CENOZOIC RECORD OF ELONGATE, CYLINDRICAL, DEEP-SEA BENTHIC FORAMINIFERA IN THE INDIAN OCEAN (ODP SITES 722, 738, 744, 758, AND 763)

Bruce W. Hayward[1,8], Ashwaq T. Sabaa[1], Ellen Thomas[2,3], Shungo Kawagata[1,4], Ritsuo Nomura[5], Claudia Schröder-Adams[6], Anil K. Gupta[7] and Katie Johnson[1]

ABSTRACT

A group of ~100 species of elongate, cylindrical deep-sea benthic foraminifera (families Stilostomellidae, Pleurostomellidae, Nodosariidae) with complex, often constricted apertural structures, became extinct during increasingly cold glacial periods in the late Pliocene to mid-Pleistocene Climate Transition (MPT, ~2.6–0.6 Ma). We document the evolutionary history and architecture of this Extinction Group (Ext. Gp) through the Cenozoic at four lower bathyal-upper abyssal Indian Ocean sites (ODP 722, 744/738, 758, 763), seeking clues to the cause of this morphologically-targeted extinction episode late in the Cenozoic.

Eighty percent of the 116 Ext Gp. species present in the Cenozoic of the Indian Ocean originated globally in the Eocene or earlier, compared with 23–37% of other Quaternary deep-sea foraminifera. The Ext. Gp had its peak species richness and relative and absolute abundances in the late Eocene. The rapid warming of the Paleocene-Eocene Thermal Maximum, that resulted in a loss of 30–50% of deep-sea foraminiferal species, had no impact on the Ext. Gp in the one Indian Ocean section (ODP 744/738) studied. Major Cenozoic changes in the Ext. Gp, including increased species turnover, changes in dominant species, a decline in abundance, loss in diversity, and finally extinction, mostly occurred during the middle Eocene to early Oligocene, middle to late Miocene, and late Pliocene to middle Pleistocene. These were times of stepped increase in the volume of polar ice, global oceanic cooling, surface-water eutrophication, seasonality of phytoplankton production, deep-water ventilation, and southern deep-water carbonate corrosiveness. The final decline and disappearance of the Ext. Gp began in the late Miocene at high latitudes (744/738), but not until the late Pliocene (758, 763) or MPT (722) at lower latitudes.

We hypothesize that the loss of the Ext. Gp of deep-sea foraminifera may have been caused by the decline or demise of their specific food source (detrital phytoplankton or bottom-dwelling microbes) that was abundant in the Greenhouse World and was decimated by the stepwise cooling, ventilation, or eutrophication of the oceans that began in the middle and late Eocene.

INTRODUCTION

GLOBAL TURNOVERS IN CENOZOIC DEEP-SEA FORAMINIFERA

The Cenozoic fossil record of deep-sea benthic foraminifera indicates that they had relatively slow background species turnover rates of ~2% myr^{-1} (Boltovskoy, 1987; McKinney, 1987; Kucera and Schönfeld, 2007). Within this period, there are four intervals of enhanced global turnover (Fig. 1). Each has been related to times of significant climate change (e.g., Thomas, 1992a; Miller and others, 1993; Hayward and others, 2007; Thomas, 2007). These turnovers were during the Paleocene-Eocene Thermal Maximum event (PETM, ~55 Ma: Thomas, 1992a), the late Eocene–early Oligocene (~36–30 Ma; Miller and others, 1993), the middle Miocene (~16–12 Ma; Miller and others, 1993), and the late Pliocene to mid-Pleistocene Climate Transition (MPT) (2.6–0.55 Ma; Weinholz and Lutze, 1989; Schönfeld, 1996; Hayward and others, 2007).

These turnovers were associated with increased numbers of species originations and extinctions, but also with major changes in the dominant deep-sea foraminiferal assemblages and populations. Up to 50% of deep-sea species died out across the PETM event (Thomas, 1998, 2007), possibly associated with the expansion of warm, oxygen-depleted, corrosive bottom waters (Katz and others, 1999). In a period of less than 10 kyrs, oceanic bottom temperatures warmed by 5–6°C (Zachos and others, 2001, 2005) and typical late Cretaceous-Paleocene faunal assemblages, dominated by *Stensioeina beccariiformis*, were replaced by late Paleogene Greenhouse World assemblages, dominated by *Nuttallides truempyi* and a variety of buliminids (e.g., Tjalsma and Lohmann, 1983; Thomas, 1990; Kaiho and others, 1996; Alegret and Ortiz, 2006; Takeda and Kaiho, 2007; Thomas, 2007; Alegret and others, 2009).

The late Eocene-early Oligocene and middle Miocene turnovers were more significant in terms of community structure but had fewer species originations or extinctions (e.g., Woodruff, 1985; Thomas, 1986, 1987; Thomas and others, 2000). These occurred at times of strengthening 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 Antarctic ice sheets (e.g., Thomas and Vincent, 1987; Thomas, 2007). *Nuttallides truempyi* and many large buliminids disappeared at the end of the Eocene, replaced by faunal assemblages transitional in composition between those of late Paleogene Greenhouse conditions and those of the late Neogene Icehouse World (Fig. 1) (e.g., Thomas, 1992a, b). The transitional and late

[1] Geomarine Research, 49 Swainston Rd, St Johns, Auckland, New Zealand.

[2] Department of Geology and Geophysics, Yale University, New Haven, CT, USA.

[3] Department of Earth and Environmental Sciences, Wesleyan University, Middletown, CT, USA.

[4] Present address: Faculty of Education and Human Sciences, Yokohama National University, 79-2 Tokiwadai, Yokohama, Japan.

[5] Faculty of Education, Shimane University, Nishikawatsu, Matsue 690-8504, Japan.

[6] Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada.

[7] Department of Geology and Geophysics, Indian Institute of Technology, Kharagpur 721 302, India.

[8] Correspondence author. Email: b.hayward@geomarine.org.nz
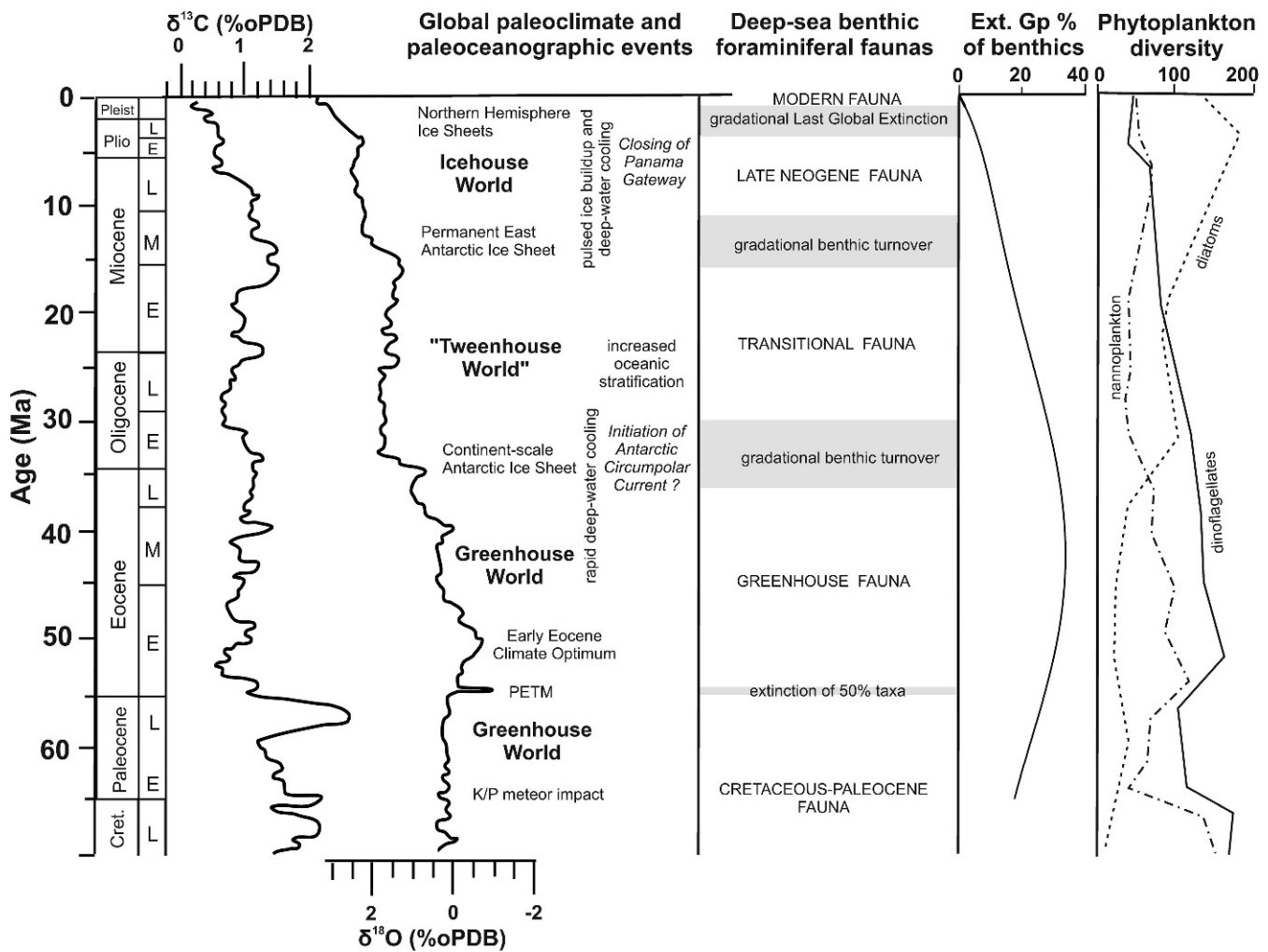
FIGURE 1.   Subantarctic, South Atlantic and South Indian Ocean compilation of benthic foraminiferal carbon and oxygen isotopic data (from Cramer and others, 2009) through the Cenozoic together with inferred timing of major global paleoclimatic and paleoceanographic events, deep-sea benthic foraminiferal 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 the diatoms, nannoplankton and dinoflagellates (from Bown and others, 2004; Stover and others, 1996; and Spencer-Cervato, 1999).

Neogene assemblages were more heterogeneous than previously, possibly reflecting the increasing geographic and bathymetric stratification of the oceans that followed the inferred establishment of the Antarctic Circumpolar Current (ACC) in the late Eocene (Fig. 2) (e.g., Diester Haass and Zahn, 1996; Cramer and others, 2009). Proponents of this view argue that the wind-driven ACC was the engine of the Oligocene through Neogene oceans, responsible for its density structure, deep circulation, formation of deep northern and southern component waters, and for the location and intensity of the upwelling of nutrient-rich deep waters, resulting in increased oceanic productivity.

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 and others, 2000; Gooday, 2003; Jorissen and others, 2007). High-latitude deep water became dominated by *Nuttallides umbonifera*, which is characteristic of cold, carbonate-

corrosive, oligotrophic, southern-sourced water (e.g., Bremer and Lohmann, 1982; Schröder-Adams, 1991; Thomas, 1992b; Jorissen and others, 2007).

Through the middle Miocene and into the early late Miocene (15–8 Ma), the transitional faunas transformed into those characteristic of the late Neogene with the evolution of *Cibicides wuellerstorfi* and further increases in seasonal phytodetritus-feeding species at bathyal depths (e.g., Thomas and Vincent, 1987; Schröder-Adams, 1991; Smart and others, 2007; Thomas, 2007), as well as the increased dominance of *Nuttallides umbonifera* at abyssal depths in lower latitudes that indicates a northward spread of vigorous, cold, corrosive deep water (e.g., Woodruff, 1985; Kurihara and Kennett, 1986; Thomas, 1992a; Hayward and others, 2004; Smart and others, 2007).

The Last Global Extinction (LGE) of deep-sea benthic foraminifera, sometimes called the "*Stilostomella* Extinction" (Weinholz and Lutze, 1989) resulted in the loss of ~20% of deep-sea foraminiferal diversity. It occurred in the late Pliocene to middle Pleistocene (~2.6–0.6 Ma) during
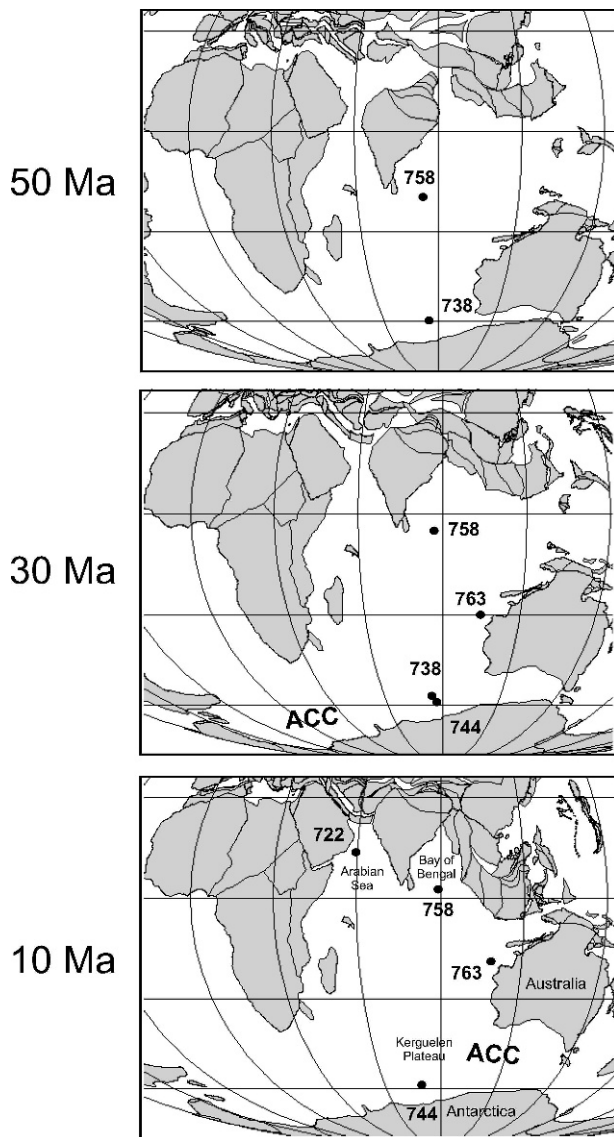
FIGURE 2. Back-tracked location of ODP study sites and hypothesized deep-ocean circulation (from Cramer and others, 2009) in the early Eocene (50 Ma), Oligocene (30 Ma) and late Miocene (10 Ma). Tectonic reconstructions are from <http://www.serg.unicam.it/Intro-Reconstr.html>. ACC = Antarctic Circumpolar Circulation.

increasingly colder glacial periods that accompanied growth of polar ice and further increases in primary productivity at lower latitudes (Hayward and others, 2007). Late Neogene faunas were replaced by those essentially similar to modern faunas, with the loss of elongate, cylindrical species during the LGE and the decline in previously abundant taxa, such as reticulate-ornamented bolivinids, *Rectuvigerina*, *Vulvulina*, *Trifarina bradyi*, *Bulimina exilis*, *Uvigerina hispida*, *Haeuslerella*, and *Bolivinita*, to be replaced with increased dominance at bathyal and upper abyssal depths by *Cassidulina carinata*, *Bulimina marginata aculeata*, *Nonionella*, *Trifarina angulosa*, and *Uvigerina peregrina* (Mackensen and others, 1992; Nomura, 1995; Hayward, 2002; Hayward and others, 2004, 2007), and by *Alabaminella weddellensis* (Kurihara and Kennett, 1986; Schröder-Adams, 1991; Yasuda, 1997; Hayward and others, 2004).

THE LAST GLOBAL EXTINCTION (*STILOSTOMELLA* EXTINCTION)

During the LGE, ~20% (19 genera and 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), one family (Stilostomellidae, 30 species) was completely wiped out and a second (Pleurostomellidae, 29 species) was decimated, leaving just one species possibly surviving through to the present (Hayward and others, 2007). The peak of extinctions (76 species) occurred during the mid-Pleistocene Climate Transition (MPT, 1.2–0.55 Ma). Unlike the PETM deep-sea extinction event (MacLeod and others, 2000), this LGE preferentially impacted specific foraminiferal morphologies (i.e., elongate, cylindrical, often uniserial tests) and types of apertures (e.g., small rounded, dentate, cribrate, lunate).

In our recent studies on 23 deep-sea core sites, we standardised the previously chaotic taxonomy of the Extinction Group of taxa (Ext. Gp), thus allowing us to document the global architecture of its populations through the late Pliocene–Recent (Hayward 2001, 2002; Kawagata and others, 2005; Hayward and others, 2006; Kawagata and others, 2006, 2007; Hayward and others, 2007; O'Neill and others, 2007; Hayward and others, 2009). These studies show widespread, pulsed declines in abundance and diversity of the Ext. Gp during more extreme glacials, with only partial interglacial recoveries. The declines started in the late Pliocene in southern-sourced deep-water masses such as Antarctic Bottom Water (AABW) and Circumpolar Deep Water (CPDW), and extended into intermediate water masses such as Antarctic Intermediate Water (AAIW) and North Atlantic Deep Water (NADW) during the MPT, with the latest declines in sites farthest downstream from high-latitude source areas of intermediate waters.

RATIONALE FOR THIS STUDY

The underlying rationale for this study is to provide an answer to this question: 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? Our approach to resolving this fundamental issue addresses the following:

1. Does the Cenozoic history of the Ext. Gp provide clues as to why it became extinct during the most recent period of rapid global cooling?
2. Was the Ext. Gp comprised of taxa with a long history of frequent turnovers?
3. Was the Ext. Gp impacted "preferentially" by the other periods of major, rapid global climate change. (i.e., the 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?
5. Has the decline of the Ext. Gp been accompanied by a major change in the other dominant deep-sea benthic foraminiferal taxa since the end of the Greenhouse World?

TABLE 1.   Location of the Indian Ocean deep-sea study sites and the number, age range and source of samples.

ODP Site	Location "Lat, Long"	Present depth	Present water mass	No. of samples	Age of samples	Size fraction	Sample sources
722	Arabian Sea 16°37′ N, 59°48′ E	2045 m	NIDW	45	Pleist	>63 μm	Kawagata and others (2006)
				16	L Mio–L Plio	>63 μm	ODP store
738	Kerguelen Plateau 62°43′ S, 82°47′ E	2252 m		31	L Cret–E Olig	>63 μm	Schröder-Adams (1991)
744	Kerguelen Plateau 61°35′ S, 80°35′ E	2308 m		24	L Eoc–Pleist	>63 μm	Schröder-Adams (1991)
758	Ninetyeast Ridge 05°23′ N, 90°22′ E	2925 m	NIDW	64	L Plio–Pleist	>63 μm	Gupta and Thomas (2003)
				9	L Plio–Pleist	>63 μm	Kawagata and others (2006)
				65	E Pal–Pleist	>150 μm	Nomura (1995)
763	NW Australia 20°35′ S, 112°13′ E	1367 m	NIDW	29	M Eoc–Pleist	>63 μm	ODP store
Total number of samples				283			

STUDY SITES

We chose four (one a composite of two nearby sites) deep-sea core sites at bathyal and abyssal depths spaced across the Indian Ocean that had well-preserved benthic foraminiferal faunas and long Cenozoic records. Age models for the sequences have been recalibrated to the latest International Commission on Stratigraphy's time scale (Gradstein and others, 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.

ODP Site 722

ODP Site 722 is located on the crest of Owen Ridge (16°37′ N, 59°48′ E, 2045 m present water depth) in the northwest Arabian Sea (Fig. 2). A 200-m-thick uppermost Miocene to Recent sequence of calcareous ooze and eolian-derived terrigenous sediment (Murray and Prell, 1991) was recovered (Table 1). Today the site is bathed in North Indian Deep Water (NIDW) with a high-salinity core layer (temperature 2°C, salinity 35.85 psu, oxygen 4.7 ml/l) originating from saline NADW (Vincent, 1974; Kawagata and others, 2006). The age model for this site combines the astronomically tuned, planktic oxygen-isotope-based model for the last ~3.7 Ma of Clemens and others (1996) with the original biostratigraphic model (Prell and others, 1989). The Last Global Extinction has been documented in detail through the Pleistocene at Site 722 (Kawagata and others, 2006) and those data are incorporated into this study.

ODP Site 758

ODP Site 758 is located on the northern end of Ninetyeast Ridge (5°23′ N, 90°22′ E, 2925 m present water depth) in the southern Bay of Bengal. A nearly continuous, 250-m-thick sequence from uppermost Eocene to Recent sequence (short hiatus in middle Miocene) plus a 50-m-thick Paleocene sequence of calcareous ooze and chalk (Pierce and others, 1989) were recovered (Table 1). Today the site is bathed in NIDW, originating from CPDW admixed with NADW (Warren, 1981). The age model for this site combines the original biostratigraphically-based model of Pierce and others (1989) with the astronomically-tuned, benthic oxygen-isotope-based model for the last ~3.6 myrs of Chen and others (1995). Previous works on the total benthic foraminiferal faunas of Site 758 has been

undertaken by Nomura (1995) on all of the, full Cenozoic sequence) and by Gupta and Thomas (2003)on the, upper Miocene-Pleistocene sequence). The Last Global Extinction has been documented in detail through the late Pliocene and Pleistocene in Site 758, (Kawagata and others, 2006) and their data have been incorporated into our study.

ODP Site 763

ODP Site 763 is located on the western side of the Exmouth Plateau (20°35′ S, 112°13′ E, present water depth 1367 m) off northwest Australia (Fig. 2). A near continuous, 250-m-thick sequence of middle Eocene-Recent (short middle-Miocene hiatus) calcareous ooze (Haq and others, 1990) was sampled. Today the site is bathed in the upper part of NIDW, originating from Circumpolar Deep Water (CPDW) admixed with NADW (Warren, 1981). The age model is based on nannofossil biostratigraphy (Siesser and Bralower, 1992) and late Neogene planktic foraminiferal biostratigraphy (Sinha and Singh, 2008). Previous work on benthic foraminifera at this site has recognized four biostratigraphic zones through the Pliocene-Pleistocene (Rai and Singh, 2004).

ODP Sites 738 and 744

ODP sites 738 (62°43′ S, 82°47′ E) and 744 (61°35′ S, 80°35′ E) are located at the southern end of the Kerguelen Plateau in the southern Indian Ocean, at present water depths of 2253 m and 2308 m respectively. To obtain a long

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)	*Ellipsopolymorphina*	
Neugeborina	*Nodosarella*	
Nodosaria mucronata, N. weaveri	*Pleurostomella*	
Orthomorphina		
Plectofrondicularia		
Proxifrons		
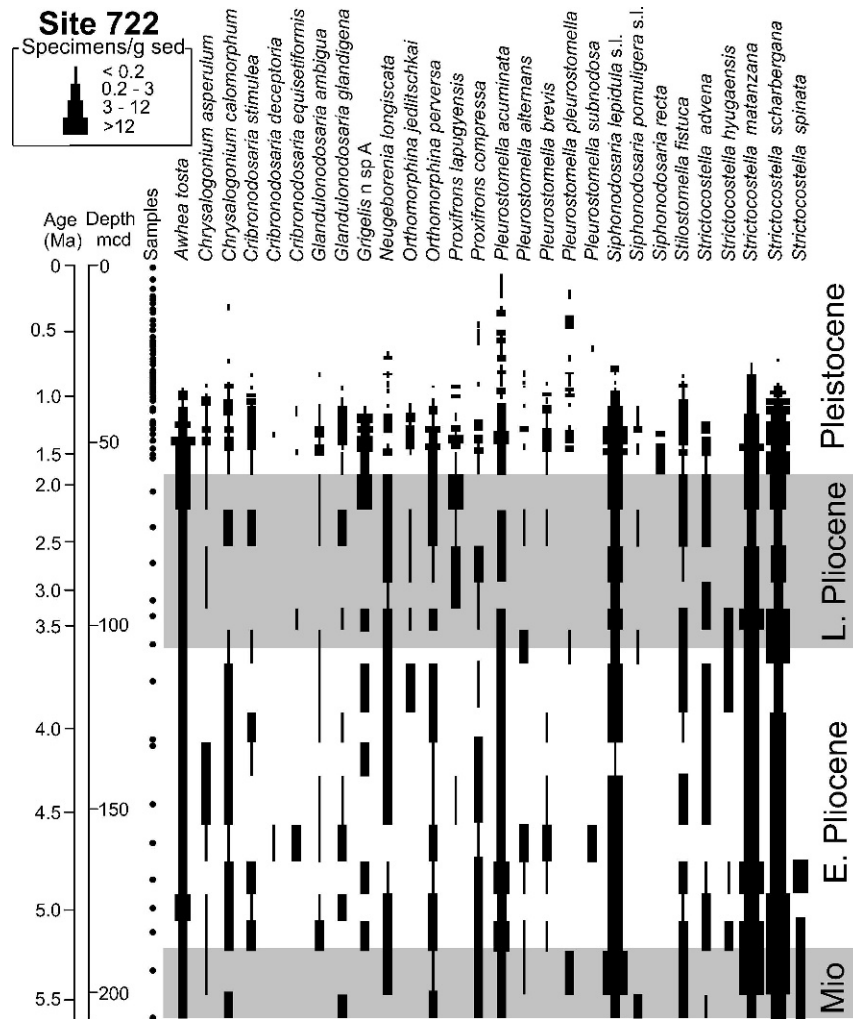
FIGURE 3. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 722.

Cenozoic record a continuous 170-m-thick upper Eocene-Recent calcareous ooze sequence from Site 744 was spliced to the top of a 190-m-thick middle-upper Eocene nanno-fossil ooze sequence recovered from Site 738 (e.g., Schröder-Adams and others, 1991). Both sites are south of the polar front and bathed in CPDW (Lindenberg and Auras, 1984). The age model is based on the biostratigraphy of Barron and others (1991) and Huber (1991).

METHODS

SAMPLE PROCESSING

Core sites were selected for their long Cenozoic carbonate-rich records from lower bathyal-middle 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 cm³ of dry sediment was weighed, washed gently with water over a 63μm sieve, and the retained sand fraction was dried. Samples washed but not picked for the benthic foraminiferal study of Schröder-Adams, (1991) were used for Site 744/738.

CENSUS COUNTS

Each sample was dry-sieved, and three size fractions (>300 μm, 150–300 μm, 63–150 μm) were picked and separately counted. The amount searched for every sample was 100% of the >300-μm fraction and, depending upon the quantity of sand in the other size fractions, 50–100% of the 150–300-μm fraction and 5–50% of the 63–150-μm fraction (using a sample splitter). The quantitative census counts were subsequently multiplied up to the number of specimens in the total sample and standardized as specimens g^{-1} sediment (bulk sediment). For most samples from Site 758, we used Nomura's (1995) quantitatively picked slides of ~300 benthic foraminifera (>63 μm) to obtain an initial census of Ext. Gp species and their relative abundance as a percentage of the total benthic foraminiferal faunas. These were supplemented by additional picking, especially of the coarser fractions (as above). All data were 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) species, which are readily distinguished by their generally elongate tests.
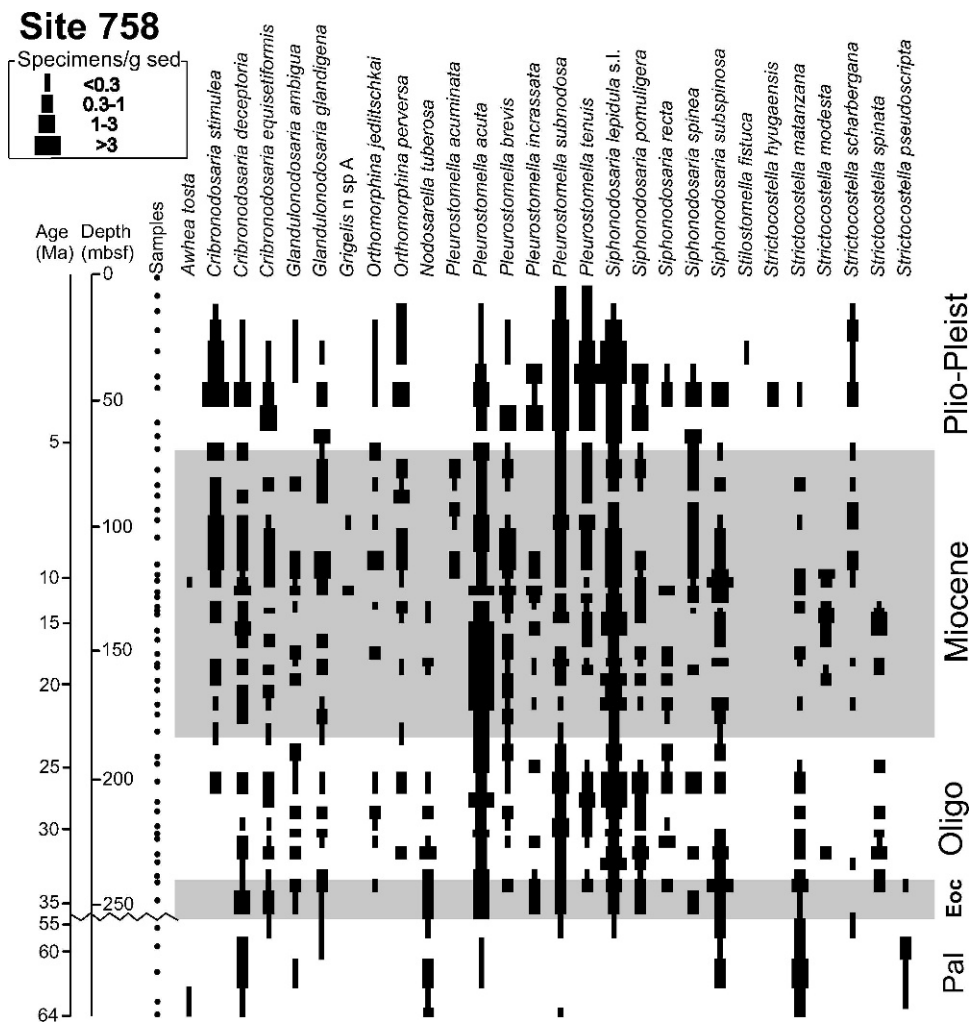
FIGURE 4. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g⁻¹ sediment) in ODP Site 758.

All Ext. Gp specimens encountered were picked from each split fraction and mounted on gummed slides for more precise identification and counting. 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 mostly found in the >150-μm fractions (Hayward and others, 2006, which were more comprehensively examined than the finest fraction, where 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 relative abundance in 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 722 and 758 (Kawagata and others, 2006) obtained by the same methodology were used for the youngest parts of these two sites.

COMPUTER METHODS

The faunal data consist of census counts (0–3120 specimens per sample) of 116 Ext. Gp foraminiferal species

from 283 samples (Appendices 1–5). For cluster analysis only the 172 samples with more than 50 Ext. Gp specimens were used. The data matrix was standardized by converting counts to percentages of sample totals. A Q-mode cluster analysis dendrogram classification was produced using the chord dissimilarity coefficient (Sneath and Sokal, 1973). The analysis was carried out using the MVSP statistical package (Kovach, 1993).

SPECIMEN ARCHIVING

Picked slides of Ext. Gp specimens used for census counts and figured specimens (prefixed by BWH) are housed in the collections of the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand.

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 3–6. A total of 117 Ext. Gp taxa were identified from the Cenozoic of the Indian Ocean (Appendix 1). Site 722 has the lowest species richness (65 spp.)
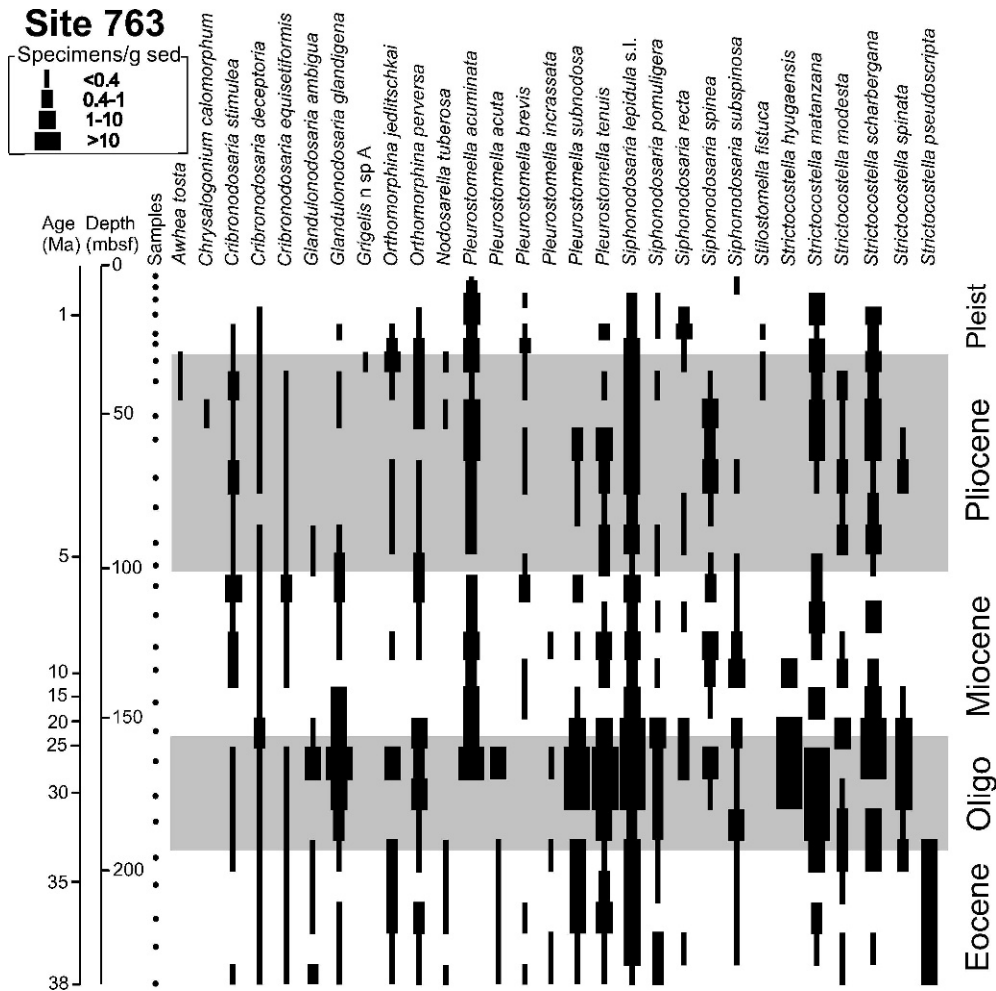
FIGURE 5. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 763.

because of its short stratigraphic range (5.6–0 Ma). In the other three sites there was a latitudinal increase in species richness from polar Site 744/738 (73 spp.) through Site 763 (82 spp.) to equatorial Site 758 (91 spp.), although this latter site also had a greater intensity of sampling (138 samples; Table 1). Eighty percent of the 110 Ext. Gp species known globally from the Pliocene–Pleistocene are recorded from the Indian Ocean. Ten of those not recorded are classified in the subfamily Plectofrondiculariinae, known to be more prevalent in shallower water (outer shelf-mid bathyal) than our sites.

ABSOLUTE ABUNDANCE AND FLUX

The absolute abundance (specimens g^{-1} sediment) and flux (specimens cm^{-2} kyr^{-1}) of the Ext. Gp (Fig. 7) were considerably greater at the two shallowest sites (722, 763). Ext. Gp absolute abundance and flux in the Paleocene was approximately half the maximum values for the late Eocene–Oligocene (sites 744/738, 758). At two sites (744/738, 763) there was a progressive overall decline in abundance from Oligocene onwards, but the decline occurred later at Site 758, from the middle Miocene on. The abundance and flux fluctuated wildly during the glacial-interglacial cycles at sites

722 and 758, with peak abundances during interglacials (Kawagata and others, 2006), and final disappearances of the Ext. Gp at all sites in the middle Pleistocene. This disappearance is particularly well documented from high-resolution sampling through the Pleistocene at sites 722 and 758 (Kawagata and others, 2006).

RELATIVE ABUNDANCE

The abundance of the Ext. Gp as a percentage of total benthic foraminifera (Fig. 7) was considerably higher at abyssal sites 744/738 and 758 (up to 45–60%) than at bathyal Site 763 (up to 17%). The most complete Cenozoic record (Site 744/738) had fairly low relative abundances of 5–25% of the Ext. Gp under Greenhouse World conditions (Paleocene–early Eocene), increasing rapidly to a peak of 20–55% during the middle Eocene–early Oligocene. Abundances declined stepwise in the middle Oligocene (to 10–27%), middle Miocene (to 4–17%), and late Miocene (to <4%).

The relative abundance pattern at Site 758 (allowing for the missing Eocene section) was remarkably similar to that at Site 744/738 (Fig. 7). Abundances peaked in the late Eocene (10–50%), then declined across the Eocene/Oligocene boundary to 10–27% in the Oligocene–early Miocene. There
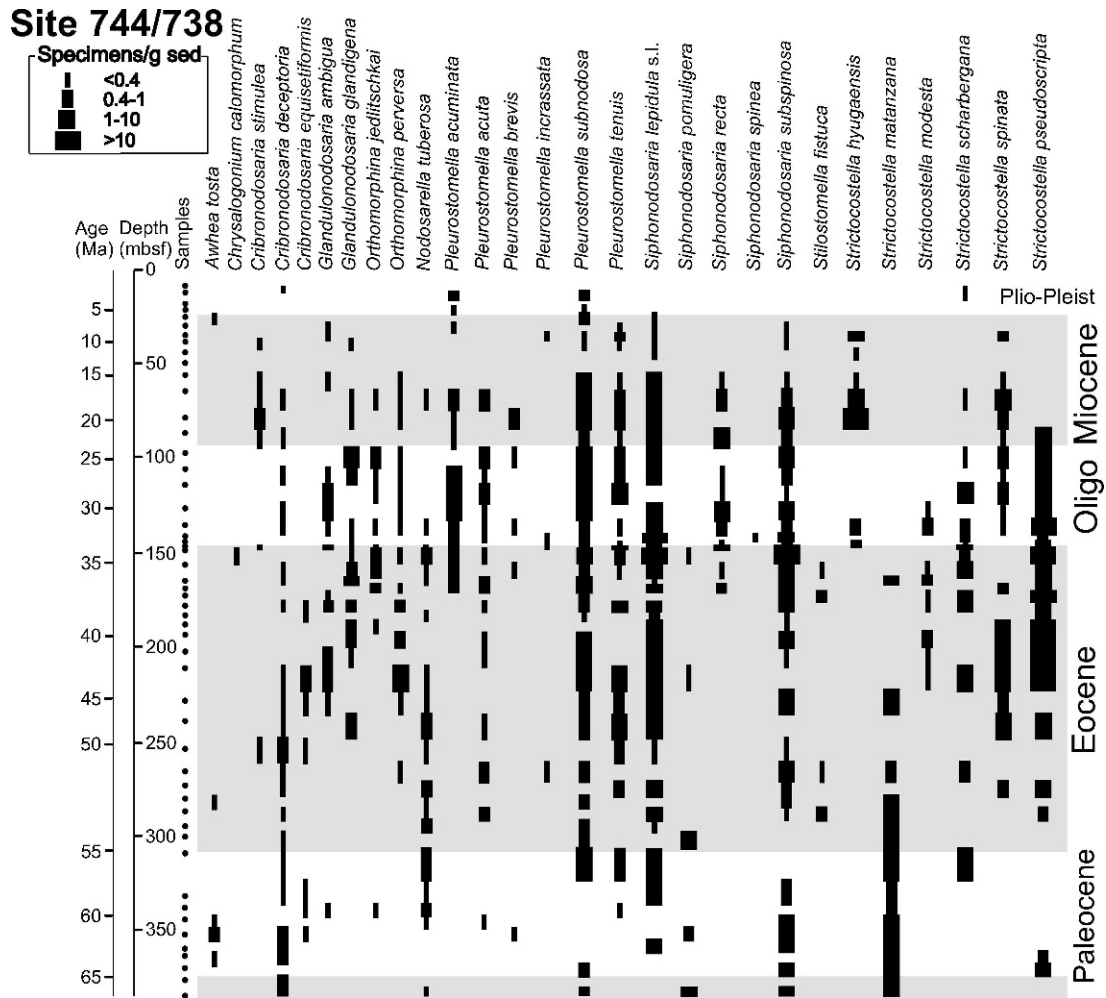
FIGURE 6. Stratigraphic records of absolute abundance of the more common Extinction Group species (specimens g^{-1} sediment) in ODP Site 744/738.

were two further stepped declines in the middle Miocene, one close to the middle-Miocene cooling event (~14 Ma), and the other in the late Miocene (~7.5 Ma). In the late Miocene–Pliocene relative abundances of the Ext. Gp were 2–10%, as compared to less than 3% in the Pleistocene.

At Site 763, the peak relative abundance of the Ext. Gp (5–13%) was in the latest Eocene to earliest Miocene, declining to less than 3% from the late early Miocene through to their disappearance in the MPT (Fig. 7).

If the Ext. Gp is broken into its three main families (Pleurostomellidae, Stilostomellidae, Nodosariidae), we find that pleurostomellids were generally more abundant at Site 758 (up to 25% compared with <8% at other sites) and stilostomellids were more abundant in sites 744/738 (up to 55% compared with <20% at other sites). At all three sites, the relative abundance of stilostomellids followed a pattern similar to that of the total Ext. Gp (Fig. 8), with increasing values from the late Cretaceous and Paleocene to a peak in the middle Eocene–earliest Miocene, followed by a progressive decline from the middle Miocene on. In the pleurostomellids, the pattern is less pronounced with a slight increase in relative abundance from the Paleocene into the Eocene, followed by a relatively flat peak through

the Eocene and Oligocene (Site 744/738), which extended through the early Miocene at Site 758. A significant drop in abundance occurred at the start of the early Miocene at Site 744/738 and at the start of the middle Miocene at Site 758, after which there was a slow, progressive decline to the extinction in the middle Pleistocene. The uniserial nodosariids (which includes many extant species) had their peak relative abundance from the Paleocene through to the early Oligocene followed by a significant drop to abundances of less than 6% since the late Oligocene, progressively declining still further from the late Miocene to the present.

SPECIES TURNOVER

The plots of Ext. Gp species richness (number of species in each sample) and overall species number (number of species present at any time, assuming continuous presence between a species' lowest and highest occurrences) for the four sites (Fig. 9) show only one interval of significant species turnover – the LGE. At the site (744/738) with the longest continuous Cenozoic record, there was a gradual increase in species richness and overall species number through the Paleocene and early Eocene, peaking at 40
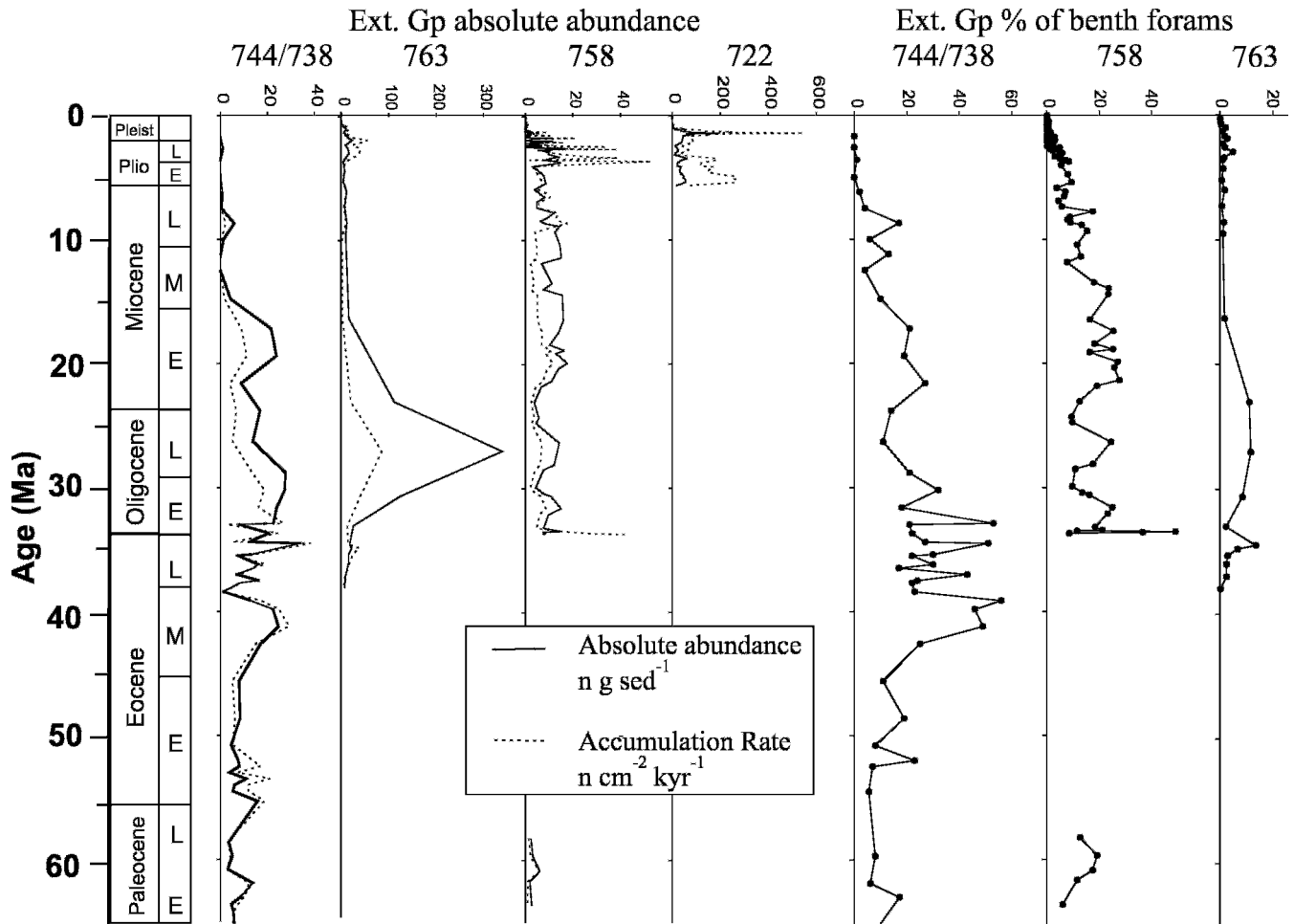
FIGURE 7. Stratigraphic records of the absolute abundance, accumulation rate (specimens $cm^{-2} kyr^{-1}$) and relative abundance (% of total benthic foraminifera) of the total Extinction Group through the Cenozoic at each study site.

species overall in the late Eocene. Species loss began in the Oligocene (11 spp.), with increased tempo of loss in the late Miocene (15 spp.). Just five species survived into the Pliocene, only to disappear completely in the MPT. At Site 763, peak species richness and number (48 spp.) also occurred in the late Eocene-earliest Oligocene, and was followed by moderate declines during the Oligocene–Miocene (10 spp. loss) and Pliocene (6 spp.), then loss of the remaining taxa (32 spp.) in the Pleistocene LGE.

The greatest Ext. Gp species richness occurred at Site 758, with its peak of overall species number (57–59 spp.) during the Oligocene-early Miocene (Fig. 9). A few species disappeared during the middle Miocene (4 spp.), with increased loss in the late Miocene (11 spp.), and early Pliocene (9 spp.). The final 35 species disappeared during the late Pliocene-middle Pleistocene LGE. In the short Pliocene–Recent record of Site 722, the peak Ext. Gp species richness (31 spp. per sample) and overall species number (50 spp.) occurred in the early Pleistocene, with the dramatic loss of all these species in the LGE.

In Site 744/738, with the longest Cenozoic record, there is evidence for a late Eocene interval of increased turnover of the Ext. Gp (increased number of lowest occurrences [LOs], and highest occurrences [HOs]) followed by a relatively

stable rate of turnover (Fig. 10). This same late Eocene peak in HOs is evident in Site 763, but the peak of LOs at this time merely reflects the start of sampling. Upper Eocene strata are not present in the other two sites. At the deeper Site 758, there is evidence for significantly increased turnovers in the number of LOs and especially HOs in the middle and late Miocene (Fig. 10). This turnover began later in Site 763, with increased LOs and HOs in the late Miocene. The major increase in HOs in the Pliocene-Pleistocene LGE is the most obvious turnover event at sites 763, 758 and 722, with the onset later (in the Pleistocene) at Site 722 than at the other two sites. Part of this last turnover also includes an increase in the number of LOs in the Pliocene at these three sites (Fig. 10), but not at Site 744/738.

When all our Indian Ocean data are combined, two peaks of LOs of Ext. Gp species are evident (Fig. 11) – in the Paleocene and the middle–late Eocene. The Paleocene peak is likely to be more evenly spread throughout the late Cretaceous (as evidenced by the number of Ext. Gp species with Cretaceous LOs – Fig. 11), which might have been clear if we had studied more Cretaceous samples, but the middle-late Eocene peak appears to have been global. The late Eocene peak of HOs at sites 744/738 and 763 was local, not ocean-wide. Similarly, the middle–late Miocene increase
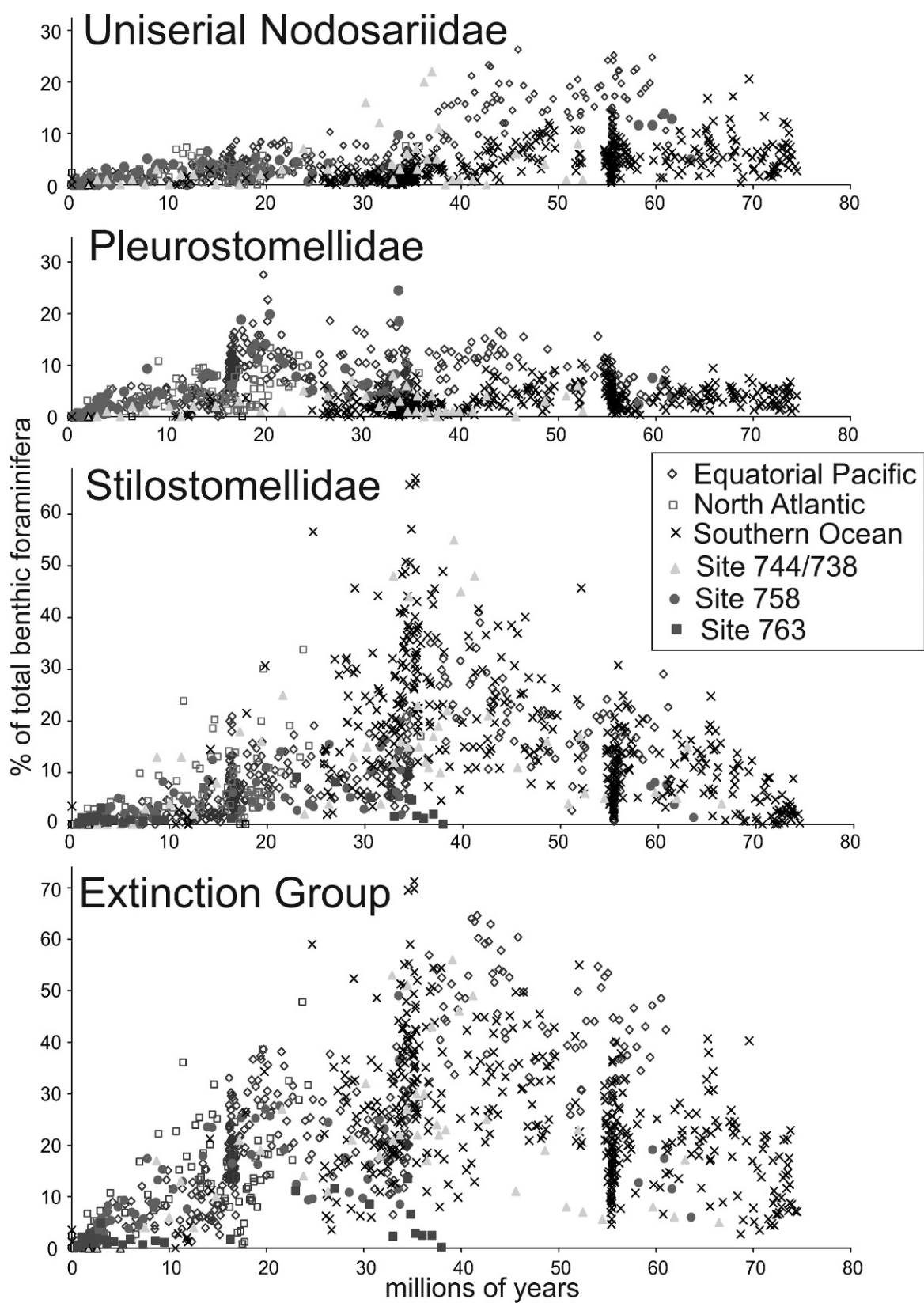
FIGURE 8. Stratigraphic record of the relative abundance of the families Stilostomellidae, Pleurostomellidae, uniserial Nodosariidae (includes extinct and extant species) and the total Extinction Group (Table 2) at Indian Ocean sites 744/738, 763 and 758 (this study), compared with the North Atlantic (Site 608), equatorial Pacific (sites 573, 574, 575, 865), and Southern Ocean (sites 689, 690) (from Thomas, 2007).

Ext. Gp Species Richness
(Number of species per sample)

Overall Species Number
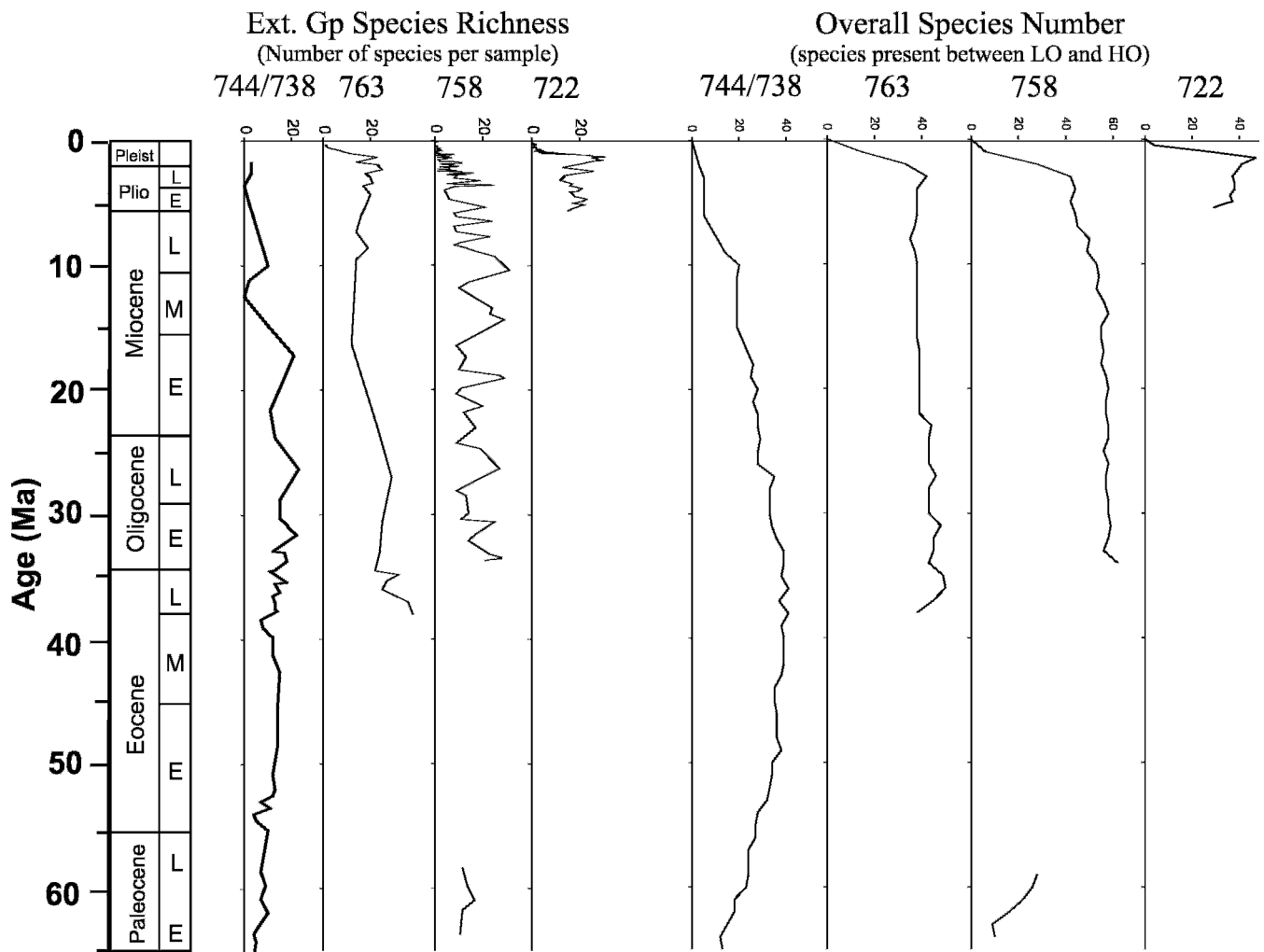(species present between LO and HO)

FIGURE 9. Stratigraphic records of the number of Ext. Gp species recorded in each sample and total number of Ext. Gp species inferred to have been present (assuming continuous presence between lowest occurrence (LO) and highest occurrence (HO) of each species) through the studied intervals at each site.

in HOs at Site 758 were not ocean-wide (Fig. 10). The increase in LOs in the late Miocene and especially Pliocene at sites 758 and 763 (Fig. 10) appears to have been more widespread in the Indian Ocean, but it was not global (Fig. 11). The major increase in HOs in the late Pliocene-middle Pleistocene (LGE) is the dominant feature of the Cenozoic history of the Ext. Gp, with 75 species (64% of Ext. Gp) disappearing from the Indian Ocean at this time (Fig. 11). The recorded global extinction of Ext. Gp species is skewed more towards the middle Pleistocene, probably because there have been more studies in Intermediate Water sites in other oceans (Hayward and others, 2007).

SPECIES DURATION

The Indian Ocean data on the timing of Ext. Gp species LOs are skewed towards the Paleocene (Fig. 11) because few Cretaceous samples were examined in this study. A large proportion 80% (93 spp.) of the Ext. Gp species have global Greenhouse World (Eocene or earlier) LOs, and this includes the majority (67%, 78 spp.) of Ext. Gp species in the Indian Ocean (Fig. 11). Five percent of Ext. Gp species seem to have

evolved globally since the middle-Miocene cooling (Icehouse World), with the remaining 15% having originated during the Oligocene-early Miocene (Tweenhouse World). The same pattern of LOs is apparent for the group of Ext. Gp species that became extinct in the Pliocene–Pleistocene in the Indian Ocean (Fig. 11b) and for a separate group of 91 Ext. Gp species recorded in Boltovskoy's (1987) global study of deep-sea foraminifera (Fig. 11a).

The dominance of Ext. Gp species with originations in the Greenhouse World contrasts with the more evenly spread originations of extant deep-sea benthic foraminiferal species across the Cenozoic epochs (Figs 11c–d). In these latter instances, 23–37% of extant species had LOs in the Cretaceous-Eocene interval. An adjunct observation from this data is that the Ext. Gp had longer mean species durations than the extant deep-sea group.

FAUNAL COMPOSITION

On the chord cluster analysis dendrogram of Ext. Gp data in all samples with more than 50 Ext. Gp specimens, we recognize nine Ext. Gp associations (Appendices 6–7). These
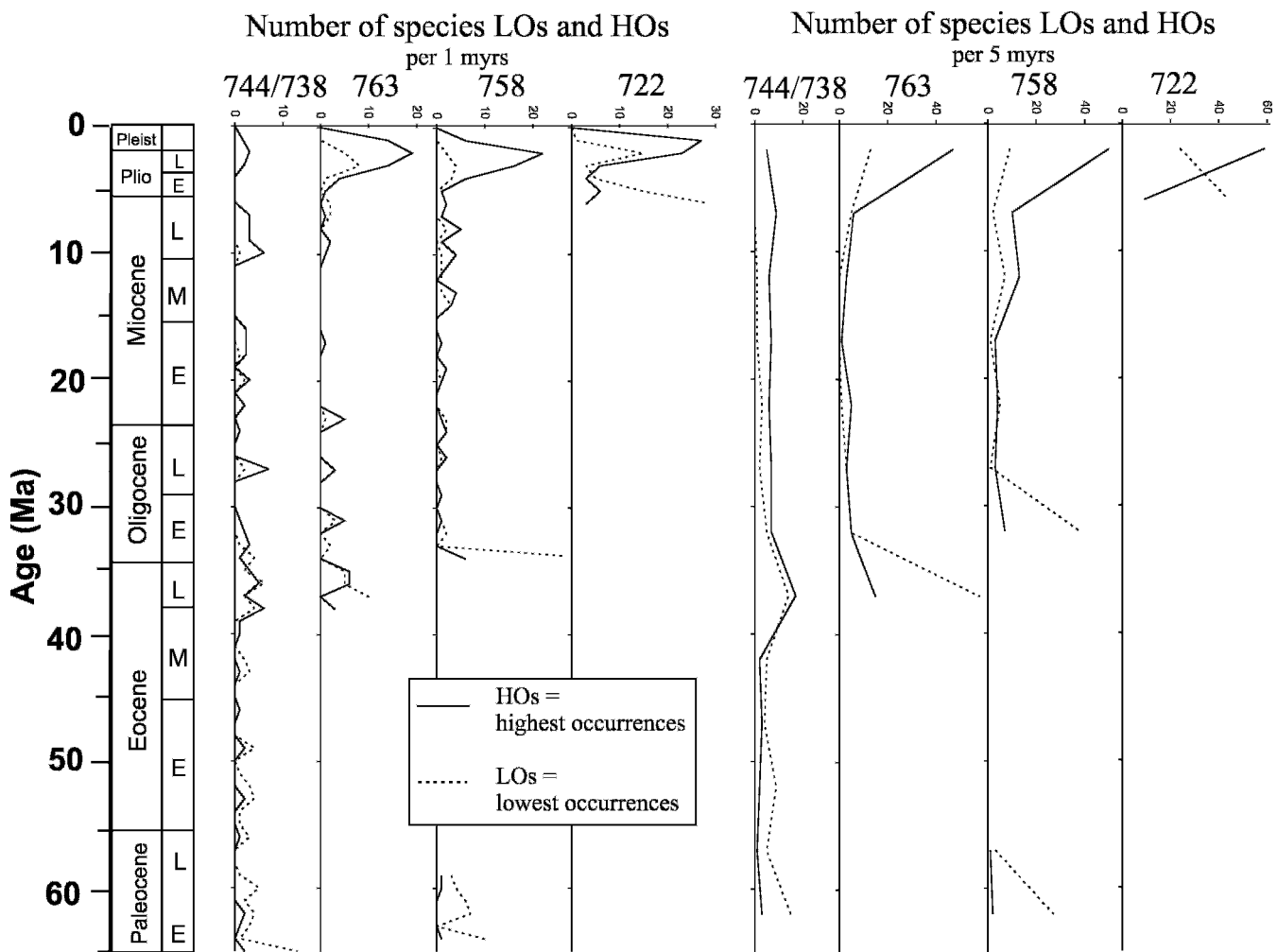
FIGURE 10.   Stratigraphic records of the number of lowest occurrences (LOs) and highest occurrences (HOs) per 1 myrs and per 5 myrs of Ext. Gp species through the studied intervals at each site.

associations have strong stratigraphic and weaker geographic and bathymetric distribution patterns (Fig. 12). Three associations (1–3) were mainly present in the Greenhouse World, two (4–5) in the Tweenhouse World (Oligocene–early Miocene), and four (6–9) in the Icehouse World.

Low-diversity assoc. 1, strongly dominated by *Strictocostella matanzana* (Figs. 14.26–14.27), only occurred in the Paleocene and earliest Eocene in the subantarctic Indian Ocean(744/738), and was not impacted by the PETM deep-sea extinction event. Assoc. 2, co-dominated by *S. matanzana* and *Siphonodosaria subspinosa* (Figs. 14.20–14.21), occurred predominantly in the latest Cretaceous–Eocene of the subantarctic, but also in the Paleocene and late Eocene deep-water of Site 758 (Fig. 12).

Assoc. 3, dominated by small, spine-bearing *Strictocostella pseudoscripta* (Figs. 14.22–14.23), was present in the subantarctic from early Eocene to earliest Miocene and also in the late Eocene of Site 763. High-diversity assoc. 4, co-dominated by *Pleurostomella acuta* (Figs. 14.10–14.12) and *Siphonodosaria lepidula* (Fig. 14.16–14.17), was the major faunal group in the Oligocene–middle Miocene of Site 758,

although it also extended into the Pliocene (Fig. 12). Assoc. 5, dominated by *Strictocostella hyugaensis*, (Figs. 14.24–14.25) occurred in the Miocene of sites 763 and 744/738, with one sample in the upper Oligocene of the former site.

Assoc. 6, which is also diverse, is dominated by *S. lepidula*, *Pleurostomella tenuis* (Figs. 14.13–14.15), and *Cribronodosaria stimulea* (Figs. 3–4), and occurred in the upper Miocene–Pliocene of sites 758 and 763, with one Oligocene sample at each site (Fig. 12). Associations 7 and 9 both occurred in the two shallowest sites 722 and 763. Assoc. 7, dominated by *Strictocostella sharbergeana*, *S. matanzana*, and *S. lepidula*, was present from the late Miocene to early Pleistocene at both sites and sporadically back to the Oligocene at Site 763 (Fig. 12). Small assoc. 8, co-dominated by *Pleurostomella incrassata* and *Siphonodosaria pomuligera* (Figs. 14.18–14.19), was rare in the middle Miocene and Pliocene of the deepest Site 758. Small, low-diversity assoc. 9, co-dominated by *Pleurostomella acuminata* (Figs. 7–9) and *S. matanzana*, only occurred near the end of the LGE close to the early/middle Pleistocene boundary (0.78 Ma), after many of the other Ext. Gp species had disappeared.
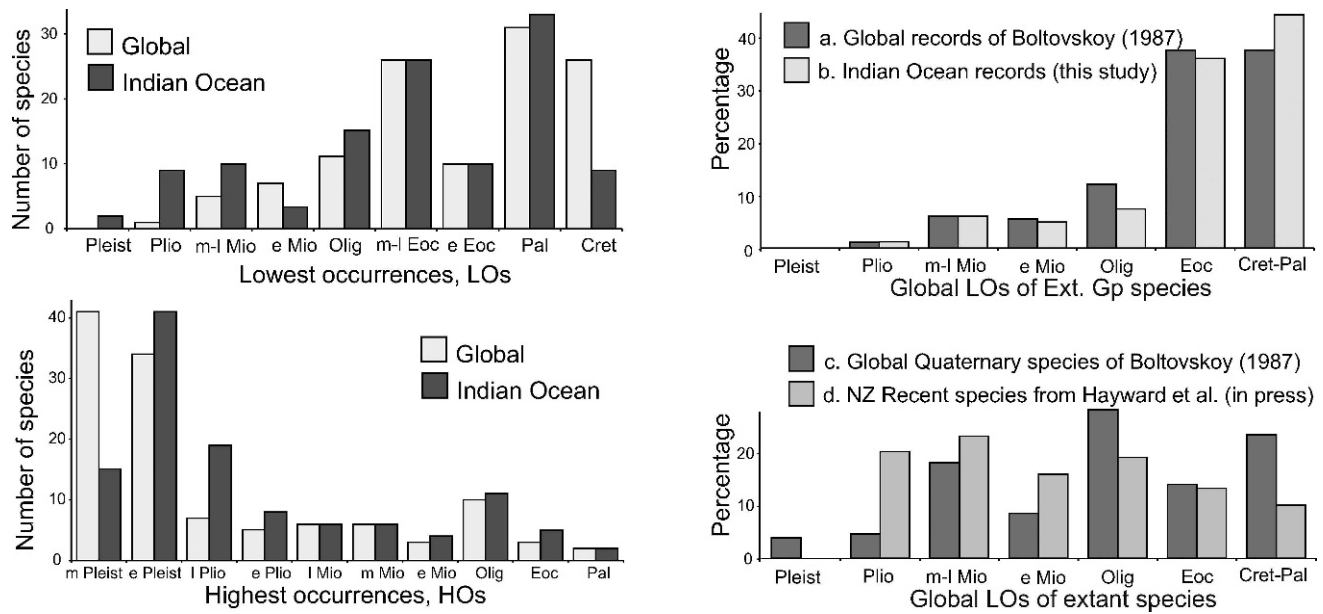
FIGURE 11. Left. Number of lowest (LO) and highest (HO) occurrences per epoch or part-epoch of Ext. Gp species in the Indian Ocean (Appendix 6) compared with the current state of knowledge globally (pers. unpubl. data). Right. Percentage of Ext. Gp species with global LOs in specified epochs or part epochs from: a. global deep-sea data set of Boltovskoy (1987), b. the present Indian Ocean study (species with Indian Ocean HOs of Pliocene or Pleistocene). Percentage of extant deep-sea benthic foraminifera with global LOs 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 and others (in press).

DISCUSSION

GLOBAL PATTERN OF EXTINCTION GROUP'S RELATIVE ABUNDANCE

The global relative abundance for the Ext. Gp through the Cenozoic, as revealed in seven deep-sea sites (Thomas, 2007) together with this study's Indian Ocean sites 744/738 and 758, increased through the Paleocene and early Eocene Greenhouse World to a middle-late Eocene peak (Ext. Gp up to 60–70%; Stilostomellidae up to 40–70%), followed by a gradual or pulsed decline (Fig. 8). Pleurostomellids increased in relative abundance through the Paleocene to a long Eocene–early Miocene peak of up to 10–25%. A rapid decline occurred at the start of the middle Miocene, followed by a more gradual decline through to the middle Pleistocene. Uniserial nodosariids had peak abundances in the late Paleocene–Eocene (up to 12–25%) with a significant decline in the late Eocene–early Oligocene, then a more gradual decline after the middle Miocene (Fig. 8). In the Paleocene–Eocene, stilostomellids appear to have been more abundant in the Southern Ocean (including Site 744/738) than elsewhere at high latitudes, whereas pleurostomellids and uniserial nodosariids were more abundant at lower latitudes, especially since the middle Eocene. The relative abundance of the Ext. Gp in Site 763 through the Cenozoic is among the lowest recorded at any deep-sea location, but the reason for this not yet clear.

TIMING OF EXTINCTION GROUP CHANGES

The major global turnovers in deep-sea benthic foraminiferal faunas (Fig. 1) have also been recorded in the Indian and Southern oceans (e.g., Gupta and Srinivasan, 1990; Schröder-Adams, 1991; Thomas, 1992b; Nomura, 1995; Smart and

others, 2007). These turnovers were associated with stepwise climatic and oceanographic changes that resulted in increased Neogene faunal complexity as the geographic and bathymetric stratification of the oceans developed (e.g., Thomas, 2007). In the northern Indian Ocean, deep-sea foraminiferal faunas were additionally influenced by the late Miocene (~8 Ma) onset of the seasonal tropical monsoons, which led to increased oceanic primary productivity and locally decreased levels of bottom-water oxygen (e.g., Gupta and Thomas, 2003; Singh and Gupta, 2004).

Paleocene-Eocene Thermal Maximum (PETM)

In the section across the PETM that we studied (Site 744/738), there were no impacts on the Ext. Gp. This contrasts with the reported 30–50% loss of total deep-sea benthic foraminiferal diversity and major changes in dominant faunal assemblage composition (e.g., Kaiho and others, 1996; Thomas, 1998). These earlier studies did not include information on the Ext. Gp. taxa at the species level; the group as a whole showed short-term decline in relative abundance during the PETM, but recovered afterwards.

Middle Eocene–Early Oligocene Cooling

In the Subantarctic (744/738), changes in the Ext. Gp faunal dominants (from assocs. 1 and 2 to assoc. 3) occurred in the middle Eocene (~47–40 Ma; Fig. 12), coincident with reported accelerated extinctions of other benthic foraminifera in the subantarctic Weddell Sea (Thomas, 1989, 1992b) during initial global cooling after the early Eocene climate optimum (Zachos and others, 2001). This was a time of increased oceanic primary productivity (Diester-Haass, 1995; Thomas and others, 2000; Diester-Haass and Zahn, 2001; Schumacher and Lazarus, 2004) and the onset of increased
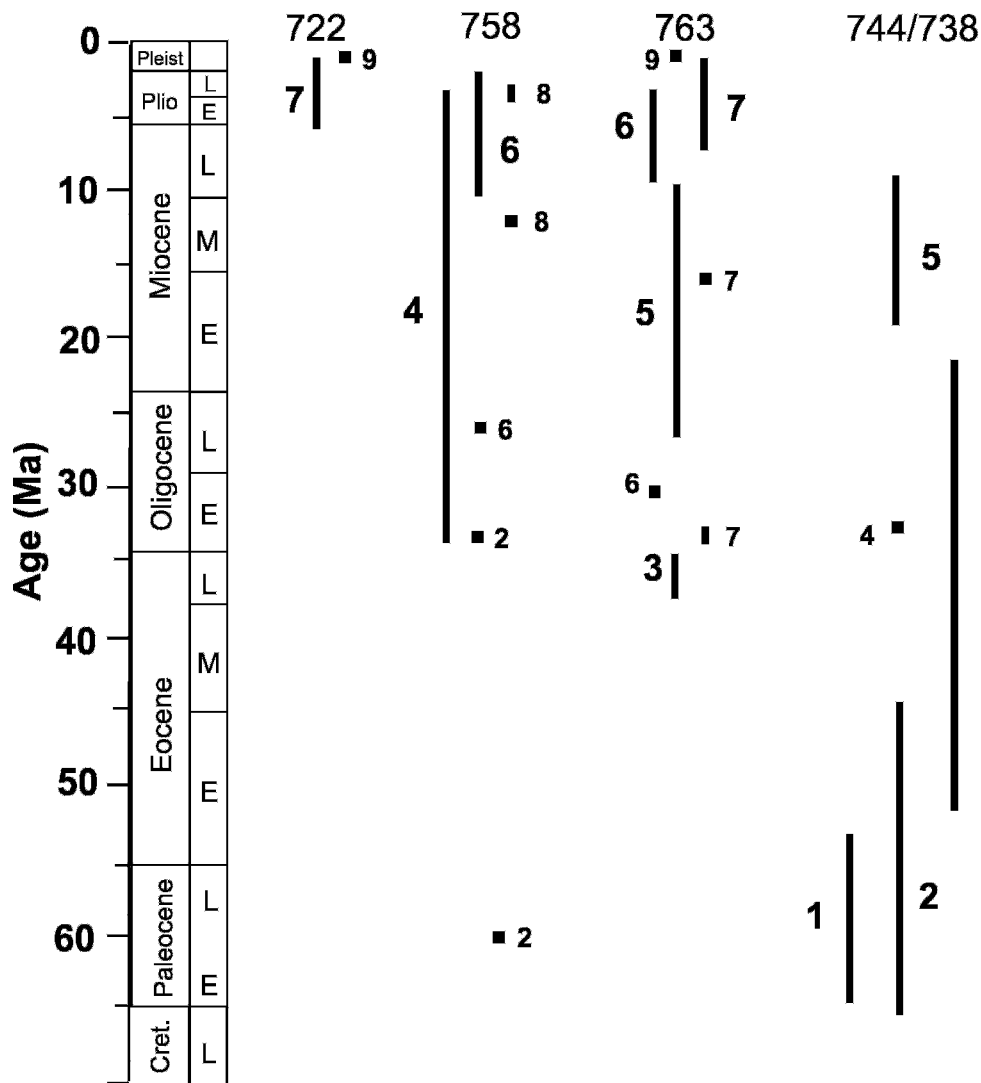
FIGURE 12. Stratigraphic distribution of the nine faunal associations (1–9) in the four ODP study sites. Solid bars represent more than one sample, small squares represent single sample records.

diatom abundance and diversity that now contribute half of export productivity in modern oceans (Falkowski and others, 2004a, b), and decreased nannoplankton diversity (Fig. 1) (e.g., Aubry, 1992; Bown, 2005). These would have resulted in major changes in the amount and composition of the food flux for Greenhouse World deep-sea benthic communities (e.g., Thomas and Gooday, 1996).

Globally, there seems to have been a slight increase in Ext. Gp originations in the middle-late Eocene period of cooling (Fig. 11). The late Eocene–early Oligocene global deep-sea benthic turnover (Fig. 1) coincided with a slightly increased turnover (both LOs and HOs) of Ext. Gp species in the two Indian Ocean sites studied (744/738, 763). There was a significant decrease in the relative abundances of Ext. Gp, stilostomellids, and uniserial nodosariids in the Indian Ocean (744/738, 758) and globally (Figs. 7–8). The overall character of the dominant Ext. Gp faunas did not change through this interval in the Subantarctic (Assoc. 3, Site 744/738), but it did change farther north (sites 758, 763), with the switch to more diverse assocs. 4, 6, and 7 faunas. Thus the Ext. Gp appears

to have been significantly impacted during the first of the global turnovers (late Eocene-early Oligocene), although Ext. Gp changes started somewhat earlier (middle Eocene) at higher latitudes (744/738), possibly associated with the first evidence of ACC development and resulting Antarctic ice (e.g., Diester Haass and Zahn, 1996).

Late Oligocene–Early Miocene Transitional Faunas

The late Oligocene–early Miocene was a fairly stable time for the transitional deep-sea benthic faunas globally (Fig. 1). There were however a few changes in the Ext. Gp in the Indian Ocean through this 10 myr interval. In the Subantarctic (744/738) there was a switch from dominant assoc. 3 to assoc. 5 faunas – a change that occurred earlier in lower latitudes (Fig. 12). The long-term decline in the overall number of Ext. Gp species began in this period and was earlier in high latitudes than low latitudes (late Oligocene at Site 744/738, early Miocene at Site 763, middle Miocene at Site 758; Fig. 9).
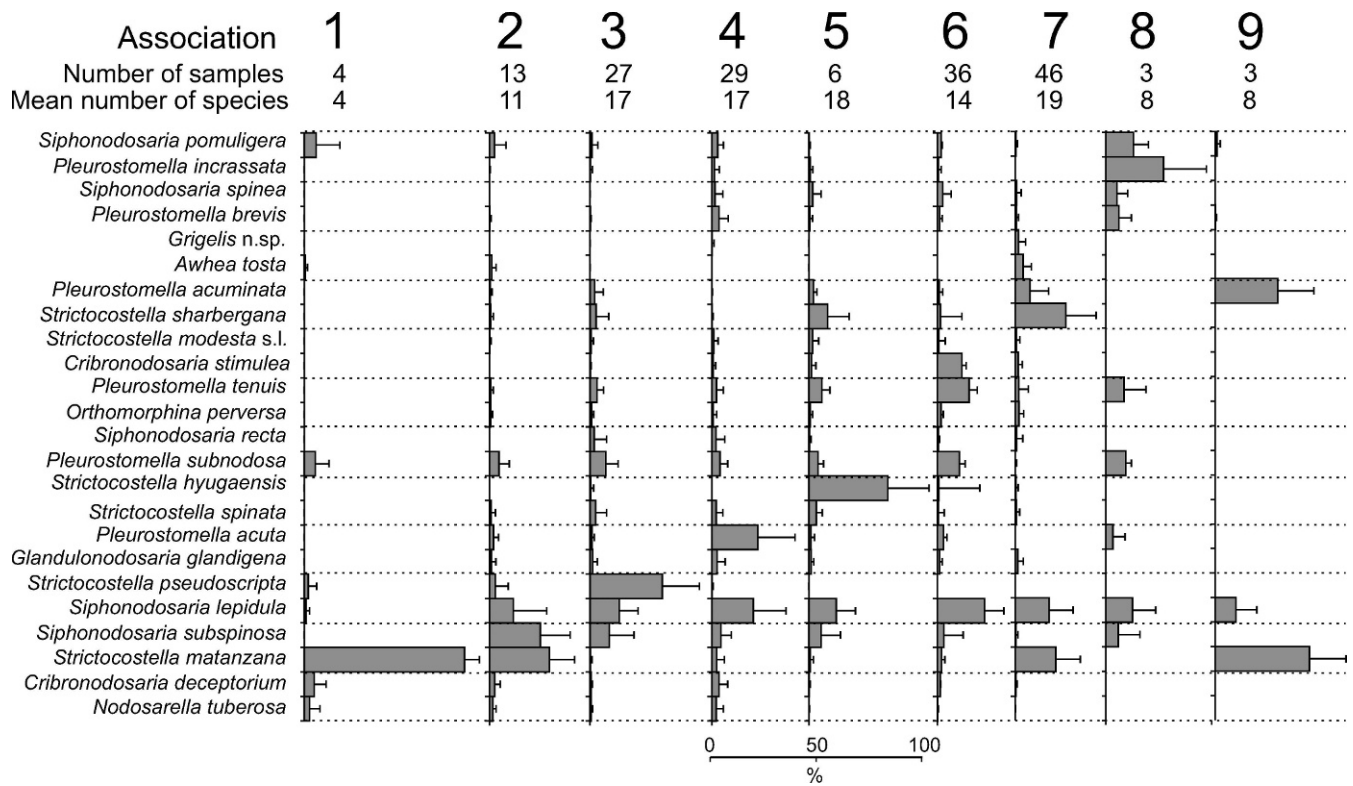
FIGURE 13. Mean relative abundance and standard deviation of the common Ext. Gp species (as proportion of the total Ext. Gp census count) in faunal associations 1–9, selected from the chord cluster analysis dendrogram (Appendix 8).

Middle Miocene Cooling

There was no apparent increased faunal turnover (LOs, HOs) of the Ext. Gp in the Indian Ocean at this time, but there was a major decline in its absolute abundance, flux, relative abundance, and species richness in the subantarctic (744/738) and in the relative abundance in the northern (758) and equatorial Indian Ocean (Smart and others, 2007), and globally (Fig. 8).

Late Miocene Cooling

There were late Miocene switches in the dominant species of Ext. Gp faunas in the east Indian Ocean from assoc. 5 to assocs. 6 and 7 (Fig. 12) but only a small increase in turnover rate (Fig. 10). In the Subantarctic (744/738), declines in Ext. Gp species richness and overall species number began in the middle and late Miocene respectively, considerably earlier than in lower latitudes (Fig. 9). The late Miocene is not noted as a time of global faunal change in the deep-sea, but significant benthic foraminiferal faunal changes at bathyal depths in the northern Indian Ocean at ~8 Ma have been attributed to the onset of tropical monsoons (e.g., Singh and Gupta, 2004). We infer however, that Ext. Gp changes, including significant declines in relative abundance, that occurred at our study sites were most probably associated with the inferred increased production of corrosive, deep Antarctic Bottom Water (AABW), which may have circulated northwards at abyssal to lower-bathyal depths in the late Miocene (e.g., Nomura, 1995; Smart and others, 2007).

Late Pliocene–Mid-Pleistocene Climate Transition, Last Global Extinction

The terminal decline in overall Ext. Gp species numbers that began in the late Miocene in the Subantarctic was completed there during the late Pliocene–Pleistocene (Fig. 9). This decline in overall number of species (loss of 74 spp., Fig. 11) began in the late Pliocene (~2.6 Ma) at sites 758 and 763 in the northeast Indian Ocean, but did not begin until onset of the MPT (~1.2 Ma) in somewhat shallower water in the northwest Indian Ocean (Site 722). The Ext. Gp associations did not change through the late Pliocene–early Pleistocene in any of our study sites (Fig. 12), with the only switch (to low-diversity assoc. 9) occurring in the early–middle Pleistocene, when many species disappeared from the two shallower sites (722, 763).

In their high-resolution study of deep Site 758 in the northern Indian Ocean, Kawagata and others (2006) recorded a stepped decline in Ext. Gp abundance and diversity at ~2.5, 1.7, and 1.2 Ma. They inferred that these glacial declines were a result of increased production of colder, well-ventilated AABW which flowed northwards over the site during pulsed increases of southern polar ice sheet volume (e.g., Elmstrom and Kennett, 1986; Froelich and others, 1991; Hodell and Venz, 1992). The Ext. Gp did not decline at shallower, intermediate water depths (Site 722) until the onset of the MPT, when the volume of cold, well-ventilated Glacial North Atlantic Intermediate Water (GNAIW) increased and spread into the Indian Ocean (e.g., Boyle, 1997; Kallel and others, 1988).
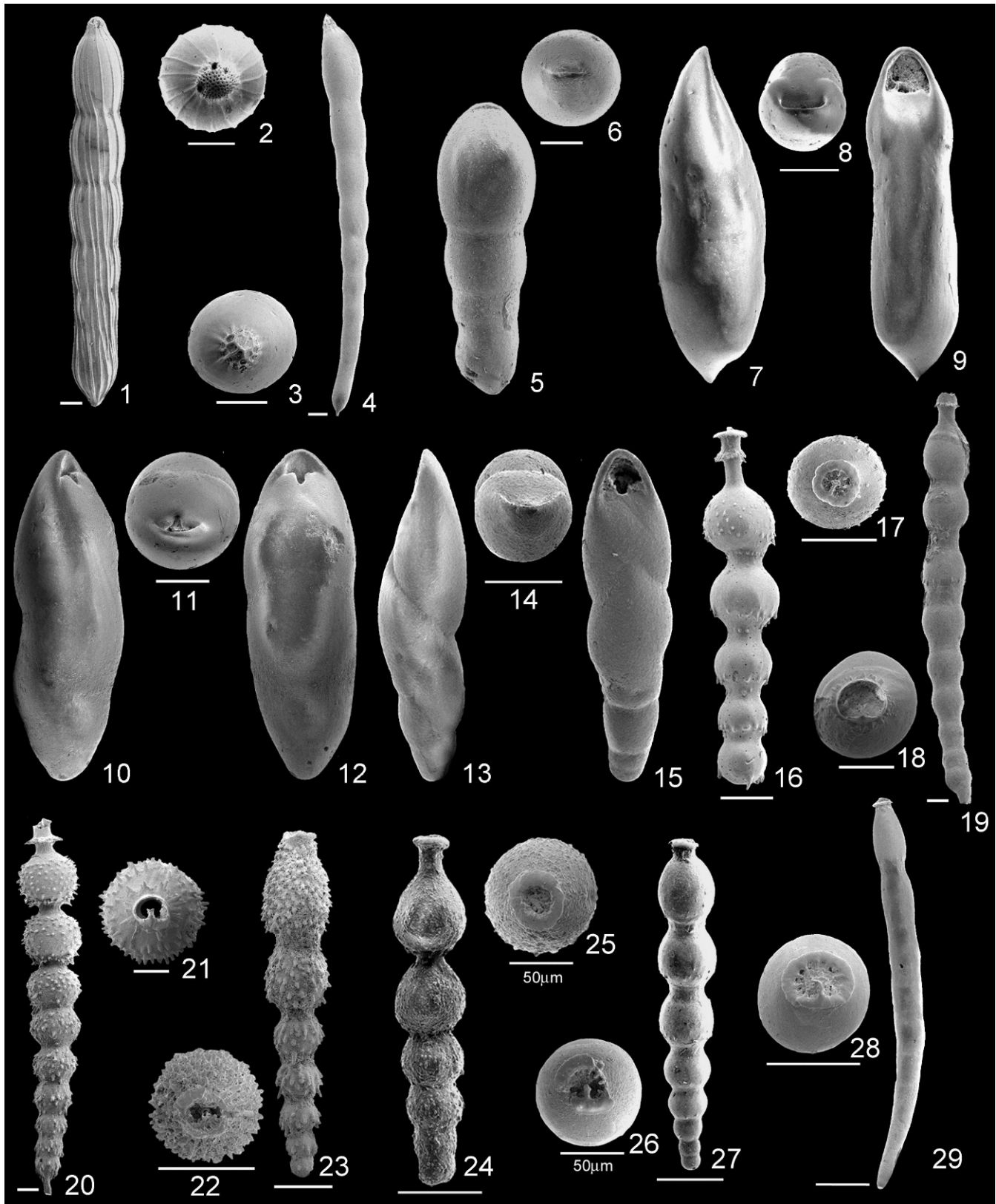
FIGURE 14. SEM images of a selection of the Extinction Group species from the Indian Ocean study sites 763, 758, and 738. Scale bar indicates 100 μm, unless otherwise labeled. All units are in μm. **1–2** *Cribronodosaria deceptoria* (Schwager, 1866). Side and apertural views, BWH 182/1, sample 763A-3H-4, 0–4 cm. **3–4** *Cribronodosaria stimulea* (Schwager, 1866). Apertural and side views, BWH 182/3, sample 763A-5H-CC. **5–6** *Nodosarella tuberosa* (Gümbel, 1868). Apertural and side views, BWH 182/5, sample 758A-25X-1, 76–78 cm. **7–9** *Pleurostomella acuminata* (Cushman, 1922). Side, apertural, and front views, BWH 182/12, sample, 763A-4H-CC. **10–12** *Pleurostomella acuta* (Hantken, 1875). Side, apertural, and front views, BWH 182/6, sample 758A-17X-3, 75–80 cm. **13–15** *Pleurostomella tenuis* (Hantken, 1883). Side, apertural, and front views, BWH 182/13, sample 758A-10H-1,

The major decline and loss of the Ext. Gp in the late Pliocene–MPT coincided with significant changes in the total deep-sea benthic faunas globally. These have been attributed to intensified cooling combined with increased upwelling and primary productivity, and in places increased strength of tropical monsoons (e.g., Gupta and Thomas, 2003).

CAUSE OF THE DECLINE AND LOSS OF THE EXTINCTION GROUP

Survival of the Ext. Gp virtually unscathed through the PETM implies that species of this group tolerated warm, possibly and locally oxygen-depleted, carbonate-corrosive bottom waters. An inferred, moderately deep-infaunal lifestyle for the Ext. Gp (Gupta, 1993; Hayward and others, 2007) might have enabled them to survive these conditions. The presence of many Ext. Gp species in Greenhouse World seas and the groups' peak global abundance towards the end of this time agree with the hypothesis that it was adapted to the warm oceans of the Greenhouse World. These oceans might have been characterized by a very different circulation pattern than that of the Icehouse World by lacking clearly delineated water masses and having much more active diapycnal mixing (e.g., Thomas and others, 2006; Huber and Thomas, 2008; Cramer and others, 2009).

The start of the Ext. Gp's decline during the middle Eocene–early Oligocene cooling of the high latitudes, and its final demise during the increasingly colder glacials of the late Pliocene and MPT, provide clues to understanding the cause of its extinction. The middle Eocene–early Oligocene experienced the most extreme drop in deep-water temperature ($\sim8^\circ$C) of the Cenozoic, probably as the result of high-latitude cooling (e.g., Zachos and others, 2001; Liu and others, 2009). The associated oceanic upheaval led to wholesale changes in oceanic phytoplankton composition and productivity (e.g., Aubry, 1992; Baldauf, 1992; Falkowski and others, 2004a, b; Bown, 2005) and probably also change in efficiency of delivery of organic matter to the seafloor (e.g., Finkel and others, 2005), and possibly its seasonality (e.g., Thomas, 2007; Eldrett and others, 2009). Physicochemical changes associated with the significant cooling of oceanic deep water included increased ventilation and increased carbonate corrosiveness (e.g., Kennett, 1977; Wright and Miller, 1996; Thomas, 2007).

Pulsed growth of polar ice sheets in the middle-late Miocene and late Pliocene MPT resulted in 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 AABW (late Miocene), and increased total food supply in the Indian Ocean (especially late Pliocene–MPT) during these cooling steps. The significant cooling of deep water during these steps would also have lowered microbial activity rates (including chemosynthetic) in bottom waters and on the seafloor, with downstream effects on any benthic foraminifera that fed on them (e.g., Thomas, 2007).

The elongate, cylindrical shape of the Ext. Gp species suggests that they may have had a moderately deep infaunal habitat tolerant of lower-oxygen conditions (Gupta, 1993). It is unlikely that the actual temperature or oxygen changes in the deep water directly impacted Ext. Gp foraminifera, as their global Neogene distribution shows they were tolerant of an extremely wide range of bottom temperature and dissolved oxygen levels (Hayward and others, 2007). The wide distribution of the Ext. Gp in oligotrophic and eutrophic regions, with sustained or highly seasonal phytoplankton productivity, also suggests that mere changes in the quantity or seasonality of food supply would not have resulted directly in the extinction of these foraminifera.

The highly specialized modifications of the apertures of most of the Ext. Gp probably contain the answer to the cause of the extinctions, but we do not know the ecological function of these modifications. We have hypothesized that they directed pseudopodial flow into and out of the shell (e.g., Hayward, 2007; Thomas, 2007), which might have been related to the collecting or rupturing of specific food sources. These specific food sources were abundant in the Greenhouse World and presumably were directly impacted by the changes that occurred during the stepwise cooling; thus, disappearance of these food sources during the MPT possibly caused the final extinction of the foraminifera that depended on them. There are several possible candidates for the specific 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, especially during the middle Eocene-early Oligocene (Aubry, 1992; Bown, 2005). Alternatively, it could have been deep-water or benthic chemosynthetic or other microscopic prokaryotes, as we know that they are more susceptible than foraminifera to small temperature changes (Thomas, 2007).

CONCLUSIONS

Our study provides some answers to the questions posed above, but it seems clear that data are needed from other ocean basins:

1. *Does the Cenozoic history of the Ext. Gp provide some clues as to why it became extinct during this most recent period of rapid cooling*? It provides clues, but no definitive answer.

←

75–80 cm. **16–17** *Siphonodosaria lepidula* (Schwager, 1866). Side and apertural views, BWH 182/7, sample 763A-5H-CC. **18–19** *Siphonodosaria pomuligera* (Stache, 1864). Apertural and side views, BWH 182/8, sample 763A-10H-CC. **20–21** *Siphonodosaria subspinosa* (Cushman, 1943). Side and apertural views, BWH 182/4, sample 763A-14H-CC. **22–23** *Strictocostella pseudoscripta* (Cushman, 1937). Apertural and side views, BWH 182/11, sample 738 B-11H-CC. **24–25** *Strictocostella hyugaensis* (Ishizaki, 1943). Side and apertural views, BWH 182/10, sample 763A-17H-CC. **26–27** *Strictocostella matanzana* (Palmer and Bermúdez, 1936). Apertural and side views, BWH 182/9, sample 763A-5H-CC. **28–29** *Strictocostella scharbergana* (Neugeboren, 1856). Apertual and side views, BWH 182/2, sample 763A-4H-CC.

2. *Did the Ext. Gp comprise taxa with a long history of frequent turnovers?* No, most of the Ext. Gp species had relatively long species durations characteristic of deep-water benthic foraminifera. They were not a group of plastic taxa subject to rapid evolutionary changes.

3. *Was the Ext. Gp impacted preferentially by the three other major periods of enhanced global turnover in deep-sea foraminifera?* The Ext. Gp survived the PETM warm event with no obvious impact. The two intervals of enhanced cooling and consequent oceanic change had some impact on the abundance and composition of the Ext. Gp in the Indian Ocean, with the much greater cooling of the middle Eocene–early Oligocene having more significant effects, including slightly enhanced turnover rates, than the middle Miocene. The LGE decline in the Ext. Gp began as early as the late Miocene in the subantarctic Southern Ocean.

4. *Were the Ext. Gp taxa some of the last remnants of the Greenhouse World deep-sea biota?* Mostly yes, with 80% of Indian Ocean members of the Ext. Gp originating in the Eocene or earlier.

5. *Has the decline of the Ext. Gp been accompanied by a major change in the other dominant deep-sea benthic foraminiferal taxa since the end of the Greenhouse World?* Yes mostly, with 63–77% of extant deep-sea foraminifera originating in the Oligocene or later, including most of the dominant species.

These observations lead us to conclude that the possible cause of the LGE of deep-sea foraminifera was the decimation of their detrital phytoplankton or deep-sea, benthic microbial food source that had been abundant in the Greenhouse World. Likely causes of this trophic alteration were the stepwise cooling, changing circulation patterns, increased ventilation and changes in oceanic primary productivity and the efficiency of the biological pump that began in the middle to late Eocene.

ACKNOWLEDGMENTS

REFERENCES

ALEGRET, L., and ORTIZ, S., 2006, Global extinction event in benthic foraminifera across the Paleocene/Eocene boundary at the Dababiya stratotype section: Micropaleontology, v. 53, p. 433–447.

———, ———, ORUE-ETXEBARRIA, X., BERNAOLA, G., BACETA, J. I., MONECHI, S., APELLANIZ, E., and PUJALTE, V., 2009, The Paleocene–Eocene Maximum: new data on microfossil turnover at the Zumaia section, Spain: Palaios, v. 24, p. 318–328.

AUBRY, M.-P., 1992, Late Paleogene calcareous nannoplankton evolution: A tale of climatic deterioration, in Prothero, D. R., and Berggren, W. A. (eds.), Eocene–Oligocene Climatic and Biotic Evolution: Princeton University Press, Princeton, New Jersey, p. 272–309.

BALDAUF, J. G., 1992, Middle Eocene through early Miocene diatom floral turnover, in Prothero, D. R., and Berggren, W. A. (eds.), Eocene–Oligocene Climatic and Biotic Evolution: Princeton University Press, Princeton, New Jersey, p. 310–326.

BARRON, J. A., BARRERA, E., and OTHERS, 1991, Biochronologic and magnetochronologic synthesis of Leg 119 sediments from the Kerguelen Plateau and Prydz Bay, Antarctica, in Barron, J. A., Larsen, B., and others, Proceedings of the Ocean Drilling Program, Scientific Results, v. 119: Ocean Drilling Program, College Station, Texas, p. 813–847.

BOLTOVSKOY, E., 1987, Tertiary benthic foraminifera in bathyal deposits of the Quaternary world ocean: Journal of Foraminiferal Research, v. 17, p. 279–285.

BOYLE, E. A., 1997, Characteristics of the deep ocean carbon system during the past 150,000 years: $\sum CO_2$ distributions, deep water flow patterns and abrupt climate change: Proceedings of the National Academy of Science, v. 94, p. 8300–8307.

BREMER, M. L., and LOHMANN, G. P., 1982, Evidence for primary control of the distribution of certain Atlantic Ocean benthonic foraminifera by degree of carbonate saturation: Deep-Sea Research, v. 29, p. 987–998.

BOWN, P. R., 2005, Calcareous nannoplankton evolution: a tale of two oceans: Micropaleontology, v. 51, p. 299–308.

———, LEES, L. A., and YOUNG, J. R., 2004, Calcareous nanno-plankton evolution and diversity through time, in Thiersten, H. R., and Young, J. R. (eds.), Coccolithophores – From Molecular Processes to Global Impact: Springer, p. 481–508.

CHEN, J., FARRELL, J. W., MURRAY, D. W., and PRELL, W. L., 1995, Timescale and paleoceanographic implications of a 3.6 m.y. oxygen isotope record from the northeast Indian Ocean (Ocean Drilling Program Site 758): Paleoceanography, v. 10, p. 21–47.

CLEMENS, S. C., MURRAY, D. W., and PRELL, W. L., 1996, Non-stationary phase of the Plio-Pleistocene Asian monsoon: Science, v. 274, p. 943–948.

CRAMER, B. S., TOGGWEILER, J. R., WRIGHT, J. D., KATZ, M. E., and MILLER, K. G., 2009, Benthic foraminiferal isotope syntheses: Ocean overturning since the Late Cretaceous: Paleoceanography, doi:10.1029/2008PA001683.

DIESTER-HAASS, L., 1995, Middle Eocene to early Oligocene pale-oceanography of the Antarctic Ocean (Maud Rise, ODP Leg 113, Site 689): change from a low to a high productivity ocean: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 113, p. 311–334.

———, and ZAHN, R., 1996, Eocene–Oligocene transition in the Southern Ocean: History of water mass circulation and biological productivity: Geology, v. 24, p. 163–166.

———, and ———, 2001, Paleoproductivity increase at the Eocene–Oligocene climatic transition: ODP/DSDP sites 763 and 592: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 172, p. 153–170.

ELDRETT, J. S., GREENWOOD, D. R., HARDING, I. C., and HUBER, M., 2009, Increased seasonality through the Eocene to Oligocene transition in northern high latitudes: Nature, v. 459, p. 969–973.

ELMSTROM, K. M., and KENNETT, J. P., 1986, Late Neogene paleoceanographic evolution of Site 590: Southwest Pacific, in Kennett, J. P. (ed.), Initial Reports of the Deep Sea Drilling Project, v. 90: Government Printing Office, Washington, D.C., p. 1361–1382.

FALKOWSKI, P. G., KATZ, M. E., KNOLL, A., QUIGG, A., RAVEN, J. A., SCHOFIELD, O., and TAYLOR, M., 2004a, The evolution of modern eukaryotic phytoplankton: Science, v. 305, p. 354–360.

———, SCHOFIELD, O., KATZ, M. E., VAN DE SCHOOTBRUGGE, B., and KNOLL, A., 2004b, Why is the land green and the ocean red?, in Thierstein, H., and Young, J. (eds.), Coccolithophores – From Molecular Processes to Global Impact: Elsevier, Amsterdam, p. 429–453.

FINKEL, Z. V., KATZ, M. E., WRIGHT, J. D., SCHOFIELD, O. M., and FALKOWSKI, P. G., 2005, Climatically driven macroevolutionary patterns in the size of marine diatoms over the Cenozoic:

Proceedings of the National Academy of Sciences, USA, v. 102, p. 8927–8932, doi: 10.1073/pnas.0409907102.

FROELICH, P. N., MALONE, P. N., and OTHERS, 1991, Biogenic opal and carbonate accumulation rates in the subantarctic South Atlantic: The late Neogene of Meteor Rise Site 704, in Ciesielski, P. F., and Kristffersen, Y. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 114. College Station, Texas, p. 515–550.

GOODAY, A. J., 2003, Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: environmental influences on faunal characteristics: Advances in Marine Biology, v. 46, p. 1–90.

GRADSTEIN, F. M., OGG, J. G., and SMITH, A. G., 2004, A Geologic Time Scale, 2004: Cambridge University Press, Cambridge, 589 p.

GUPTA, A. K., 1993, Biostratigraphic vs. paleoceanographic importance of Stilostomella lepidula (Schwager) in the Indian Ocean: Micropaleontology, v. 39, p. 47–52.

———, and SRINIVASAN, M. S., 1990, Response of northern Indian Ocean deep-sea benthic foraminifera to global climates during Pliocene-Pleistocene: Marine Micropaleontology, v. 16, p. 77–91.

HAQ, B. U., VON RAD, U., and others., 1980, Proceedings of the Ocean Drilling Program, Initial Reports, v. 122: Ocean Drilling Program, College Station, Texas.

HAYWARD, B. W., 2001, Global deep-sea extinctions during the Pleistocene ice ages: Geology, v. 29, p. 599–602.

———, 2002, Late Pliocene to middle Pleistocene extinctions of deep-sea benthic foraminifera ("Stilostomella Extinction") in the Southwest Pacific: Journal of Foraminiferal Research, v. 32, p. 274–307.

———, GRENFELL, H. R., CARTER, R., and HAYWARD, J. J., 2004, Benthic foraminiferal proxy evidence for the Neogene palaeoceanographic history of the Southwest Pacific, east of New Zealand: Marine Geology, v. 205, p. 147–184.

———, KAWAGATA, S., GRENFELL, H. R., DROXLER, A. W., and SHEARER, M., 2006, Mid-Pleistocene extinction of bathyal benthic foraminifera in the Caribbean Sea: Micropaleontology, v. 52, p. 53–73.

———, ———, ———, SABAA, A. T., and O'NEILL, T., 2007, The last global extinction in the deep sea during the mid-Pleistocene climate transition: Paleoceanography, v. 22, PA3103, doi:10.1029/2007PA001424.

———, SABAA, A. T., KAWAGATA, S., and GRENFELL, H. R., 2009, The early Pliocene re-colonisation of the deep Mediterranean Sea by benthic foraminifera and their pulsed late Pliocene-middle Pleistocene decline: Marine Micropaleontology, v. 71, p. 97–112.

———, TENDAL, O. S., CARTER, R., GRENFELL, H. R., MORGANS, H. E. G., SCOTT, G. H., STRONG, C. P., and HAYWARD, J. J., in press, Phylum Foraminifera. Foraminifera and Xenophyophores, in Gordon, D. P. (ed.), New Zealand Inventory of Biodiversity. A Species 2000 Symposium Review: Canterbury University Press, Christchurch.

HODELL, D. A., and VENZ, K., 1992, Toward a high-resolution stable isotopic record of the southern ocean during the Pliocene–Pleistocene (4.8 to 0.8 Ma). The Antarctic paleoenvironment: a perspective on global change: Antarctic Research Series, v. 56, p. 265–310.

HUBER, B. T., 1991, Paleogene and early Neogene planktonic foraminiferal biostratigraphy of sites 738 and 744, Kerguelen Plateau (southern Indian Ocean), in Barron, J. A., Larsen, B., and others (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 119: Ocean Drilling Program, College Station, Texas, p. 427–450.

HUBER, M., and THOMAS, E., 2008, Paleoceanography: greenhouse climates, in Steele, J. H., Thorpe, S. A., and Turekian, K. K. (eds.), Encyclopedia of Ocean Sciences, 2nd edition: Elsevier, New York, p. 4229–4239.

JORISSEN, F. J., FONTANIER, C., and THOMAS, E., 2007, Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics, in Hillaire-Marcel, C., and de Vernal, A. (eds.), Proxies in late Cenozoic Paleoceanography: Pt. 2: Biological tracers and biomarkers: Elsevier, Amsterdam, p. 263–326.

KAIHO, K., and OTHERS, 1996, Latest Paleocene benthic foraminiferal extinction and environmental changes at Tawanui, New Zealand: Paleoceanography, v. 11, p. 447–465.

KALLEL, N., LABEIRIE, L. D., JUILLET-LECLERC, A., and DUPLESSY, J.-C., 1988, A deep hydrological front between intermediate and deep-water masses in the glacial Indian Ocean: Nature, v. 333, p. 651–655.

KATZ, M. E., PAV, D. M., DICKENS, G. R., and MILLER, K. G., 1999, The source and fate of massive carbon input during the latest Paleocene thermal maximum: Science, v. 286, p. 1531–1533.

KAWAGATA, S., HAYWARD, B. W., GRENFELL, H. R., and SABAA, A. T., 2005, Mid-Pleistocene extinction of deep-sea foraminifera in the North Atlantic Gateway (ODP sites 980 and 982): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 221, p. 267–291.

———, ———, and GUPTA, A. K., 2006, Benthic foraminiferal extinctions linked to late Pliocene-Pleistocene deep-sea circulation changes in the northern Indian Ocean (ODP sites 722 and 758): Marine Micropaleontology, v. 58, p. 219–242.

———, ———, and KUHNT, W., 2007, Extinction of deep-sea foraminifera as a result of Pliocene-Pleistocene deep-sea circulation changes in the South China Sea (ODP sites 1143 and 1146): Quaternary Science Reviews, v. 26, p. 808–827.

KENNETT, J. P., 1977, Cenozoic evolution of Antarctic glaciation, the Circum-Antarctic Ocean, and their impact on global paleoceanography: Journal of Geophysical Research, v. 82, p. 3843–3859.

KOVACH, W. L., 1993, MVSP shareware, multivariate statistics package: Kovach Computing Services, Pentraeth, Wales.

KUCERA, M., and SCHÖNFELD, J., 2007, The origin of modern oceanic foraminiferal faunas and Neogene climate change, in Williams, M., Haywood, A. M., Gregory, F. J., and Schmidt, D. N. (eds.), Deep Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies: The Micropalaeontological Society, Special Publication v. 2, p. 409–426.

KURIHARA, K., and KENNETT, J. P., 1986, Neogene benthic foraminifers: Distribution in depth traverse, Southwest Pacific, in Kennett, J. P., von der Borch, C. C., and others. (eds.), Initial Reports of the Deep Sea Drilling Project, v. 90: U.S. Government Printing Office, Washington, D.C., p. 1037–1077.

LINDENBERG, H. G., and AURAS, A., 1984, Distribution of arenaceous foraminifera in depth profiles of the Southern Ocean (Kerguelen Plateau area): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 48, p. 61–106.

LIU, Z., PAGANI, M., ZINNIKER, D., DECONTO, R., HUBER, M., BRINKHUIS, H., SHAH, S. R., LECKIE, R. M., and PEARSON, A., 2009, Global cooling during the Eocene-Oligocene climate transition, Science, v. 323, p. 1187–1189. doi 10.1126/science.1166368.

MACKENSEN, A., BARRERA, E., and HUBBERTEN, H.-W., 1992, Neogene circulation in the southern Indian Ocean: evidence from benthic foraminifers, carbonate data, and stable isotope analyses (site 751): in Wise, S. W., and Schlich, R. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 120: Ocean Drilling Program, College Station, Texas, p. 867–880.

MACLEOD, N., ORTIZ, N., FEFFERMAN, N., CLYDE, W., SCHULTER, C., and MACLEAN, J., 2000, Phenotypic response of foraminifera to episodes of global environmental change, in Culver, S. J., and Rawson, P. F. (eds.), Biotic Response to Global Change: The Last 145 Million Years: Cambridge University Press, Cambridge, p. 51–78.

MCKINNEY, M. L., 1987, Taxonomic selectivity and continuous variation in mass and background extinctions of marine taxa: Nature, v. 325, p. 143–145.

MILLER, K. G., KATZ, M. E., and BERGGREN, W. A., 1993, Cainozoic deep-sea benthic foraminifera: A tale of three turnovers, in Takayanagi, Y., and Saito, T. (eds.), Studies in Benthic Foraminifera: Tokai University Press, Tokyo, p. 67–75.

MURRAY, D. W., and PRELL, W. L., 1991, Pliocene to Pleistocene variations in calcium carbonate organic carbon, and opal on the Owen Ridge, northern Arabian Sea, in Prell, W. J., Niitsuma, N., and others. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 117: Ocean Drilling Program, College Station, Texas, p. 343–363.

NOMURA, R., 1995, Paleogene to Neogene deep-sea paleoceanography in the eastern Indian Ocean: benthic foraminifera from ODP sites 747, 757 and 758: Micropaleontology, v. 41, p. 251–290.

O'NEILL, T. A., HAYWARD, B. W., KAWAGATA, S., SABAA, A. T., and GRENFELL, H. R., 2007, Pleistocene extinctions of deep-sea foraminifera: the South Atlantic record: Palaeontology, v. 50, p. 1073–1102.

PEIRCE, J., WEISSEL, J., and OTHERS (eds.), Proceedings of the Ocean Drilling Program, Initial Reports, v. 121: Ocean Drilling Program, College Station, Texas.

PRELL, W. L., NIITSUMA, N., and OTHERS, 1989, Proceedings of the Ocean Drilling Program, Initial Reports, v. 122: Ocean Drilling Program, College Station, Texas.

RAI, A. K., and SINGH, V. B., 2004, Late Neogene deep sea benthic foraminiferal biostratigraphy of ODP sites 762B and 763A (Exmouth Plateau), eastern Indian Ocean: Journal of the Geological Society of India, v. 63, p. 415–429.

SCHÖNFELD, J., 1996, The 'Stilostomella Extinction'. Structure and dynamics of the last turnover in deep-sea benthic foraminiferal assemblages, in Moguielsky, E. A., and Whatley, R. (eds.), Microfossils and Oceanic Environments: Aberystwyth Press, University of Wales, Aberystwyth, p. 27–37.

SCHRÖDER-ADAMS, C. J., 1991, Middle Eocene–Holocene benthic foraminifera, Kerguelen Plateau (south Indian Ocean), in Barron, J. A., Larsen, B., and others (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 119: Ocean Drilling Program, College Station, Texas, p. 611–630.

SCHUMACHER, S., and LAZARUS, D., 2004, Regional differences in pelagic productivity in the late Eocene to early Oligocene – a comparison of southern high latitudes and lower latitudes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 214, p. 243–263.

SIESSER, W. G., and BRALOWER, T. J., 1992, Cenozoic calcareous nannofossil biostratigraphy on the Exmouth Plateau, eastern Indian Ocean, in Proceedings of the Ocean Drilling Program Scientific Results, v. 122: Ocean Drilling Program, College Station, Texas, p. 601–631.

SINGH, R. K., and GUPTA, A. K., 2004, Late Oligocene–Miocene paleoceanographic evolution of the southeastern Indian Ocean: evidence from deep-sea benthic foraminifera (ODP Site 757): Marine Micropaleontology, v. 51, p. 153–170.

SINHA, D. K., and SINGH, A. K., 2008, Late Neogene planktic foraminiferal biochronology of the ODP Site 763a, Exmouth Plateau, southeast Indian Ocean: Journal of Foraminferal Research, v. 38, p. 251–270.

SMART, C. W., THOMAS, E., and RAMSAY, A. T. S., 2007, Middle–late Miocene benthic foraminifera in a western equatorial Indian Ocean depth transect: paleoceanographic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 247, p. 402–420.

SNEATH, P. H. A., and SOKAL, R. R., 1973, Numerical Taxonomy: Freeman, San Francisco, 573 p.

SPENCER-CERVATO, C., 1999, The Cenozoic deep-sea microfossil record: explorations of the DSDP/ODP sample set using the Neptune database: Paleontologica Electronica 2, art. 5.

STOVER, L. E., BRINKHUIS, H., DAMASSA, S. P., DE VERTEUIL, L., KELEY, R. J., MONTEIL, E., PARTRIDGE, A. D., POWELL, A. J., RIDING, J. B., SMELROR, M., and WILLIAMS, G. L., 1996, Mesozoic-Tertiary dinoflagellates, acritarchs and prasinophytes, in Jasonius, J., and McGregor, D. C. (eds.), Palynology: Principles and Applications, v. 2: American Association of Stratigraphic Palynologists Foundation, p. 641–750.

TAKEDA, K., and KAIHO, K., 2007, Faunal turnovers in central Pacific benthic foraminifera during the Paleocene-Eocene Thermal Maximum: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 251, p. 175–197.

THOMAS, E., 1986, Changes in composition of Neogene benthic foraminiferal faunas in equatorial Pacific and North Atlantic: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 53, p. 47–61.

———, 1987, Late Oligocene to Recent deep-sea benthic foraminifera from the central equatorial Pacific Ocean, in Ruddiman, W. F., Kidd, R. B., and others. (eds.), Initial Reports of the Deep Sea Drilling Project, v. 94: U.S. Government. Printing Office, Washington, D.C., p. 997–1032.

———, 1989, Development of Cenozoic deep-sea benthic foraminiferal faunas in Antarctic waters: Geological Society London Special Publication, v. 47, p. 283–296.

———, 1990, Late Cretaceous–early Eocene mass extinctions in the deep sea. In: Sharpton, V. L., and Ward, P. D. (eds.), Global Catastrophes in Earth History: Geological Society of America, Special Publication, v. 247, p. 481–495.

———, 1992a, Cenozoic deep-sea circulation: evidence from deep-sea benthic foraminifera, in Kennett, J. P., and Warnkke, D. A. (eds.), The Antarctic Paleoenvironment: A Perspective on Global Change: Antarctic Research Series, v. 56, Washington D.C., p. 141–165.

———, 1992b, Middle Eocene–late Oligocene bathyal benthic foraminifera (Weddell Sea): faunal changes and implications for ocean circulation, in Prothero, D. R., and Berggren, W. A. (eds.), late Eocene–Oligocene and Biotic Evolution: Princeton University Press, Princeton, New Jersey, p. 245–271.

———, 1998, Biogeography of the late Paleocene benthic foraminiferal extinction, in Aubry, M.-P., Lucas, S., and Berggren, W. A. (eds.), Late Paleocene–Early Eocene Biotic and Climatic Events in the Marine and Terrestrial Records: Columbia University Press, New York, p. 214–243.

———, 2007, Cenozoic mass extinctions in the deep sea: what perturbs the largest habitat on earth?, in Monechi, S., Coccioni, R., and Rampino, M. R. (eds.), Mass Extinctions and Other Large Ecosystem Perturbations: Extraterrestrial and Terrestrial Causes: Geological Society of America, Special Paper 424, p. 1–23.

———, BRINKHUIS, H., HUBER, M., and RÖHL, U., 2006, An ocean view of the early Cenozoic Greenhouse World: Oceanography (Special Volume on Ocean Drilling), v. 19, p. 63–72.

———, and GOODAY, A. J., 1996, Deep-sea benthic foraminifera: tracers for Cenozoic changes in oceanic productivity? Geology, v. 24, p. 355–358.

———, and VINCENT, E., 1987, Major changes in benthic foraminifera in the equatorial Pacific before the middle Miocene polar cooling: Geology, v. 15, p. 1035–1039.

———, ZACHOS, J. C., and BRALOWER, T. J., 2000, Deep-sea environments on a warm Earth: latest Paleocene–early Eocene, in Huber, B., MacLeod, K., and Wing, S. (eds.), Warm Climates in Earth History: Cambridge University Press, Cambridge, p. 132–160.

TJALSMA, R. C., and LOHMANN, G. P., 1983, Paleocene–Eocene bathyal and abyssal benthic foraminifera from the Atlantic Ocean: Micropaleontology, Special Publication, v. 4, p. 1–90.

VINCENT, E., 1974, Cenozoic planktic biostratigraphy and paleoceanography of the tropical western Indian Ocean, in Fisher, R. L., Bunce, E. T., and others (eds.), Initial Reports of Deep Sea Drilling Project, v. 73: U.S. Government Printing Office, Washington, D.C., p. 1111–1150.

WARREN, B. A., 1981, Transition hydrographic section at Lat. 18°S. Property distribution and circulation in the South Indian Ocean: Deep-Sea Research, v. 28, p. 759–788.

WEINHOLZ, P., and LUTZE, G. F., 1989, The Stilostomella extinction, in Ruddiman, W. F., Sarnthein, M., and others. (eds.), Proceedings of Ocean Drilling Program, Scientific Results, v. 108: ODP, College Station, Texas, p. 113–117.

WOODRUFF, F., 1985, Changes in Miocene deep-sea benthic foraminiferal distribution in the Pacific Ocean: Relationship to paleoceanography, in Kennett, J. P. (ed.), The Miocene Ocean: Paleoceanography and Biogeography: Geological Society of America Memoir, 163, p. 131–175.

WRIGHT, J., and MILLER, K., 1996, Control of North Atlantic Deep Water circulation by the Greenland-Scotland Ridge: Paleoceanography, v. 11, p. 157–170, doi: 10.1029/95PA03696.

YASADA, H., 1997, Late Miocene–Holocene paleoceanography of the western equatorial Atlantic: evidence from deep-sea benthic foraminifers, in Shackleton, N. J., Curry, W. B., Richter, C., and Bralower, T. J. (eds.), Proceedings of the Ocean Drilling Program, Scientific Results, v. 154: ODP, College Station, Texas, p. 395–431.

ZACHOS, J. C., PAGANI, M., SLOAN, L., THOMAS, E., and BILLUPS, K., 2001, Trends, rhythms, and aberrations in global climate 65 Ma to present: Science, v. 292, p. 686–693.

———, and OTHERS, 2005, Extreme Acidification of the Atlantic Ocean at the Paleocene-Eocene Boundary (~55 Mya): Science, v. 308, p. 1611–1615.

APPENDICES 1–8

These appendices can be found on the Cushman Foundation website in the JFR Article Data Repository (http://www.cushmanfoundation.org/jfr/index.html) as item number JFR‗DR400001.

APPENDIX 1

Taxonomic list of deep-sea benthic foraminiferal species of the Extinction Group recorded in this study from Indian Ocean sites 722, 738, 744, 758, and 763. The original description is listed for each species, together with reference to a recent image (if available) and the documented time of extinction based on our studies to date.

APPENDIX 2

Census data of Ext. Gp species in ODP Site 722.

APPENDIX 3

Census data of Ext. Gp species in ODP Site 758.

APPENDIX 4

Census data of Ext. Gp species in ODP Site 763.

APPENDIX 5

Census data of Ext. Gp species in ODP Site 744/738.

APPENDIX 6

Relative abundance of Ext. Gp species in samples from all four Indian Ocean study sites grouped in clusters 1–9, obtained from chord cluster analysis (Appendix 8). Sample prefixes: A = Site 722, B = Site 758, C = Site 763, D = Site 744/738; samples suffixes are ages in myrs.

APPENDIX 7

Dendrogram classification of all samples from the four ODP study sites with >50 Ext. Gp specimen counts produced using the chord measure of dissimilarity. Sample identifiers are prefixed by A–D to identify site and have a numerical suffix that records the samples age in myrs. A = Site 722, B = 758, C = 763, D = 738 and 744. Five samples were unclustered.

APPENDIX 8

Lowest occurrences (LOs) and highest occurrences (HOs) in Ma of Ext. Gp species in the Indian Ocean study sites and as currently known globally.