig. 13. Distribution of Ext. Gp species durations as a percentage of the species in the North Atlantic and equatorial Pacific study sites, and also globally — includes records from the Indian Ocean (Hayward et al., 2010).

It would seem that conditions in the deep-sea were optimal for the Ext. Gp throughout the relatively warm Eocene.

6.4. Latest Eocene–early Oligocene rapid cooling

Deep ocean waters cooled rapidly associated with the growth of a continent-wide, Antarctic ice sheet at this time (Fig. 1). There was no concurrent rapid change in the Ext. Gp, but after the rapid cooling there was an elevated level of species turnover (numbers of FOs and LOs) in the early Oligocene at all three study sites that spanned this interval (Fig. 11) as well as globally (Fig. 19). Overall changes in Ext. Gp composition during the middle Eocene–early Oligocene cooling at our sites consisted of the replacement of mainly lower diversity Ext. Gp faunas, dominated by high abundances of just one or two species (Assocs. 1–3), by higher diversity faunas (Assocs. 4–6), with a more even distribution of species abundances (Figs. 14 and 16). The most significant faunal turnover in the non-Ext. Gp benthic foraminifera since

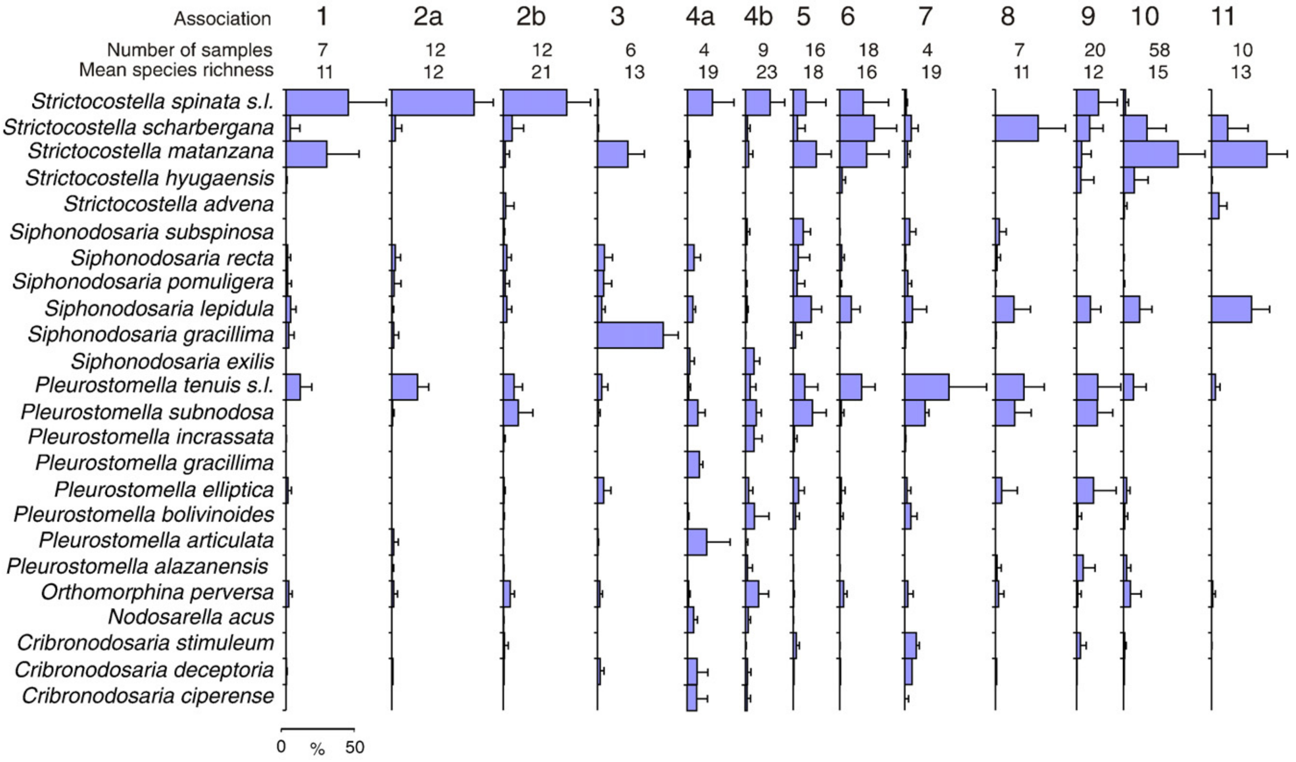

Fig. 14. Mean relative abundance and standard deviation of the common Ext. Gp species (as proportion of the total Ext. Gp census count) in faunal Assocs. 1–11, selected from the chord cluster analysis dendrogram (Appendix K).

the PETM occurred across this boundary at North Atlantic Site 548 and in abyssal depths in equatorial Pacific Sites 317 and 574, (Thomas, 1985; Boltovskoy et al., 1992; Boltovskoy and Watanabe, 1994).

6.5. Late Oligocene–early Miocene Tweenhouse World

This period appears to have had relatively stable global climate with a low level of benthic foraminiferal turnover (e.g. Miller et al., 1993; Katz et al. 2003). Ext. Gp species turnover was also at a low level in our study sites and globally (Figs. 11 and 19). Species richness and the overall number of Ext. Gp species remained stable in the North Atlantic sites (546 and 608), but declined regionally at both equatorial Pacific sites (317 and 865) (Fig. 10). Conversely Ext. Gp absolute abundance, flux and relative abundance declined somewhat in the North Atlantic, but remained steady or slightly increased in the equatorial Pacific (Fig. 12). There was no significant change in Ext. Gp faunal composition through this interval at three of the study sites, but at abyssal depths in the equatorial Pacific (317) there was a shift from Assoc. 4b to Assocs. 2b and 5 during the early Miocene (Figs. 16 and 17).

6.6. Middle and late Miocene cooling

The middle Miocene has been recognized as an interval of enhanced global turnover of deep-sea benthic foraminifera (e.g. Miller et al., 1993; Woodruff, 1985; Woodruff and Savin, 1989). There is a slight increase in both FOs and LOs of Ext. Gp species in both North Atlantic study sites

Table 3
Characteristic species, age and site distribution of foraminiferal associations selected from the cluster analysis dendrogram produced using a chord dissimilarity coefficient on square-root transformed census data (Appendix K).

Assoc.	Dominant species present	No. of sites spp.		Age range	Depth
1	*Strictocostella spinata–Strictocostella matanzana*	32	865	Pal-e Eoc	l bath
			548	e Eoc, l Mio	l bath
2a	*Siphonodosaria gracillima–S. matanzana*	32	865	l Pal-m Eoc	l bath
2b	*S. spinata–Pleurostomella tenuis*	46	865	l Pal-e Olig	l bath
			317	e-m Mio	u abys
3	*S. spinata–Pleurostomella subnodosa*	62	548	Pal-e Eoc	l bath
4a	*S. spinata–Pleurostomella articulata*	34	317	m-l Eoc	u abys
4b	*S. spinata–Orthomorphina perversa*	52	317	Olig-e Mio	u abys
5	*S. matanzana–P. subnodosa–Siphonodosaria lepidula*	54	317	e-m Mio	u abys
			608	l Olig-e Pli	m abys
6	*Strictocostella scharbergana–S. matanzana–S. spinata*	59	548	Olig-l Pli	l bath
			865	e Mio	l bath
7	*P. tenuis–P. subnodosa*	32	317	l Mio	u abys
8	*S. scharbergana–P. tenuis–P. subnodosa–S. lepidula*	32	608	l Mio-l Pli	m abys
9	*S. spinata–P. tenuis–P. subnodosa–P. elliptica*	38	317	KR e-l Plio	u abys
10	*S. matanzana–S. scharbergana–S. lepidula*	57	548–980	e Pli-e Pleis	l bath
			982	L Pli-e Pleis	u abys
			1055	e Pleis	l bath
11	*S. matanzana–S. lepidula*	28	1012	e Pleis	l bath

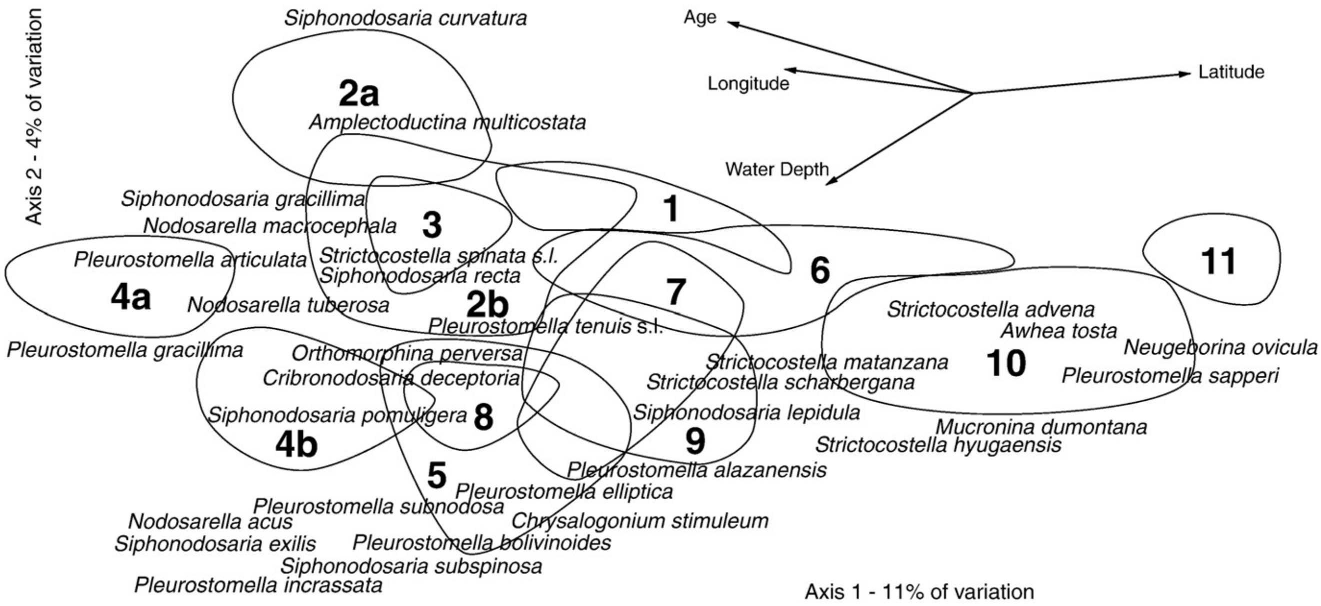

Fig. 15. Two-dimensional ordination of the 200 faunal samples (simplified and shown as faunal Assocs. 1–11) and more common species produced by detrended Canonical Correspondence Analysis (CCA). Vector axes show strength of faunal relationship with age, water depth and geographic location. Full DCA ordination with plots of individual samples is given in Appendix K.

(548 and 608) but none in the equatorial Pacific site (317) (Fig. 11). In the late Miocene however, both abyssal sites (317 and 608) experienced slightly increased Ext. Gp LOs and resultant decreased overall species number (Figs. 10, 11 and 19), whereas the one bathyal site that spans this interval (548) did not. The absolute abundance, flux and relative abundance of the Ext. Gp declined through the middle–late Miocene at all sites, although it increased again in the Pliocene (Fig. 12). No significant faunal changes occurred through this period at bathyal depths in the North Atlantic (548) but at abyssal depths in both oceans (317 and 608) there was a switch from Assoc. 5 to Assoc. 7 or 8 at ~10 Ma (Figs. 16 and 17).

6.7. Pliocene to mid-Pleistocene Climate Transition, Last Global Extinction

By far the largest species turnover in the Cenozoic history of the Ext. Gp occurred in the Pleistocene with a loss of 40% of its diversity in the equatorial Pacific sites and 60% loss in the North Atlantic and

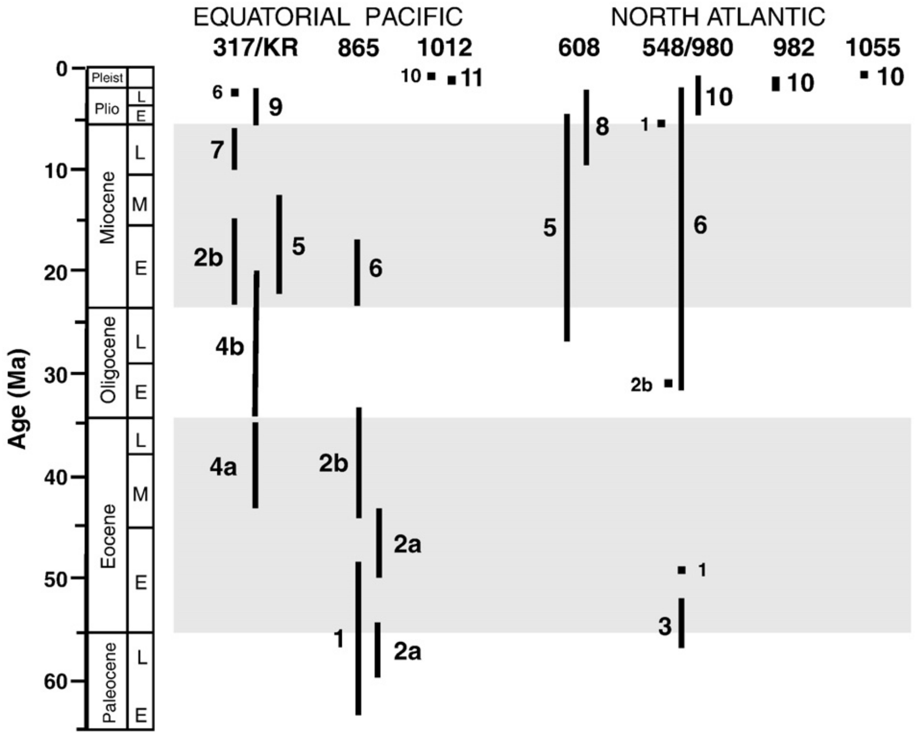

Fig. 16. Stratigraphic distribution of the eleven faunal associations (1–11) in the five single and two composite deep-sea study sites in the equatorial Pacific and North Atlantic. Assocs. 1–11 (Table 3) were selected from the chord cluster analysis dendrogram (Appendix K). Solid bars represent more than one sample, small squares represent single sample records. Non-clustered samples are not shown. Eocene and Miocene shaded.

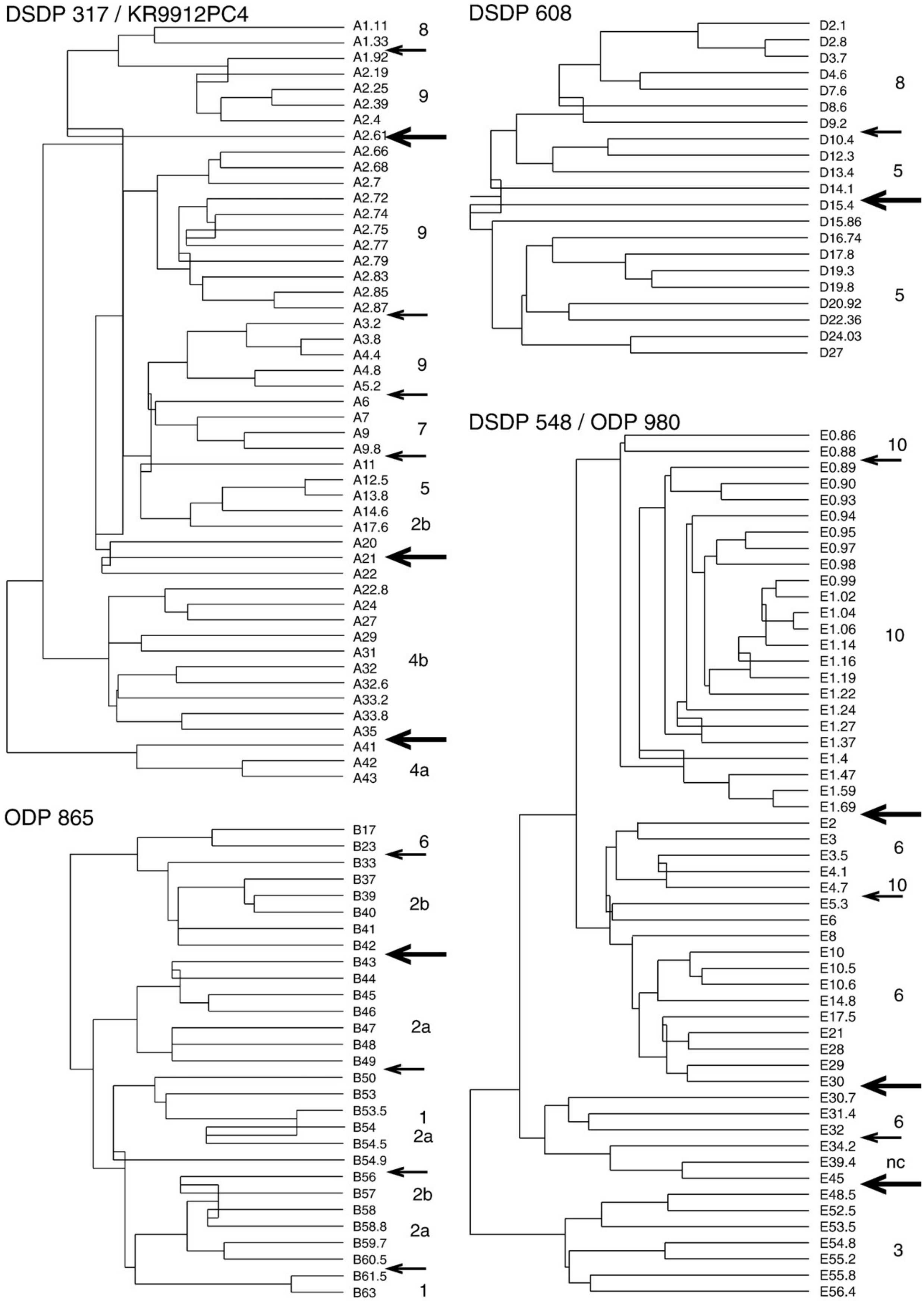

Fig. 17. Constrained cluster analyses (using Ext. Gp census data standardized as proportions) of samples with a minimum of eight Ext. Gp species, conducted separately on the four longer deep-sea sections or composite sections. Arrows indicate location of significant changes in the composition of the Ext. Gp faunas. Numbers are the faunal associations obtained from the cluster analysis (Table 3). nc = not clustered.

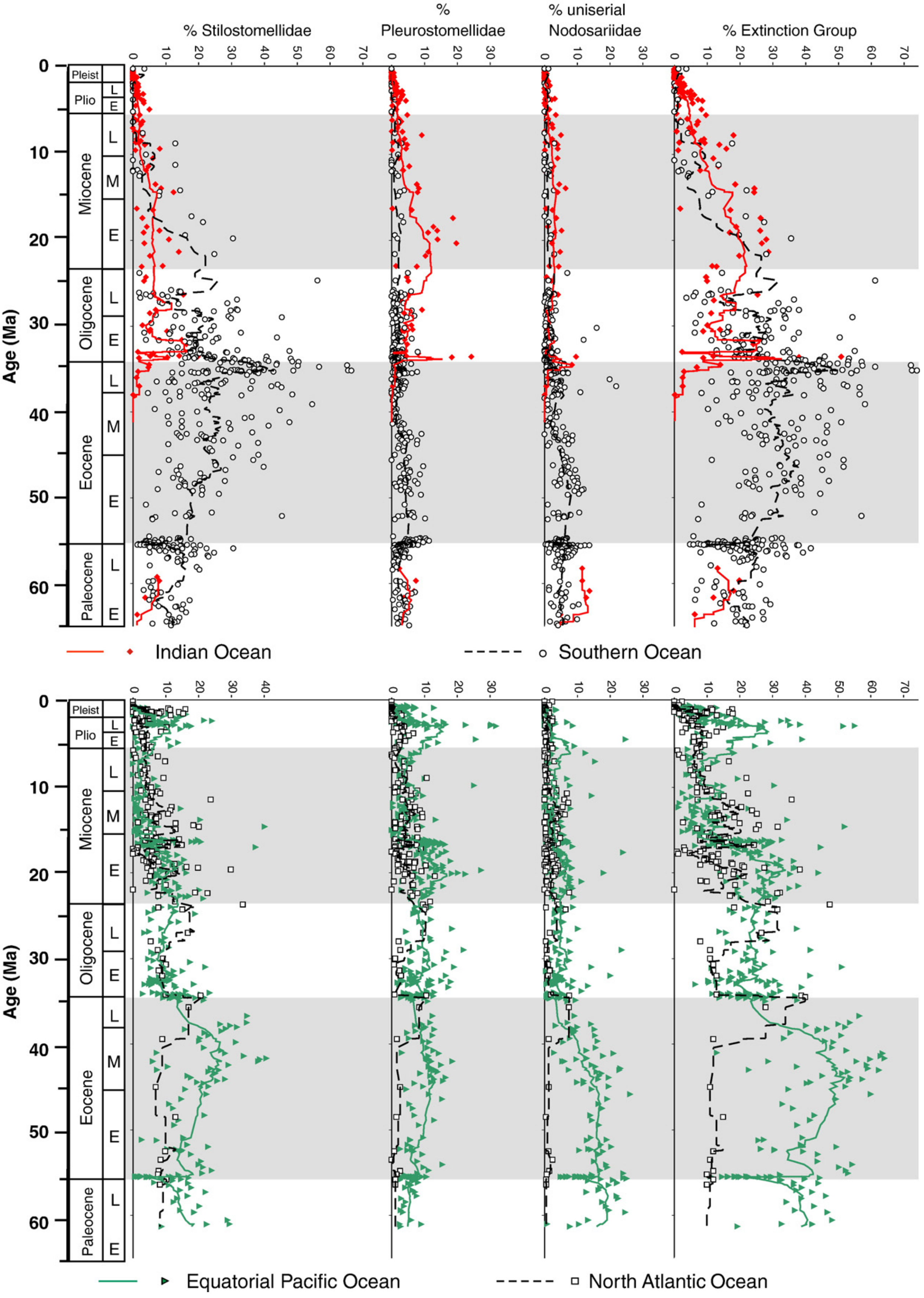

Fig. 18. Stratigraphic record of the relative abundance of the families Stilostomellidae, Pleurostomellidae, uniserial Nodosariidae and the total Extinction Group from the Indian Ocean (Sites 763 and 758) and Southern Ocean (Sites 689, 690, and 744/738) compared with the North Atlantic (Sites 548, 608, 980, 982, and 1055) and equatorial Pacific (Sites 317, 573, 574, 575, 865, 1012, and KR9912) (from Thomas, 2007; Hayward et al., 2010; this study). Trendlines for data from each ocean are the moving average of the 15 nearest points. Eocene and Miocene shaded.

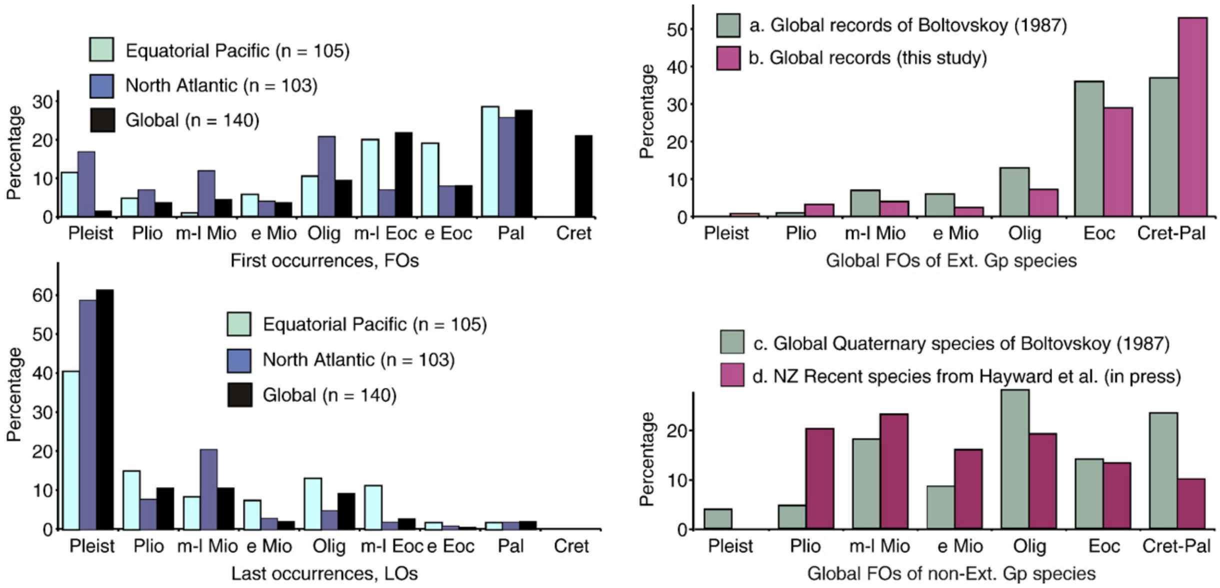

Fig. 19. Left: Percentage of first (FO) and last (LO) occurrences per epoch or part-epoch of Ext. Gp species in the equatorial Pacific and North Atlantic (Appendix I) compared with our current knowledge globally of these species. Right upper: Percentage of Ext. Gp species with global FOs in specified epochs or part epochs from: a. global deep-sea data set of Boltovskoy (1987), b. our group's current global data set of the total Extinction Group, based on this and previous studies (Hayward et al., 2007; 2010). Right lower: Percentage of non-Ext. Gp Quaternary deep-sea benthic foraminifera with global FOs in specified epochs or part epochs from: c. global deep-sea data set of Boltovskoy (1987), d. New Zealand deep-sea data set of Hayward et al. (in press).

globally (Fig. 19). Last occurrences were also slightly elevated (~10%) in the Pliocene. There were few originations globally during the Pliocene and Pleistocene, with the ~10% of originations in the Pleistocene in the study regions (Figs. 11 and 19) being an artifact of inclusion of more sites with only a Pleistocene record from a wider range of water depths. Species richness and overall species number remained relatively high throughout the Pliocene in the two shallower study sites (317 and 548), but continued the middle–late Miocene decline in the mid abyssal North Atlantic site (608) (Fig. 10). The three study sites that document most of the Neogene record exhibited a similar trend in overall species decline to that observed previously in the Indian Ocean. The decline started earliest (middle Miocene) in the deepest site (mid abyssal 608) with a relatively steady loss of species through to the last disappearance in the MPT. At upper abyssal depths (317 and KR9912), beneath upper Circumpolar Deep Water, the major decline started in the latest Pliocene–early Pleistocene and was steady through to the final MPT disappearance (Figs .4 and 10). At lower bathyal depths (980, 1012 and 1055), there was hardly any decline in overall Ext. Gp species number until the onset of the MPT, during which the major loss of the Ext. Gp fauna occurred (Figs. 8–10).

In the two abyssal sites (KR9912 and 608) there were Pliocene peaks of absolute and relative abundance of the Ext. Gp prior to their major decline in abundance starting in the late Pliocene in Site 608 and in the early Pleistocene in KR9912. In the bathyal site (548/980) absolute abundance and flux were extremely low throughout this period but there were secondary peaks of relative abundance (~20%) in the late Pliocene and early Pleistocene (Fig. 12).

Changes in overall faunal composition occurred near the Miocene–Pliocene boundary in the two shallower sites (317 and 548) with the lower diversity Assocs. 9 and 10 replacing Assocs. 7 and 6 (Figs. 16 and 17).

6.8. Middle Pleistocene

In two study sites, one in the North Atlantic (1055) and one in the equatorial Pacific (KR9912) there are rare records of Ext. Gp species above the MPT (Figs. 4 and 9 and Table 4). Records of single isolated specimens of a species could be a result of reworking, but more consistent higher records of just a few species suggest that they survived in low numbers higher into the middle Pleistocene. The species involved are *Pleurostomella acuminata*, *P. bolivinoides*, *P. pleurostomella*, *P. subnodosa*, *Strictocostella matanzana* and *Mucronina* n. sp. A. The latter species is known elsewhere to be one of only two members of the Ext. Gp to have possibly survived through to the present day (Hayward

Table 4
More frequent Ext. Gp species with global time ranges of potential stratigraphic value. Data are from this study and Hayward et al. (2007, 2010). Synonyms and figured examples are given in Appendix A.

	FO	LO
Chrysalogonium setosum (Schwager, 1866)	l Olig	e Pleist
Cribronodosaria laeve (Cushman & Bermúdez, 1936)	e Pal	e Mio
Ellipsopolymorphina russitanoi (Silvestri, 1904)	e Mio	e Pleist
Muconina compressa (Costa, 1855)	Olig	m Pleist
Mucronina dumontana (Reuss, 1861)	Mio	m Pleist
Mucronina elongata (Costa, 1855)	Olig	m Pleist
Mucronina silvestriana (Thalmann, 1952)	Plio	e Pleist
Neopleurostomella pendula (Boltovskoy & Watanabe, 1985)	l Eoc	l Olig
Nodosaria acutecosta (Silvestri, 1872)	e Olig	Plio
Nodosaria weaveri Finger & Lipps, 1990	m Mio	e Pleist
Parafrondicularia antonina (Karrer, 1878)	l Mio	e Pleist
Plectofrondicularia paucicostata (Cushman & Jarvis, 1929)	l Eoc	e Olig
Pleurostomella articulata (Brotzen, 1936)	l Cret	m Mio
Pleurostomella gracillima (Cushman, 1933)	l Cret	e Olig
Pleurostomella greatvalleyensis Trujillo, 1960	l Cret	l Olig
Pleurostomella obesa Cushman & Bermúdez, 1937	e Olig	l Mio
Pleurostomella sapperi Schubert, 1911	Plio	m Pleist
Pleurostomella wintereri (Trujillo, 1960)	l Cret	m Mio
Siphonodosaria annulifera (Cushman & Bermúdez, 1937)	l Pal	l Mio
Siphonodosaria curvatura (Cushman, 1939)	Pal	m Mio
Siphonodosaria dentaliniformis (Cushman & Jarvis, 1934)	Olig	m Pleist
Siphonodosaria exilis (Cushman, 1936)	l Cret	l Olig
Siphonodosaria hispidula (Cushman, 1917)	l Cret	e Mio
Strictocostella jabacoensis (Bermúdez, 1937)	e Eoc	l Eoc
Strictocostella pseudoscripta (Cushman, 1937)	Cret	e Mio

et al., 2007). Three of the four *Pleurostomella* species have been reported surviving up into the late middle Pleistocene (0.45–0.2 Ma) in the Indian Ocean, South China and Mediterranean Seas (Kawagata et al., 2006, 2007; Hayward et al., 2009). These are the first indications that *P. bolivinoides* or *S. matanzana* may also have survived longer.

7. What caused the decline of the Extinction Group?

The elongate, cylindrical shape of the Ext. Gp species provides a high surface to volume ratio, which has been interpreted by a number of workers to be indicative of a moderately deep infaunal habitat tolerant of lower oxygen conditions with high organic carbon flux (e.g. Boersma 1990, Gupta, 1993, Thomas et al., 2000). Proxy studies have also shown a high positive correlation between Ext. Gp abundance and low oxygen/high food supply indicators prior to the group's decline (e.g., Kawagata et al., 2005, 2006; O'Neill et al., 2007). The specialized modifications to the constricted apertures of most of the Ext. Gp probably contain the answer to the cause of the extinctions, especially as the two families that became extinct (Stilostomellidae and Pleurostomellidae) are defined by the character of the apertures. Unfortunately we do not know the ecological function of these specialized apertural modifications. We have hypothesized that they directed pseudopodial flow into and out of the shell, which may have been related to the collecting and/or rupturing of specific food sources (e.g., Hayward et al., 2007; Thomas, 2007). The observation that many stilostomellid specimens have incomplete, apparently dissolved, apertural neck and collar might indicate that these forms lived in an upright orientation within the sediment with their apertural necks extending into the more carbonate-corrosive bottom water above the sediment–water interface. This too, could have been an adaptation to collecting a specific type of suspended or surface-dwelling food.

The Cenozoic history of the Ext. Gp provides some clues as to the cause of the decline of the Ext. Gp and its eventual extinction. The Ext. Gp was at its maximum relative abundance as a percentage of the deep-sea benthic foraminifera in the middle Eocene–earliest Oligocene during relatively warm Greenhouse World conditions and the first major Cenozoic cooling of the Earth's climate. Survival of the Ext. Gp virtually unscathed through the PETM implies that species of this group tolerated warm, locally oxygen-depleted, carbonate-corrosive, bottom waters consistent with their inferred, moderately deep infaunal lifestyle.

Clearly, the Ext. Gp was well-adapted to the warm oceans of the Greenhouse World, when oceanic circulation was quite different from Icehouse World conditions in which they died out (Emanuel, 2002). In the warmer Paleogene oceans there were no clearly delineated water masses and probably more active diapycnal mixing (Thomas et al., 2006). This possibly resulted in more common and intense upwelling on short time scales over the now oligotrophic central oceanic gyre regions (e.g., Huber and Thomas, 2008). Thus the food flux to the ocean floor may have been more variable on short time scales (months), but more homogeneous over longer time scales (i.e., on the time scale of circulation of the oceans, one or several millennia). These conditions presumably better suited the Ext. Gp than the Icehouse oceans with well-defined water-masses and more heterogeneous distribution of eutrophic and oligotrophic regions.

The decline and loss of the Ext. Gp occurred in a number of steps. The first occurred during and soon after the rapid latest Eocene–earliest Oligocene global cooling. At this time the Ext. Gp started to decline in relative abundance (Fig. 18), changed from faunas strongly dominated by one or two species to more even and more diverse faunas (Figs. 14 and 16), and suffered from the first small episode of enhanced extinctions (Figs. 11 and 19).

The second phase of decline followed nearly 15 Myr of relatively stable climate during the Oligocene–early Miocene Tweenhouse World (Fig. 1). During the middle–late Miocene period of fairly rapid cooling, the absolute abundance, flux and relative abundance of the Ext. Gp once again declined (Fig. 12) and the number of regional LOs and global extinctions increased significantly (Figs. 11 and 19). Ext. Gp faunal changes occurred in deeper (abyssal) sites at this time (Figs. 16 and 17) and the overall number of species started declining at mid abyssal depths (Site 608), but not at shallower sites (Fig. 10).

This pattern of earlier impacts in deeper water continued during the third and last phase of Ext. Gp decline in the late Pliocene–middle Pleistocene (Hayward et al., 2007). Major loss of Ext. Gp species started in the late Pliocene–early Pleistocene at upper abyssal depths (317, KR9912) (Fig. 10), but not until the onset of the MPT at bathyal sites (980, 1012, and 1055), during which the major loss of the Ext. Gp fauna occurred (Figs. 8–10). Whatever was the cause of the loss of the Ext. Gp had to change earlier in deeper waters and progressively impact shallower waters through the stepwise coolings of the middle–late Miocene, late Pliocene–early Pleistocene, and MPT.

Pulsed growth of polar ice sheets is inferred to have occurred during these steps, resulting in equatorwards migration of regions of deep-water formation, further deep-water cooling, more clearly demarcated water masses, and increased deep-sea ventilation. Overall benthic foraminiferal changes point to further increased seasonality in food supply (especially in the middle Miocene), increased production of corrosive Antarctic Bottom Water (late Miocene) and increased total food supply (especially late Pliocene–MPT) during these cooling steps. It is hard to conceive how any of these changes directly impacted the Ext. Gp species and brought about their demise. Increased seasonality of food certainly appears to have advantaged other benthic foraminifera, which may have outcompeted the Ext. Gp and resulted in declines in their relative abundance. The widespread bathymetric and geographic distribution of the Ext. Gp in Miocene–Pliocene deep-water sediment indicates that they were tolerant of a broad range of bottom oxygen and temperature conditions, and that the small changes in these physical properties that accompanied the stepwise middle Miocene–MPT cooling would not have been sufficient, in themselves, to wipe out the Ext. Gp.

Maybe these cooling steps impacted more directly the specific food source of the Ext. Gp. There are several possible candidates for this food source. It could have been a phytoplankton group, as we know the hard skeleton-bearing phytoplankton were greatly impacted by the periods of cooling, starting in the middle Eocene (Aubry, 1992; Bown, 2005). Parallel to the stepwise cooling there was a decline in the diversity of dinoflagellates and calcareous nannoplankton and greatly increased diversity of diatoms (Fig. 1 — Stover et al., 1996; Spencer-Cervato, 1999; Bown et al., 2004). Progressive decline in the delivery of specific phytoplankton particles to the seafloor could have impacted deeper water sites earlier than shallower ones, because of the progressive consumption of sinking particles that occurs during their downward path (e.g., Berger and Wefer, 1990).

Another candidate food group could have been deep-water chemosynthetic or other microscopic prokaryotes, as we know that microbial activity rates are more susceptible to smaller temperature changes than in foraminifera (e.g., Thomas, 2007). Today a large part of ocean productivity (especially in relatively oligotrophic regions) is by prokaryotes rather than diatoms and nannoplankton (e.g., Zwirgmaijer et al., 2008). Paerl and Huisman (2008) have argued that in the Greenhouse World oceans a larger proportion of primary productivity was by prokaryotes than at the present time. During the stepwise Neogene cooling of deep waters, the deepest watermasses would have always cooled through certain threshold temperatures earlier than shallower deep-water masses. Thus a specific type of prokaryotic food for the Ext. Gp could also have declined earlier deeper in the oceans and produced the pattern of decline and extinction we have documented.

8. Conclusions

1. Eighty percent of the elongate, cylindrical benthic foraminiferal species belonging to families and genera that became extinct during the MPT (Ext. Gp), originated in the Cretaceous–Eocene Greenhouse World. This contrasts with ~30% of non-Ext. Gp

species of Quaternary deep-sea benthic foraminifera that originated at this time. Thus the Last Global extinction in the deep sea mostly killed off long-ranging species that had evolved in the warm, deep water of the Greenhouse World.

2. The Ext. Gp was largely unaffected by the Paleocene–Eocene Thermal Maximum event which killed off ~30–35% of benthic foraminiferal species within the warmer, more-corrosive deep water.
3. Maximum relative abundances and overall species diversity of the Ext. Gp occurred towards the end of Greenhouse World times (middle Eocene–early Oligocene) suggesting optimal conditions in the deep sea for this group.
4. The decline and loss of the Ext. Gp was progressive with three identifiable intervals of enhanced turnover, faunal changes and abundance declines, which coincide with previously identified periods of faunal turnover in the total deep-sea benthic foraminiferal faunas.
5. The first of these occurred in the latest Eocene–early Oligocene with slightly increased levels of species turnover (origination and extinction) and changes in the composition of dominant species in the Ext. Gp, possibly as a result of major changes in oceanic circulation and primary productivity associated with rapid global cooling.
6. The second occurred during the middle–late Miocene cooling with declines in Ext. Gp abundance and flux and slightly enhanced species loss. Major Ext. Gp faunal changes occurred at mid abyssal depths.
7. The overall number of Ext. Gp species present at any one site, began declining earlier at mid abyssal depths (middle Miocene) than at upper abyssal (late Pliocene–early Pleistocene) or lower bathyal depths (MPT).
8. The third and final interval of enhanced turnover occurred in the late Pliocene–middle Pleistocene with the final significant declines in abundance and extinction of most of the Ext. Gp species. The abundance declines were pulsed, usually coinciding with increasingly colder glacial stages. Six species may have survived through the MPT in low numbers in scattered refuges, with two of these possibly surviving up into the present.
9. The strongest clues to the cause of the Last Global Extinction in the deep sea come from the specialized apertural modifications of the targeted species and the coincidence of periods of decline and loss with times of increased global and deep-water cooling.
10. We infer that the apertural modifications may be related to the method of food collection or processing, and that it may have been the decline or disappearance of their specific phytoplankton or prokaryote food group that was more directly impacted by the coolings, that resulted in the extinctions of these deep-sea benthic foraminifera.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the on-line version, at doi:10.1016/j.marmicro.2010.01.001.

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