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Planktonic Foraminiferal Response to Middle Miocene Cooling in the Southern Ocean (ODP Site 747, Kerguelen Plateau)

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The response of planktonic foraminifera to changing oceanographic conditions during Middle Miocene Climate Transition (MMCT) ~14 million years ago (Ma) at ODP Site 747 (Kerguelen Plateau) is investigated. Faunal changes are presented in the background of sea surface temperature (SST) estimates and multi-taxon $\delta^{18}O$ and $\delta^{13}C$ data presented in other studies. Four faunal transitions are distinguished between 15.0 and 12.2 Ma. The first two affected only a limited number of taxa, and do not lead to large-scale assemblage reorganizations. They are only minor assemblage changes within the pre-MMCT fauna. The first (14.5–14.4 Ma) is marked by a reduction in the *Globorotalia zealandica* plexus in favor of the *Globorotalia praescitula* plexus, coupled with the first signs of increased seasonality. The second (14.3–14.2 Ma) is characterized by recovery and diversification of the *G. zealandica* plexus and an increase in *Turborotalita quinqueloba* in response to further enhanced seasonality. The third faunal transition across the Middle Miocene Shift (MMS) in $\delta^{18}O$ (13.9–13.8 Ma) affects almost all planktonic foraminifera, leading to dismembering of the pre-MMCT assemblage. These changes were triggered by the SST drop by ~7°C, followed by reduced sea-surface salinity following the MMS, which favored the opportunistic *Neogloboquadrina continuosa*. Its dominance spans the transitional period (13.8–13.2 Ma), during which several planktonic foraminiferal events gradually shaped the post-MMCT assemblage. The fourth faunal threshold took place during the hiatus in the ODP Hole 747A record spanning 13.2–12.5 Ma. It is expressed by the establishment of an assemblage dominated by *Globorotalia praescitula* and *Globigerina bulloides* in association with diminishing of the low-salinity surface layer. The two dominant taxa exhibit well-defined morphologies, much different from their earlier relatives. The microperforate foraminifera show relatively few morphological changes, probably due to their morphological conservatism. Their changes are thought to herald the large foraminiferal transformations, especially in case of the third and fourth faunal transition thresholds.

Key words: Planktonic foraminifera, climate change, Middle Miocene, Kerguelen Plateau, Southern Ocean.

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Introduction

The cooling of MMCT is one of the three major steps in Cenozoic climatic evolution. It terminated the Mid-Miocene Warmth and reached a threshold at ~14 Ma, which is marked by a world-wide and rapid shift in $\delta^{18}O$ (MMS) (Flower and Kennett 1994). The MMS is interpreted as being related to a rapid, major expansion of the East Antarctic Ice Sheet that was coupled with increased global cooling (Shackleton and Kennett 1975; Shevenell et al. 2008). The climatic effects of the MMCT were much pronounced in the southern high latitudes where significant cooling and hydrographic changes took place (Shevenell and Kennett 2004; Lewis et al. 2008). At ~14 Ma, SST are interpreted to have decreased by ~7°C in the Southern Ocean (Shevenell et al. 2004; Verducci et al. 2007), while deep waters cooled by 1.5 to 3.0°C (Lear et al. 2000; Billups and Schrag 2002; Shevenell et al. 2008). This cooling was accompanied by major reorganization of oce-

anic circulation and an increased production of Southern Component Deep Water (Woodruff and Savin 1989; Flower and Kennett 1994). Global-scale changes in ocean circulation accompanying the MMCT resulted in the so-called "silica switch" that marked the transfer of biosiliceous deposition from the North Atlantic to the North Pacific and Indian Oceans (Keller and Barron 1983; Flower and Kennett 1994).

The progressing thermal isolation of Antarctica, that begun with the Eocene opening of the Drake Passage (Livermore et al. 2007) and was coupled with increased global cooling, eventually resulted in a major turnover in planktonic organisms and development of the Neogene fauna (Keller and Barron 1983). At ~14 Ma, the southern high-latitude modern-like calcareous nannoplankton assemblage developed (Haq 1980). During roughly the same time, an abrupt turnover in planktonic foraminifera followed the 7°C decrease in SST as reported from ODP Hole 747A (Verducci et al. 2007), located on the central Kerguelen Plateau (Fig. 1).
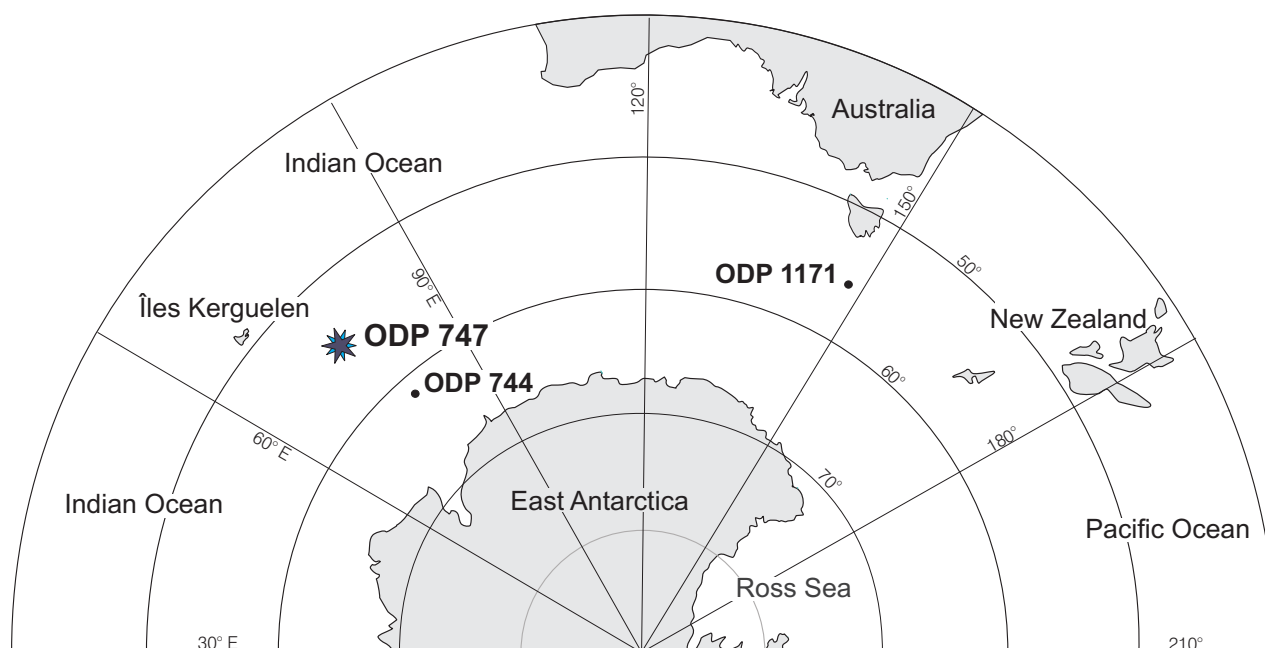
Fig. 1. Location of ODP Sites 747, 744, and 1171 on a paleogeographic reconstruction for 15 Ma modified from Lawver et al. (1992).

The high quality of foraminiferal record at this ODP Site was highlighted by Berggren (1992) and Li et al. (1992), who conducted initial micropaleontological studies. Moreover, detailed investigations of Shevenell et al. (2004) and Verducci et al. (2007) helped to unravel SST changes in the Middle Miocene Southern Ocean, while multi-taxon stable isotopic studies (Majewski and Bohaty 2010) provided insights into the local hydrography, including changes in seasonality and salinity in the water-column at this site. In this paper, the complex changes in the planktonic foraminiferal assemblages are traced across the MMCT between 15.0 and 12.2 Ma in that robust paleoceanographic background (Fig. 2).

Middle Miocene climatic history of the Indian sector of the Southern Ocean.—The Mg/Ca paleotemperature estimates for ODP Hole 1171C (Shevenell et al. 2004) and Hole 747A (Verducci et al. 2007) both highlight the strong SST cooling by ~7°C at ~14 Ma just preceding the MMS and the Mi3 glaciation. Both records show short term SST variations throughout the Middle Miocene; however, they are not always concurrent (Fig. 2). Prior to the MMS, the stable isotopic records derived from benthic and planktonic foraminifera, suggest decreasing strength on thermocline and/or increased seasonality with cooler early-spring and/or late-fall temperatures (Majewski and Bohaty 2010). The later seems to be especially well supported by a reversed planktonic $\delta^{18}O$ hierarchy between *Globorotalia praescitula* and *Globigerina bulloides* at Site 747. Brief episodes of the reversed planktonic $\delta^{18}O$ hierarchy took place also before, as early as ~14.45 Ma, but it became more or less prevailing feature between 14.35 and 13.9 Ma (Majewski and Bohaty 2010). During MMS, almost identical $\delta^{18}O$ values recorded by *Globigerina bulloides* and *Globorotalia praescitula* suggest a

possible reduction in differences between niches inhabited by these two planktonic species.

During the initiation of the Mi3 glaciation at ~13.9 Ma, the $\delta^{18}O$ values of *Globigerina bulloides* diverged significantly from benthic and at ~13.8 Ma also from *Globorotalia praescitula* values, resulting in a ~0.5‰ increase in the benthic to *Globigerina bulloides* $\delta^{18}O$ gradient across the MMS. The observed changes in $\delta^{18}O$ gradients were interpreted as due to decrease in surface-water salinity of up to ~2 salinity units persisting until at least ~13.2 Ma (Majewski and Bohaty 2010). The interpreted freshening of the upper water-column at Site 747 occurred in direct association with the Mi3 cooling and glaciation event interpreted from the benthic foraminiferal $\delta^{18}O$ record, but it appears to lag surface cooling interpreted from planktonic foraminiferal Mg/Ca records derived by Shevenell et al. (2004) and Verducci et al. (2007) (Fig. 2). The combination of cooling and upper-water freshening seems to point to a strengthening of temperature and salinity gradients across the polar frontal zone (Majewski and Bohaty 2010) and/or its northward migration (Verducci et al. 2009).

Planktonic species.—Taxonomic discrimination between planktonic foraminifera investigated in this study was based on several former works. The planktonic foraminifera from the interval between 15 and 12 Ma, in ODP Hole 747A, were initially investigated by Berggren (1992) and Li et al. (1992), and subsequently by Verducci et al. (2009). Their results disagree due to different approach to foraminiferal taxonomy. In this paper, the taxonomic approach of the earlier workers is applied after some modifications and supplemented with rich SEM documentation. Cifelli and Scott (1986) and Scott et al. (1990) investigated Miocene southern-hemisphere globorotalids and used plexi to demonstrate phyletic relations
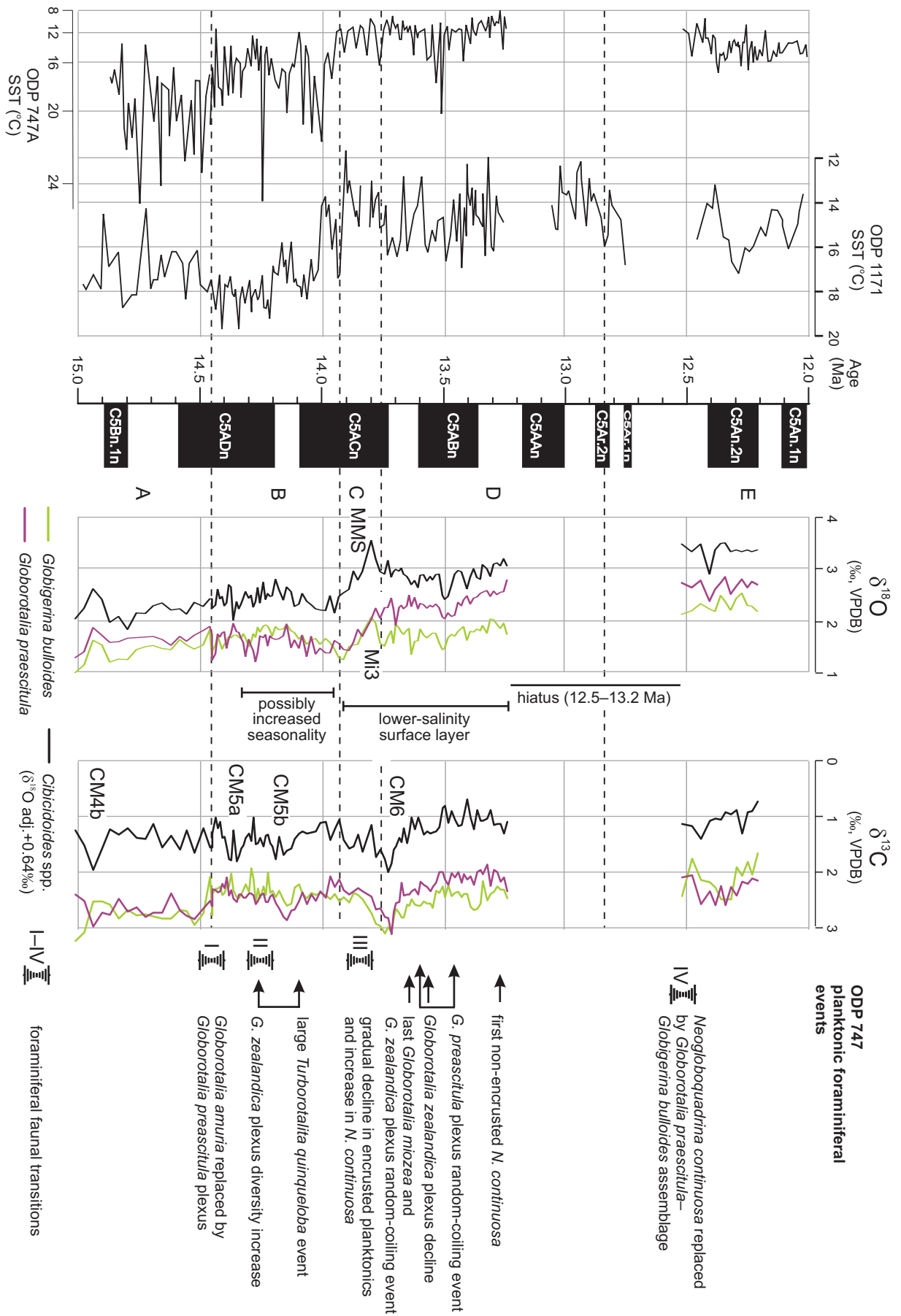
Fig. 2. Major foraminiferal and paleoenvironmental events at ODP Site 747A (15.0–12.2 Ma) discussed in this paper, related to age after Majewski and Bohaty (2010). Oxygen MI3, Mi4 and carbon CM4, CM5, CM6 stable isotopic events as well as Middle Miocene δ18O shift (MMS) are indicated on the stable isotopic plots. Dashed lines show limits of the five isotopic intervals (A–E) from Majewski and Bohaty (2010). The paleotemperature records from Shevenell et al. (2004) and Verducci et al. (2007).

within this foraminiferal group. They also pointed to numerous difficulties in making precise discrimination between different forms within these phyletic groups. Majewski (2002, 2003) encountered similar problems, finding the plexus concept to be very practical in quantifying high latitude Miocene globorotalids.

Scott et al. (1990) provided criteria for discriminating between members of the *Globorotalia zealandica* plexus, including *Globorotalia amuria* and *Globorotalia conica*. The latter species tended to exhibit more depressed sutures and possessed less highly arched apertures. *Globorotalia conica* exhibited more a compressed periphery and ventroconical outline than *G. amuria*. On the other hand, Scott et al. (1990) suggested that it was possible to distinguish between populations rather than individual specimens of *Globorotalia praescitula* and *Globorotalia miozea*. Large specimens of typical *G. miozea* often showed sharp chamber peripheries, less depressed sutures than *G. praescitula*, and thick encrustation. Scott et al. (1990) also noted that within the *G. praescitula* plexus immature specimens were practically impossible to discriminate.

Both Berggren (1992) and Li et al. (1992), who investigated planktonic foraminifera in ODP Hole 747A for the interval between 15 and 12 Ma, documented the occurrence of reticulate *Neogloboquadrina continuosa*, the kummeform *Neogloboquadrina nympha*, and spinose *Turborotalita quinqeloba*, as well as only two globigerinid species, *Globoturborotalita woodi* and *Globigerina bulloides*. They did not identify *Globigerina praebulloides* as did Verducci et al. (2009). This foraminifer, however, shares numerous morphologic characteristics with *Globigerina bulloides*, and a precise differentiation between them is therefore, rather problematic. According to Kennett and Srinivasan (1983), the range of *G. praebulloides* spans the Middle Miocene interval investigated here. Chaproniere (1988), who restudied the holotype section of *Globoturborotalita woodi*, noted that there appeared to be a gradation in overall test morphology between this foraminifer and *Globigerina praebulloides*. However, the cancellate test wall, typical for *Globoturborotalita woodi*, appeared suddenly, showing no gradation in this morphocharacter. Therefore, the presence of strongly encrusted, coarsely pitted, cancellate wall could be treated as the main discriminating factor between *Globoturborotalita woodi* and *Globigerina praebulloides–Globigerina bulloides*.

Li et al. (1992) investigated microperforate tenuitellinids from ODP Hole 747A, a group, which because of their minute size, was rarely studied elsewhere. They distinguished several low trochospiral species with 4 to 5 chambers in the final whorl, including *Tenuitella clemenciae*, *Tenuitella jamesi*, *Tenuitellinata pseudoedita*, and *Tenuitellinata selleyi*. The low to medium trochospiral taxa, with 3 to 4 chambers in the final whorl, were represented by *Globigerinita juvenilis*, which had a low-arch aperture with a thin lip, *Globigerinita glutinata* with an aperture covered by a "true" bulla that tended to be flat and with more than one opening, and finally *Globigerinita boweni* which bears an inflated, bulla-like final chamber covering the umbilicus. In case of the last two minute species, they were difficult to differentiate. Therefore, both *Globigerinita* species were assigned by Li et al. (1992) to *Globigerinita glutinata* s.l. The final species, the highly trochospiral *Globigerinita uvula*, was shown to be linked with *G. glutinata* by morphological intermediates (Li et al. 1992).

Abbreviations.—mbsf, meters below sea floor; MMCT, Middle Miocene Climate Transition; MMS, Middle Miocene Shift; mwd, meters water-depth; ODP, Ocean Drilling Project; rmbsf, rescaled meters below sea floor; SST, sea surface temperature.

Methods

The interval between 15.0 and 12.2 Ma at ODP Site 747 Hole A (54°48.68'S, 76°47.64'E, 1696 mwd; meters water-depth) on the Central Kerguelen Plateau is investigated (Fig. 1). The age model for ODP Hole 747A, which identifies an hiatus at ~65.5 mbsf (13.2–12.5 Ma) is discussed in Majewski and Bohaty (2010) and applied accordingly. Similarly as in that paper, corrected core depths are used, to accommodate for overlapping core sections at ~66.1 and ~75.5 mbsf resulting from post-recovery core expansion. They are expressed in "rescaled meters below sea floor" (rmbsf).

The section between 79.89 (747A-9H-4, 148–150 cm) and 62.03 mbsf (747A-7H-5, 8–10 cm) was sampled every 30 cm. The sediment samples were dry-weighted, then soaked in de-ionized water and washed over a 63 µm sieve. The residue was dry sieved through a 150 µm sieve and split into coarse- (>150 µm) and fine-fractions (63–150 µm). A total of 150 or more randomly selected planktonic foraminifera from both fractions were picked and identified. The maximum test diameter of picked *Globigerina bulloides* was measured optically at 63× magnification with ±16 µm precision. Coiling directions and the presence of incrustation were investigated in some key taxa.

Results

All samples yield abundant planktonic foraminifera in both >150 µm and 63–150 µm fractions. Thirteen taxa are identified within >150 µm and 8 taxa within 63–150 µm size fraction (Appendix 1). Some of these taxa are in fact evolutional or morphological groups of species, which are difficult to discriminate. Foraminiferal census data and some morphological changes through the analyzed interval are presented in Figs. 3, 6, 7, 9. On these figures, the stable isotopic intervals identified by Majewski and Bohaty (2010) are indicated along with the absolute ages, and these are used throughout the subsequent discussion.

***Globorotalia zealandica* plexus** (Figs. 3, 4).—Two species within this globorotalid plexus, *Globorotalia amuria* and
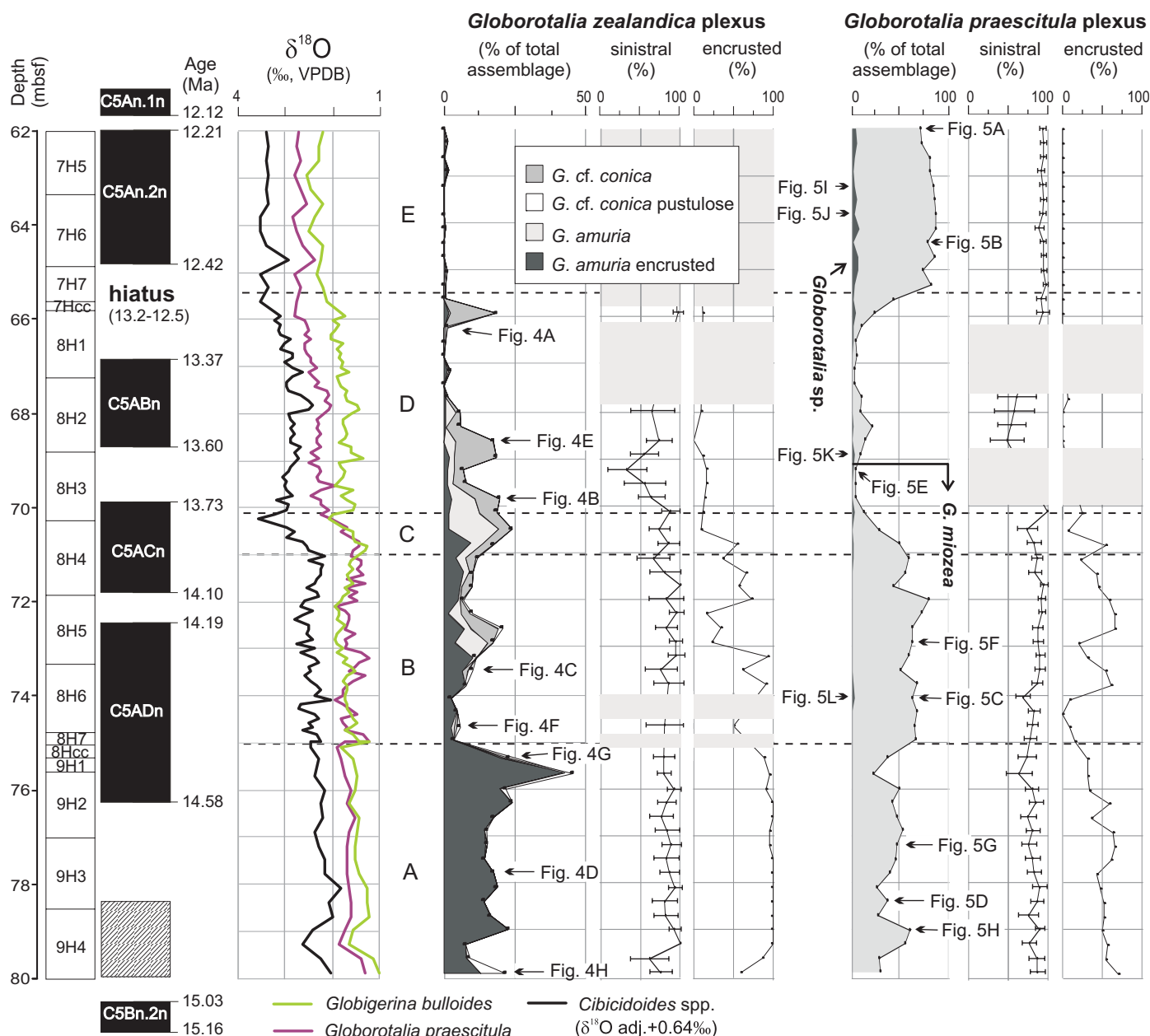
Fig. 3. Large fraction (>150 μm) *Globorotalia* percentages in ODP Hole 747A between 15.0 and 12.2 Ma together with coiling ratios and percentages of encrusted individuals. Note 95% confidence intervals marked on the coiling ratio plots. Descriptions with arrows show stratigraphic position of foraminiferal specimens shown on Figs. 4 and 5. Note δ18O data and the five isotopic intervals (A–E) after Majewski and Bohaty (2010).

Globorotalia cf. *conica,* are distinguished (Fig. 4). Both taxa include specimens with an additional calcite crust, although *Globorotalia* cf. *conica* shows a lower degree of massive encrustation than *G. amuria*, which results in a pustulose wall texture (Fig. 4G, H). Abundances of the two foraminifera, as well as the proportion of encrusted individuals, vary greatly within the stratigraphic succession examined. Some discrete fluctuations in coiling ratios are also present (Fig. 3).

Throughout Interval A, strongly encrusted *Globorotalia amuria* (Fig. 4C, D) dominates the plexus, with the only exception being the oldest sample at ~15.0 Ma, where pustulose *Globorotalia* cf. *conica* constitutes ~40% of the plexus. During Interval A, the *Globorotalia zealandica* plexus is at its

peak (8–44% of large fraction assemblage). It decreases to ~4% at the beginning of Interval B, then increases to ~20%, drops again and reaches almost 24% in Interval C. Beginning from ~14.3 Ma, non-encrusted *Globorotalia amuria* and *Globorotalia* cf. *conica* become progressively more dominant. During Interval C, encrusted *G. amuria* dwindles to just few specimens per sample and never rises again. From mid Interval C until mid Interval D, at ~13.5 Ma, *G.* cf. *conica* is the most abundant component of the plexus. After ~13.5 Ma, only single individuals of *G. zealandica* plexus are noted, with the exception of a single sample in the later Interval D at ~13.25 Ma, when they reach 18% of the total large fraction. Coiling directions within the *Globorotalia zealandica* plexus are
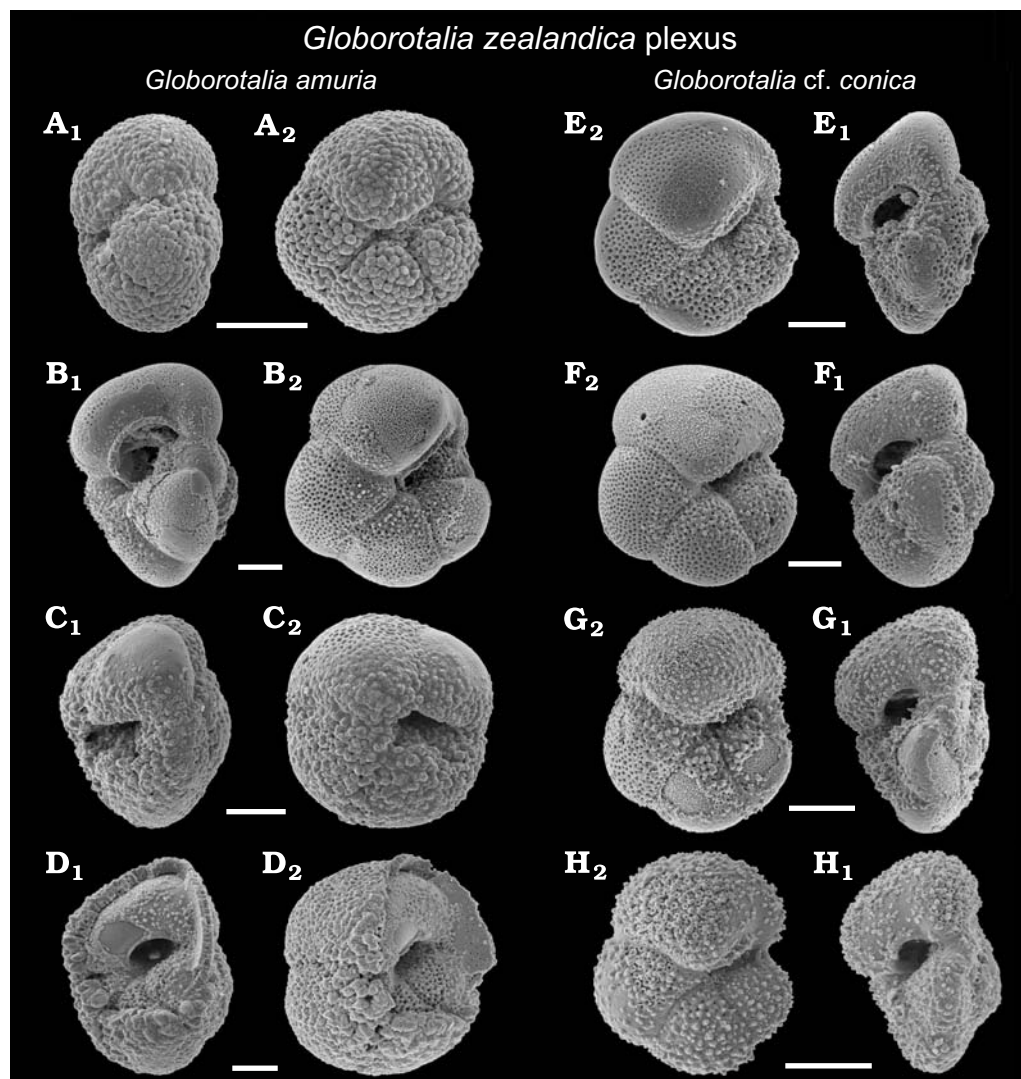
Fig. 4. Middle Miocene planktonic foraminifer *Globorotalia zealandica* plexus from ODP Site 747, Kerguelen Plateau. **A–D**. *Globorotalia amuria*. Encrusted: 8H-1, 38–40 cm (**A**); 8H-6, 28–30 cm (**C**); 9H-3, 98–100 cm (**D**). Non-encrusted: 8H-3, 100–102 cm (**B**). **E–H**. *Globorotalia* cf. *conica*. Non-pustulose: 8H-2, 128–130 cm (**E**); 8H-6, 146.5–148.5 cm (**F**). Pustulose: 9H-1, 4–6 cm (**G**); 9H-4, 148–150 cm (**H**). A_1–H_1 axial view, A_2–H_2 umbilical view. All SEM images. Scale bars 100 μm. The stratigraphic position of pictured specimens is indicated on Fig. 3.

~85% sinistral through episodes A and B. It falls from ~14.1 Ma and exhibits more random values in early Interval D. The sample at ~13.25 Ma, with a large population of *Globorotalia* cf. *conica,* shows again almost exclusively sinistral forms.

***Globorotalia praescitula* plexus** (Figs. 3, 5).—It is difficult to distinguish between single individuals of *Globorotalia praescitula* and *Globorotalia miozea*, especially among smaller specimens. In the ODP Hole 747A succession, the presence of morphologies typical for both species are traced. *G. praescitula* (Fig. 5A–D) is present throughout and includes few, if any, encrusted individuals. Specimens are significantly smaller than *G. miozea* (Fig. 5E–H). The largest individuals frequently have five chambers in the final whorl. It appears that the percentage of encrusted specimens among the *G. praescitula* plexus closely parallels fractions of *G. miozea*. The *Globorotalia* sp. morphotype (Fig. 5I–L) is also placed

together with the *G. praescitula* plexus (Fig. 3). It represents rather minute specimens with 4.5–5 chambers in the final whorl and a more or less rounded periphery. They seem to blend gradually into the major *G. praescitula* population in the earlier occurrences, but become progressively more distinctive where the late *G. praescitula* specimens show a more strongly compressed periphery.

The *Globorotalia praescitula* plexus spans the entire section analyzed; however, distinct trends are observed (Fig. 3). Throughout Interval A, the *G. praescitula* plexus constitutes 25–60% of the total assemblage; but it exceeds 50% only occasionally. Encrusted individuals (presumably *G. miozea*) decline from just over 50% of this plexus to only 2% at the beginning of Interval B (at ~14.4 Ma). The encrusted individuals are quite variable in abundance throughout Intervals B and C (10–70%) and they decline totally just after Interval C. The last *G. miozea* specimen is noted at ~13.65 Ma, just at
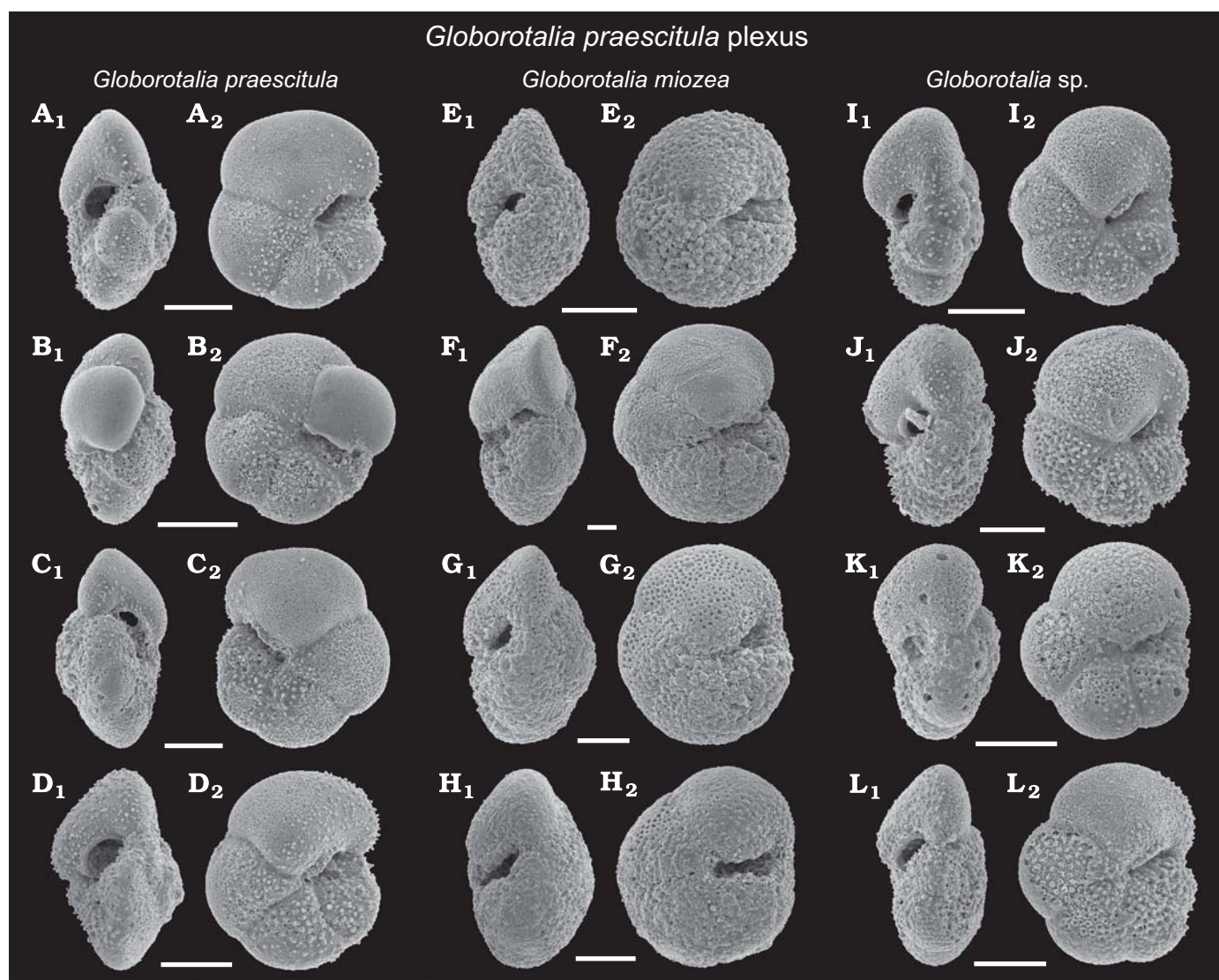
Fig. 5. Middle Miocene planktonic foraminifer *Globorotalia preascitula* plexus from ODP Site 747, Kerguelen Plateau. **A–D**. *Globorotalia praescitula*: 7H-5, 8–10 cm (**A**); 7H-6, 98–100 cm (**B**); 8H-6, 88–90 cm (**C**); 9H-3, 148–150 cm (**D**). **E–H**. *Globorotalia miozea*: 8H-3, 40–42 cm (**E**); 8H-5 118–120 cm (**F**); 9H-3, 28–30 cm (**G**); 9H-4, 58–60 cm (**H**). **I–L**. *Globorotalia* sp.: 7H-5, 128–130 cm (**I**); 7H-6, 30–40 cm (**J**); 8H-3, 10–12 cm (**K**); 8H-6, 88–90 cm (**L**). In axial (A₁–L₁) and umbilical (A₂–L₂) views. All SEM images. Scale bars 100 μm. Stratigraphic position of pictures specimens is indicated on Fig. 3.

the beginning of Interval D. Throughout Interval B, the total *G. praescitula* plexus achieves ~50–70% of the total large assemblage, only to decline gradually during Interval C to just 3% at the beginning of Interval D. Above this level, the *G. praescitula* morphotype greatly dominates the plexus. Although *Globorotalia* sp. becomes gradually more frequent and more morphologically distinct from *G. praescitula*, it remains only a minor (up to 6.6%) component of the total fauna. During Interval D, the *G. praescitula* plexus is subordinate, constituting only 3–10% of the total large fauna and reaches almost 20% only at 13.55 Ma. In contrast, *G. praesctitula* increases since ~13.25 Ma and is most dominant after 12.5 Ma in Interval E, strongly dominating the >150 μm assemblage (68–84%). In the same interval, its population is composed of small individuals with clearly thin walls and rather strongly compressed periphery (Fig. 5A, B).

A distinct trend in coiling direction within the *G. praescitula* plexus (Fig. 3) is also observed. In Intervals A and B, where both *G. praescitula* and *G. miozea* are present, it appears that both species show similar ratios, i.e., ~75–90% sinistral. During Interval C, when the *G. praescitula* plexus abundance rapidly declines, the coiling ratio begins to change, and it reaches ~50% in mid Interval D (13.65–13.45 Ma). Late in Interval D and throughout Interval E, the coiling ratio climbs up again to become a consistent 90–95% sinistral.

Globigerina bulloides (Fig. 6).—This species occurs throughout the analyzed succession. Its test shape shows considerable variation in chamber arrangement, aperture size, and wall thickness. Some specimens from the lower portion of the section may represent the ancestral thicker-walled *Globigerina praebulloides* (e.g., Fig. 6D). No variations in coiling ratios
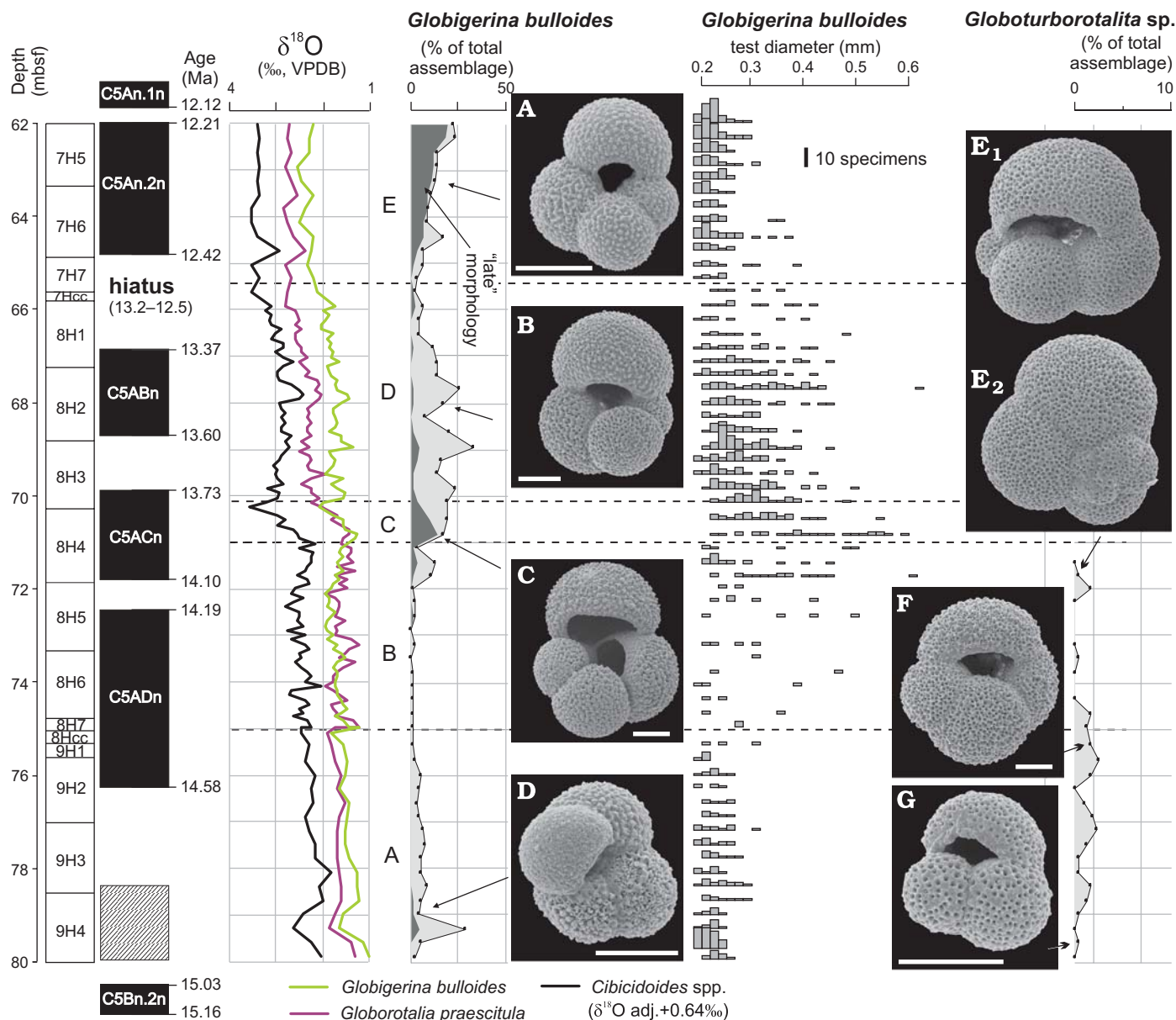
Fig. 6. Planktonic foraminifers *Globigerina bulloides* and *Globoturborotalita* sp. percentages in ODP Hole 747A between 15.0 and 12.2 Ma. Note $\delta^{18}O$ data and the five isotopic Intervals (A–E) after Majewski and Bohaty (2010). SEM foraminiferal images. **A–D**. *G. bulloides*: 7H-5, 128–130 cm (**A**); 8H-2, 68–70 cm (**B**); 8H-4, 48–50 cm (**C**); 9H-4, 58–60 cm (**D**). **E–G**. *Globoturborotalita* sp.: 8H-4, 136.5–138.5 cm (**E**); 9H-1, 4–6 cm (**F**); 9H-4, 118–120 cm (**G**). E[1] umbilical view, E[2] spiral view. Scale bars 100 μm.

occur. The populations are ~50% sinistral throughout. However, their test size and the fraction of so called "late" specimens varies significantly (Fig. 6). The "late" morphological type is characterized by chambers rapidly increasing in size, strongly depressed sutures, thin walls, and wide-open aperture (Fig. 6A, C), giving a distinctively less massive appearance than that of the earlier forms.

Throughout Interval A, *Globigerina bulloides* populations constitute ~5% of the large fraction planktonic foraminifera. They are small in size, with no large specimens. Only a few "late" morphologies are noted within the interval of high *G. bulloides* abundance at ~14.9 Ma. During Interval B, a significant reduction of *G. bulloides* populations to 1–2% is observed, which is accompanied by much increased test-size variability (Fig. 6). Its population surpasses 10% of the large fraction only shortly before Interval C. In the same Interval, a few "late" morphologies are noted.

During Interval C, a significant increase in population size (up to 20%) and the highest test-size variability is noted. Rarely, the "late" type specimens exceed 50% of the total *G. bulloides* population. Throughout Interval D, the population size gradually declines; however, test-size remains variable. The "late" morphologies once more become only a minor component. Finally, during Interval E, population size increases steadily from only 3% up to well over 20% of the large fraction assemblage. The *G. bulloides* populations be-
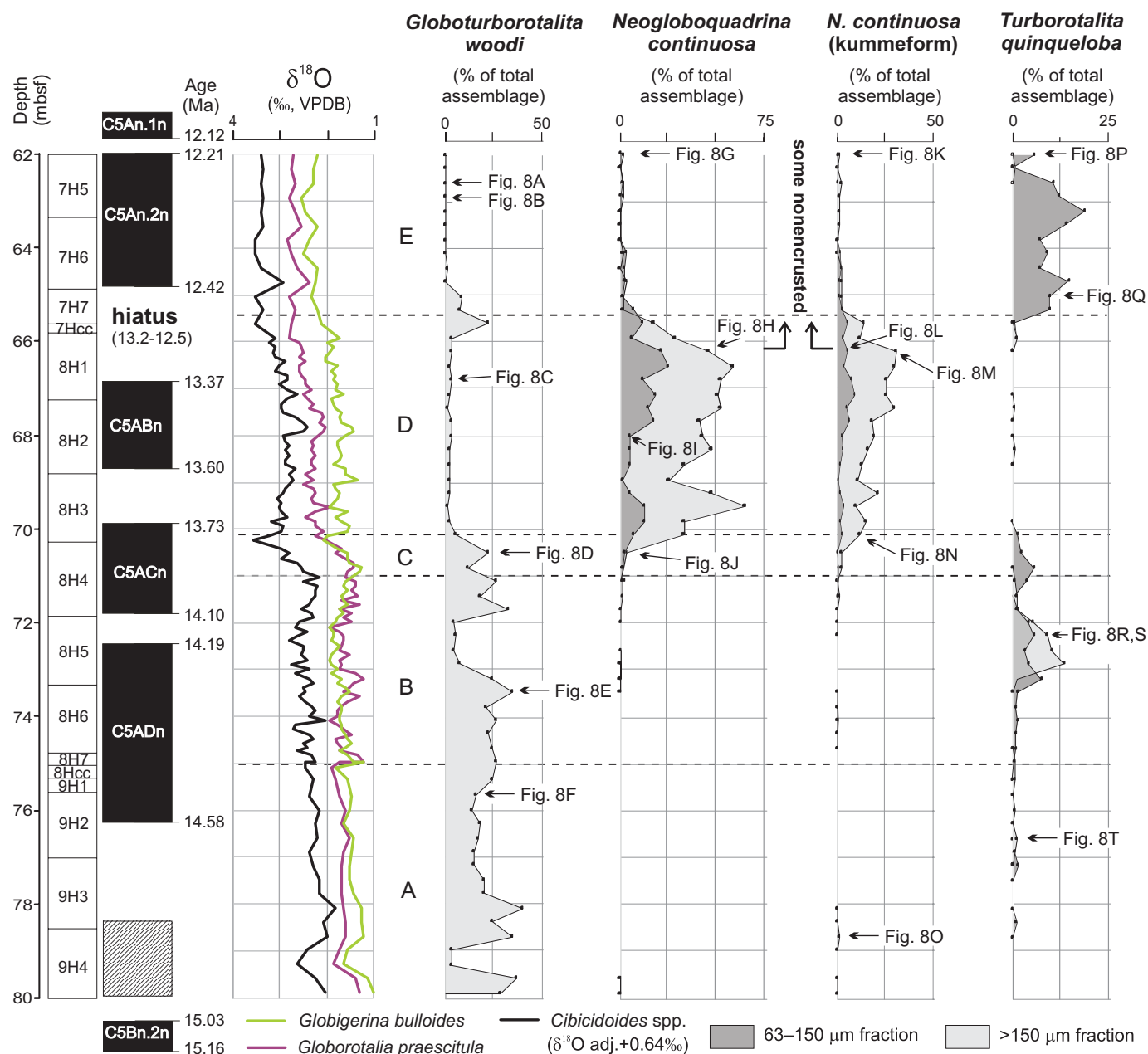
Fig. 7. Percentages of some planktonic foraminifera in ODP Hole 747A between 15.0 and 12.2 Ma. Descriptions with arrows show the stratigraphic position of foraminiferal specimens shown on Fig. 8. Note δ¹⁸O data and the five isotopic intervals (A–E) after Majewski and Bohaty (2010).

come strongly dominated by rather minute specimens representing the "late" morphological type.

Globoturborotalita sp. (Fig. 6).—This species is linked to reticulate *Globoturborotalita woodi* based on the presence of distinctive pore pits as in Majewski (2002). It differs from *G. woodi* by lower and wider aperture, more compact outline and less depressed sutures (Figs. 6, 8). In the analyzed section, *Globoturborotalita* sp. occurs in low numbers (up to 2.5% of the assemblage) only in Intervals A and B. No specimens are found since ~14.0 Ma, during and after the MMS threshold.

Globoturborotalita woodi (Figs. 7, 8).—Specimens of this taxon represent a broad range of morphologies (A–F on Fig.

8), and are likely to belong to more than one species. The wall structure is used as the primary character to distinguish *Globoturborotalita woodi* (sensu lato, see Chaproniere 1988) from *Globigerina bulloides*.

Globoturborotalita woodi is present throughout the succession; however, its frequencies varied greatly (Fig. 7). It constitutes 15–30% of large fraction assemblages throughout Intervals A–C with the exception of just two episodes ~14.85 and 14.3–14.1 Ma, when it declined to 3–7%. On the other hand, it constitutes only ~3% of the large fraction during Interval D. It increases to 22% near the 13.2–12.5 Ma hiatus, which may be due to its greater robustness. There are only a few single occurrences of this foraminifer during Interval E.
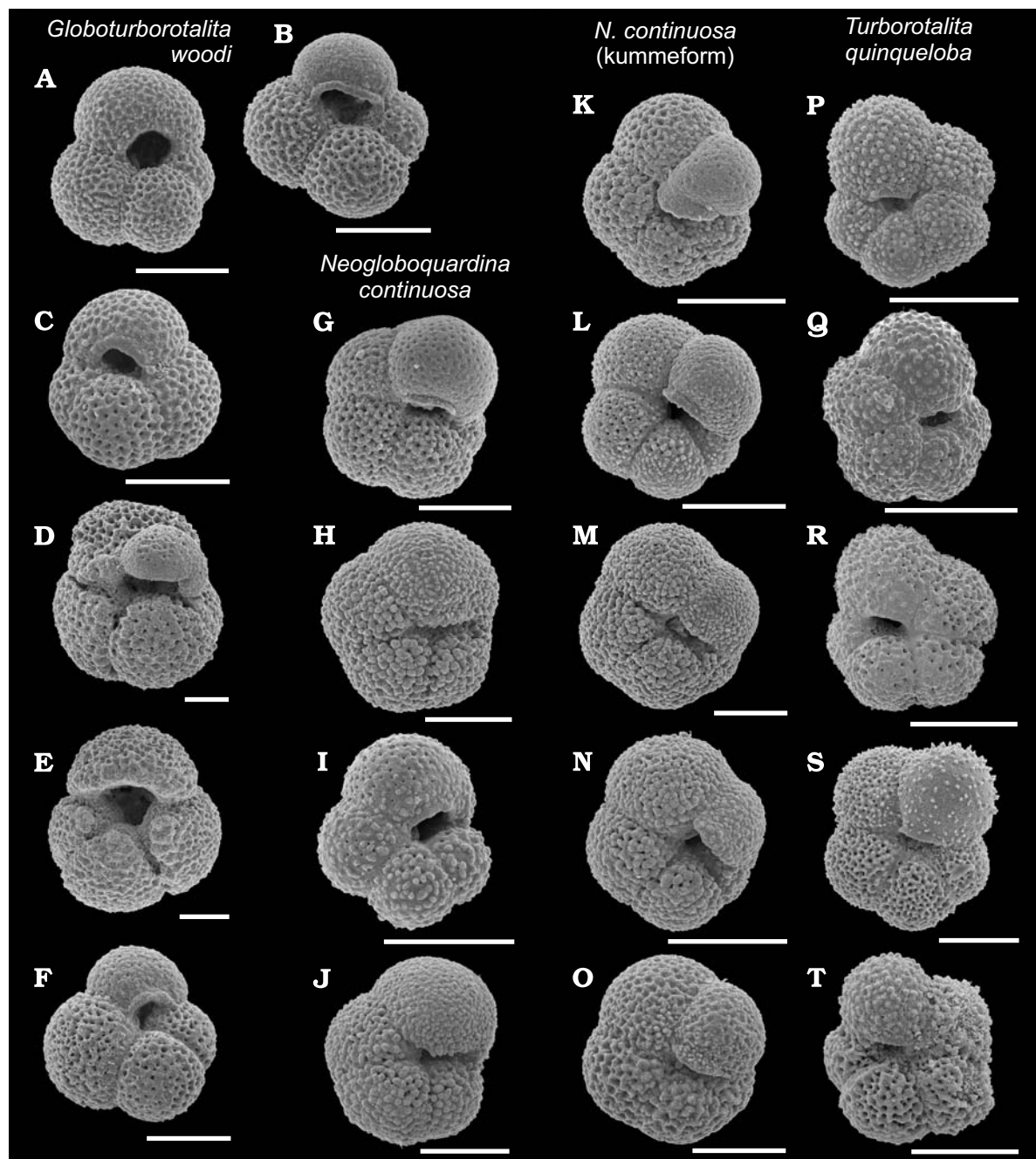
Fig. 8. Planktonic foraminifers from ODP Site 747, Kerguelen Plateau. **A–F**. *Globoturborotalita woodi*: 7H-5, 68–70 cm (**A**); 7H-5, 98–100 cm (**B**); 8H-1, 97.5–99.5 cm (**C**); 8H-4, 18–20 cm (**D**); 8H-6, 28–30 cm (**E**); 9H-2, 28–30 cm (**F**). **G–O**. *Neogloboquadrina continuosa*. **G–J**. Non-kummeform: 7H-5, 8–10 cm (**G**); 8H-1, 38–40 cm (**H**); 8H-2, 68–70 cm (**I**); 8H-4, 18–20 cm (**J**). **K–O**. Kummeform: 7H-5, 8–10 cm (**K**); 8H-1, 38–40 cm (**L, M**); 8H-3, 100–102 cm (**N**); 9H-4, 28–30 cm (**O**). **P–T**. *Turborotalita quinqueloba*: 7H-5, 8–10 cm (**P**); 7H-7, 8–10 cm (**Q**); 8H-5, 58–60 cm (**R, S**); 9H-2, 118–120 cm (**T**). All SEM images. Scale bars 100 μm. The stratigraphic position of pictured specimens is indicated on Fig. 7.

Neogloboquadrina continuosa (Figs. 7, 8).—Both Berggren (1992) and Li et al. (1992) documented the occurrence of two *Neogloboquadrina* species, *Neogloboquadrina nympha* and *Neogloboquadrina continuosa* in ODP Hole 747A. In this study, two morphological forms were noted, *N. continuosa* with the last chamber larger than the penultimate and *N. continuosa* (kummeform) with larger penultimate chamber. They show no other convincing morphological differences, which suggests that they are a single species. Both possess

coarsely pitted (reticulate) walls, are usually significantly thickened and crystalline (Fig. 8). Populations are dominated by sinistrally coiled specimens (~80–90%).

The stratigraphic distribution of the two morphologies is fully comparable in the succession analyzed here (Fig. 7). They co-occur throughout; however, non-kummeform *Neogloboquadrina continuosa* is twice as abundant as the kummeform form. Both are recognizable in the large and small fractions. Throughout Intervals A and B, only single, exclusively en-
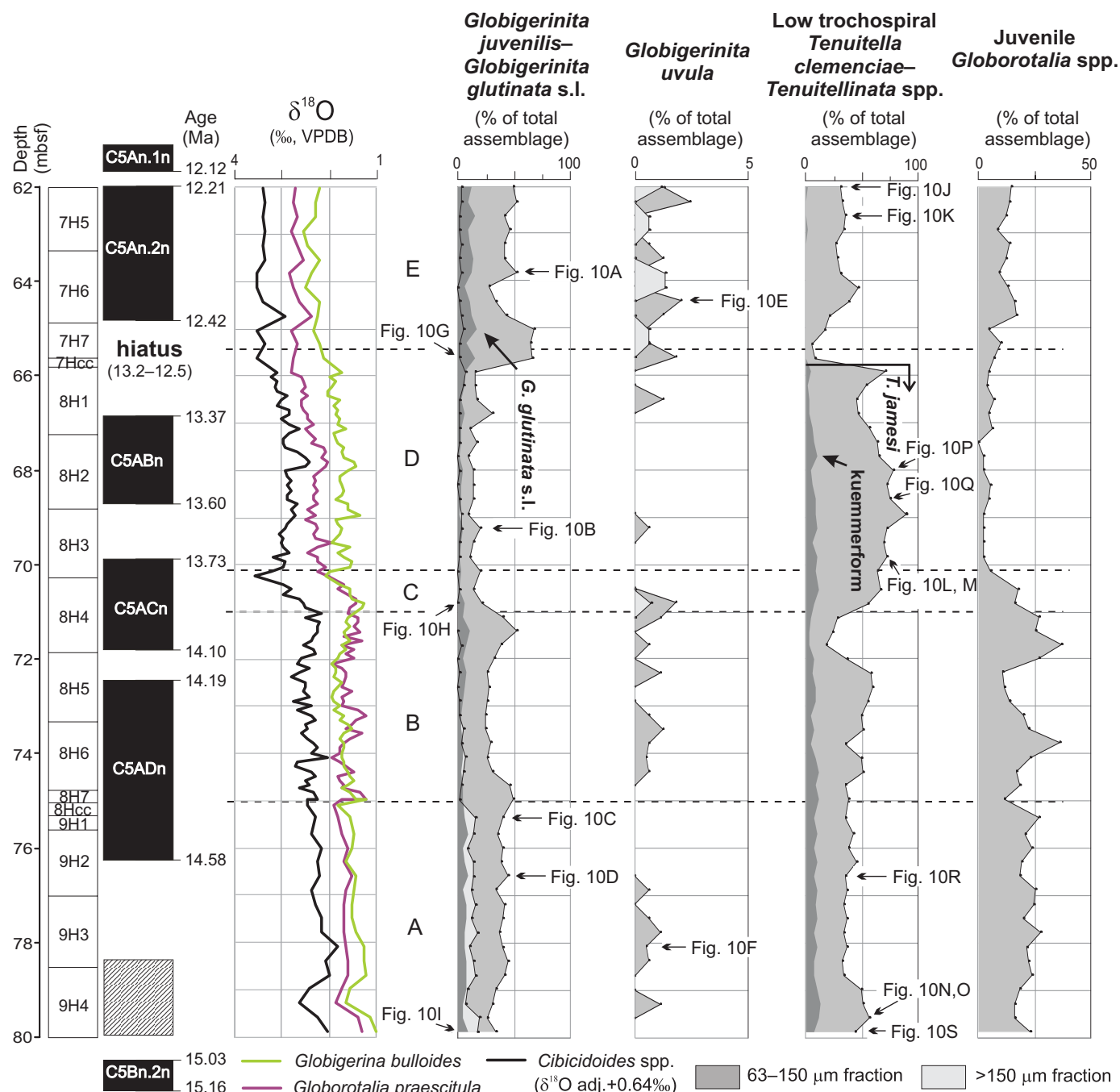
Fig. 9. Microperforate planktonic foraminifera and small fraction (63–150 μm) juvenile *Globorotalia* percentages in ODP Hole 747 between 15.0 and 12.2 Ma. Descriptions with arrows show stratigraphic position of foraminiferal specimens shown on Fig. 10. Note δ^{18}O data and the five isotopic Intervals (A–E) after Majewski and Bohaty (2010).

crusted specimens are recognized. They rapidly increase in abundances in Interval C and reach their long-lasting highs throughout Interval D, where they dominate the large fraction, comprising together 33–88% of the large and up to 30% of the small fraction assemblage. Non-encrusted forms first appear in late Interval D at ~13.3 Ma (sample 747A-8H-1, 38–40 cm), and they reach up to 25% of the sharply declining *N. continuosa* population in early Interval E at ~12.45 Ma. In Interval E, *N. continuosa* remains as a minor (~2% in >150 μm and ~1% in <150 μm fraction) but continuously present compo-

nent. Its populations include both encrusted and non-encrusted individuals.

Turborotalita quinqeloba (Figs. 7, 8).—This species is present in both fractions throughout the succession analyzed (Fig. 7). Only a few *Turborotalita quinqeloba* specimens are noted in Interval A. It becomes relatively abundant between 14.3 and 14.1 Ma within Interval B, where it reaches 4–8% of the fine fraction and as much as 6–13% of the large fraction assemblage. In fact, this is the only interval in which large (>150 μm)
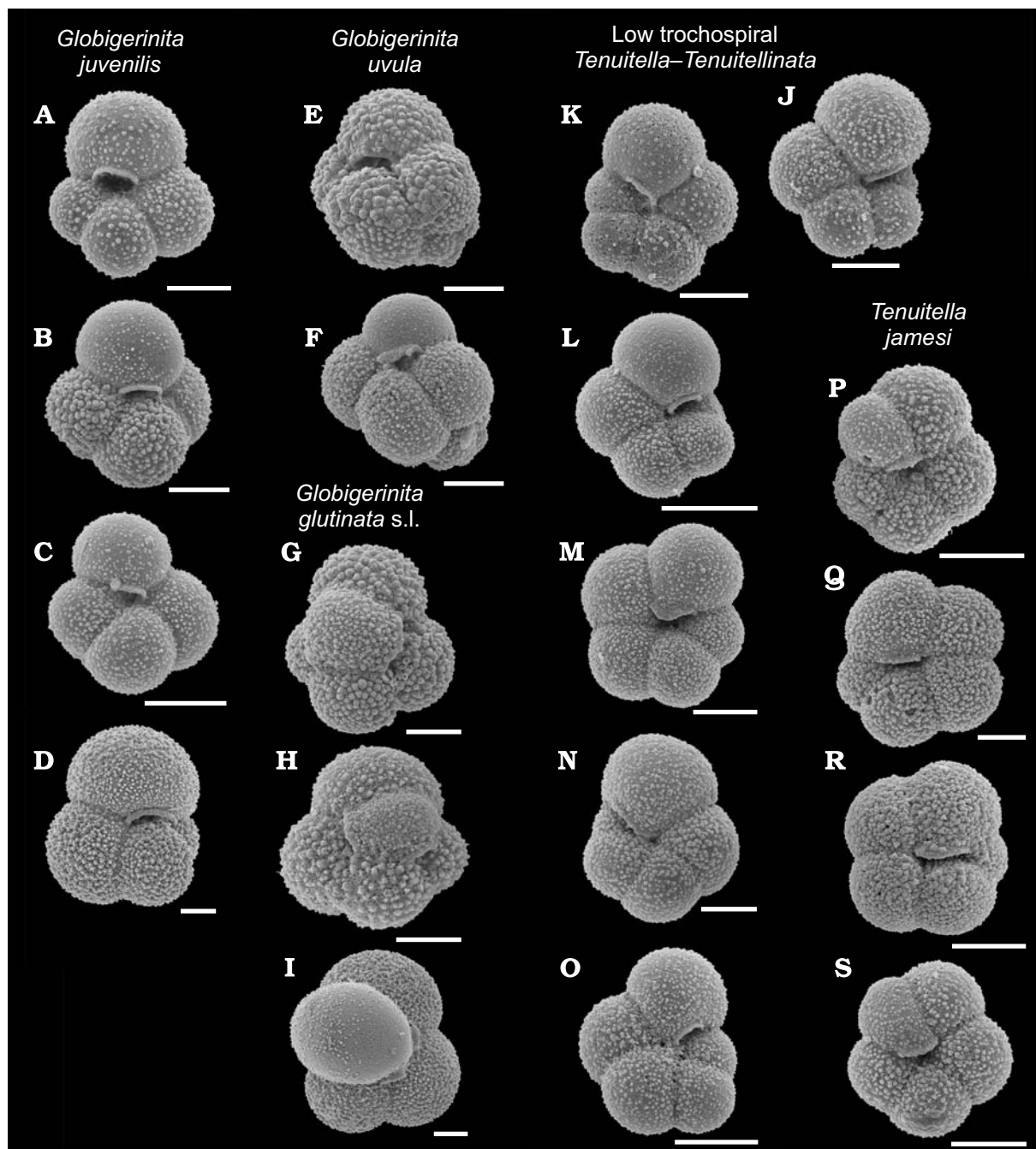
doi:10.4202/app.2009.0088

Fig. 10. Middle Miocen microperforate planktonic foraminifera from ODP Site 747, Kerguelen Plateau. **A–D**. *Globigerinita juvenilis*: 7H-6, 38–40 cm (**A**); 8H-3, 40–42 cm (**B**); 9H-1, 4–6 cm (**C**); 9H-2, 118–120 cm (**D**). **E, F**. *Globigerinita uvula*: 7H-6, 98–100 cm (**E**); 9H-3, 118–120 cm (**F**). **G–I**. *Globigerinita glutinata* s.l.: 7H-7, 8–10 cm (**G**); 8H-4, 48–50 cm (**H**); 9H-4, 148–150 cm (**I**). **J–S**. Low trochospiral *Tenuitella–Tenuitellinata*: 7H-5, 8–10 cm (**J**); 7H-5, 68–70 cm (**K**); 8H-3, 100–102 cm (**L, M**); 9H-4, 118–120 cm (**N, O**); including *Tenuitella jamesi*: 8H-2, 68–70 cm (**P**); 8H-2, 128–130 cm (**Q**); 9H-2, 118–120 cm (**R**); 9H-4, 118–120 cm (**S**). All SEM images. Scale bars 50 µm. The stratigraphic position of pictured specimens is indicated on Fig. 9.

T. quinqeloba specimens are an important component of the total assemblage. Minute *T. quinqeloba* are present through Interval C (2–6%); however, they are extremely rare during Interval D. They reappear as a considerable component (up to 19%) of the small fraction assemblage throughout Interval E.

***Globigerinita juvenilis–Globigerinita glutinata* sensu lato** (Figs. 9, 10).—This is a group of microperforate minute, pus-

tulate, low to medium trochospiral taxa with 3 to 4 chambers in the final whorl (Fig. 10). *Globigerinita juvenilis* and *Globigerinita glutinata* s.l. (sensu Li et al. 1992) are encountered in both size fractions; although, they are definitely more abundant in the 63–150 µm fraction. The largest specimens show walls uniformly covered by subconical crystallites (pustules) (e.g., H on Fig. 10), but these are less developed among the minute specimens. In the ODP Hole 747A succession, both

taxa are present throughout. *Globigerinita glutinata* s.l. is generally less abundant than *G. juvenilis* by approximately one-fifth, and only by approximately one-third in the youngest Interval E. Nevertheless, it appears that the two taxa co-varied throughout the succession (Fig. 9).

The bullate and nonbullate individuals of this group of species together constitute ~25–40% of the small and as much as ~15% of the large fraction assemblage throughout Interval A. In Interval B, the minute specimens remain at a similar level, then decreased across the B/C boundary to 10–20% of the total minute assemblage, and they remain at this level throughout Interval D. Early in Interval E, they increase to ~65% and then to ~40% during late Interval E. The large specimens of this group never truly recovered after their decline at the end of Interval A, and they remain only a minor component of the large fraction assemblage.

Globigerinita uvula (Figs. 9, 10).—In the ODP Hole 747A succession, *Globigerinita uvula* is noted in both fractions (Fig. 9). Minute specimens (63–150 μm) occur throughout in similar low (up to 2.4%) and sparse numbers. During Interval D, they are the least abundant. Large fraction specimens of *G. uvula* are recorded only in Intervals C and E. They occur in similarly low numbers as in the small fraction.

Low trochospiral *Tenuitella* and *Tenuitellinata* (Figs. 9, 10).—This minute microperforate group includes several pustulose, low trochospiral species with 4 to 5 chambers in the final whorl. They include *Tenuitella clemenciae*, *Tenuitella jamesi*, *Tenuitellinata pseudoedita*, *Tenuitellinata selleyi*, and probably additional unidentified species. Due to their small size, limited number of distinctive features, and numerous intermediate forms it is impossible at this point to quantify their abundances.

This low trochospiral microperforate group occurs throughout the succession (Fig. 9). In Interval A through mid B, it constitutes more than one third of the total small fraction assemblage. The group slightly surpasses 50% during the 14.95–14.85 and 14.45–14.15 Ma intervals. It declines to ~20% just before Interval C, at which time it increases to over 50% and remains at the ~60–80% level throughout Interval D. It appears that the Interval C–D high abundance levels of the low trochospiral microperforates are mostly due to an increase in *Tenuitella jamesi*, together with more variable abundances of *Tenuitella clemenciae*, whereas *Tenuitellinata pseudo-edita–Tenuitellinata selleyi* abundances remain at rather moderate levels. *Tenuitella jamesi* and bullate, low-trochospiral microperforates disappear by the end of Interval D (at ~13.25 Ma). At the same time, the remainder of the group falls sharply to only 6–8%; however, the surviving taxa recover rapidly by ~12.35 Ma to 45% and remain steady at ~30% until 12.2 Ma.

Remarks

Li et al. (1992) identified *Tenuitellinata pseudoedita* and *Tenuitellinata selleyi* in the Middle Miocene of ODP Hole

747A. They noted a close size-relationship between these two species; they differed primarily by the presence of a partially smooth wall in the latter species. However, these two species are found to be rather difficult to differentiate. Moreover, Li et al. (1992) indicated the sudden disappearance of all the taxa included in the low trochospiral group, i.e., *Tenuitella clemenciae*, *Tenuitellinata pseudoedita*, *Tenuitellinata selleyi*, and *Tenuitella jamesi* near the hiatus (13.2–12.5 Ma). The present study confirms only the disappearance of the last species (*T. jamesi*) during this time interval. It appears that morphologies typical for the other species survive this interval and range into younger sediments. This inconsistency highlights the need for further investigation of the *Tenuitella–Tenuitellinata* group of planktonic foraminifera.

Discussion

Morphological features

Test encrustation.—Numerous authors have reported on examples of encrustation among modern and extinct planktonic foraminifera. They stressed the importance of the gametogenetic and non-gametogenetic encrustation as it may strongly affect stable isotopic and trace-element composition of tests (Bé 1980) as well as alter assemblage composition in deep-sea sediments (Hemleben et al. 1979). In well preserved samples, the percentage of encrusted specimens may be suggestive of environmental change and/or reproduction success of foraminiferal populations (Bé 1980); however, it may be to some degree overwritten by selective dissolution of non-encrusted tests.

At ODP Site 747, both *Globigerina bulloides* and *Globoturborotalita* sp. show no clear indications of encrustation; however, the thickness and robustness of *G. bulloides* tests is clearly variable. Its older populations, which resemble *Globigerina praebulloides*, are more massive. On the other hand, the "late" morphotype has an obviously thinner and more fragile test (Fig. 6A). Possible signs of encrustation are also noted among another spinose species, i.e., *Turborotalita quinqueloba*; however, this feature was not extensively studied under the light microscope, due to the small size of specimens.

On the other hand, common signs of encrustation are encountered in *Globoturborotalita woodi* (e.g., Fig. 8D, E). In fact, Kennett and Srinivasan (1983) considered this species as ancestral to Recent *Globigerinoides sacculifer*, which undergoes calcification coupled with spine resorption prior to a gamete release (Bé 1980; Caron et al. 1990). It seems likely that the encrustation in *Globoturborotalita woodi* is also gametogenetic in nature, in which case it bears no paleoenvironmental significance.

Hemleben et al. (1985, 1989) noted that a non-gametogenetic calcite crust may be also deposited at low temperatures in some non-spinose globorotalids. The authors cultured subtropical *Globorotalia truncatuloides*, *Globorotalia hirsuta*, and *Globorotalia inflata* under cool conditions be-

low 10 and 15°C, where they developed a calcite crust identical to that observed in field-collected populations. A large proportion of globorotalids in the ODP Hole 747A succession is heavily encrusted (see Figs. 4–6). It is assumed that as with the Recent members of this genus, this is the result of non-gametogenetic encrustation, so the percentage of encrusted forms does not indicate reproductive success among the Middle Miocene populations but reflects environmental and/or evolutionary changes.

Within the *Globorotalia zealandica* plexus, encrusted forms dominate early populations throughout Intervals A and B and then rapidly and almost completely disappeared during the MMS (Fig. 3). This abrupt change appears to be environmental in origin for two reasons. First, single encrusted *Globorotalia amuria* occurs practically throughout later Intervals D and E. Second, according to Scott et al. (1990), *G. amuria* had only slightly shorter stratigraphic range than *Globorotalia conica*, and both forms ranged younger than 12 Ma. The observed decline in encrusted forms takes place during the well documented cooling of the MMS, which contrasts with the situation for cool temperature induced encrustation among modern subtropical globorotalids. Apparently, other mechanisms stimulated encrustation processes within the Middle Miocene *G. zealandica* plexus in contrast to the Recent subtropical globorotalids. A similar trend of sharp reduction in encrusted forms across the MMS was also observed within the *Globorotalia praescitula* plexus (Fig. 3). It appears, however, that this change could be related to the disappearance of *Globorotalia miozea* at ODP Site 747 at ~13.65 Ma, which correlates well with the extinction of *G. miozea* in New Zealand (Scott et al. 1990).

A decline of less importance in percent encrusted forms in the *G. zealandica* plexus takes place at ~14.25 Ma and appears to initiate a fluctuations towards the major reduction of encrusted forms at the MMS. It correlates with an increase in non-encrusted *G. amuria* and *G.* cf. *conica* as well as with an abrupt and brief appearance of unusually large-test populations of *Turborotalita quinqueloba* (Fig. 7), which suggests environmental driving of this reduction in encrustation. It coincides roughly with increased seasonality with cooler early-spring and/or late-fall temperatures prior to the MMCT between 14.35 and 13.9 Ma, as suggested by the stable isotopic data (Majewski and Bohaty 2010). On the other hand, some minor changes in the percent of encrusted forms in the *G. praescitula* and *G. zealandica* plexi (at ~14.4 Ma) coincided with SST decline (Verducci et al. 2007) at the boundary between Intervals A and B. Nevertheless, the direct driving forces of these morphological trends remain enigmatic.

In high latitudes, encrustation in *Neogloboquadrina pachyderma*, which Kennett and Srinivasan (1980) derived directly from *Neogloboquadrina continuosa*, is rather non-gametogenetic in nature, and it occurs at all depths or at the main pycnocline (Kohfeld et al. 1996). Until now, no indications suggesting the gametogenetic nature of *N. pachyderma* encrustation have been reported. However, it is well established that its Antarctic populations have thicker tests, and

have stronger crystalline and encrusted forms than subantarctic ones (Kennett and Srinivasan 1980). Srinivasan and Kennett (1974) investigated a South Pacific Late Miocene–Pleistocene succession and noted high percentages of crystalline (encrusted) *N. pachyderma* during cool episodes, a time when this species was also more abundant. It appears, therefore, that the appearance of non-encrusted *Neogloboquadrina* late in Interval D (at ~13.3 Ma), and coinciding with a strong decline in the abundance of this genus (Fig. 7), may indicate a trend towards warmer conditions. However, Verducci et al. (2007) suggested only ~2°C SST increase at the boundary between Intervals D and E. On the other hand, late Interval D marks the decline of low-salinity surface layer conditions (Majewski and Bohaty 2010). Therefore, the decline in *N. continuosa* and increase number of thin-wall specimens may be also in conjunction with that event.

Test size.—*Globigerina bulloides* is among the most studied foraminifera for variation in test size. This species is commonly found throughout the Middle Miocene in ODP Hole 747A. Despite moderate sampling resolution and number-limited populations, this foraminifer showed a strong increase in its mean test-size beginning at ~14.4 Ma and reversing to uniformly small test-size populations at ~12.3 Ma. Average test-size reached its climax at ~13.9 Ma, during the MMS (Figs. 6, 11).

In the southern Indian Ocean, *G. bulloides* was reported to increase test size with decreasing water temperatures (Malmgren and Kennett 1976). Comparison of paleontological (Figs 2, 6) and paleotemperature record from Southern Ocean (Shevenell et al. 2004, Verducci et al. 2007) indicates that the size variations in *G. bulloides* were predominantly temperature driven and its size increase between 14.3 and 13.9 Ma coincides especially well with the temperature decline interpreted by Shevenell et al. (2004) (Fig. 11). The variable test-size pattern during Interval D seems to correlate with temperature variations during this time. It appears, however, that the final reduction in *G. bulloides* test size since 12.5 Ma was due to the development and dominance of a single phenotype or cryptic species. Hecht (1976) warned that the size differences between phenotypes may obscure test-size results derived from undifferentiated populations. The results of genetic studies (De Vargas et al. 1999; Darling et al. 1999, 2000; Darling and Wade 2008) reinforced the probability for the existence of phenotypes now considered as genotypes or cryptic species.

Test-size variations are also observed within some smaller foraminiferal taxa (Fig. 9). *Globigerinita glutinata* s.l. tends to be larger and have a thicker wall during Interval A, which represents warmer conditions of the late Mid-Miocene Warmth. On the other hand, *Globigerinita uvula* larger size during Interval E may reflect rather progressive cooling. *Turborotalita quinqueloba* provides another example with populations at ~14.3–14.1 Ma being larger in size than those from Interval E (Fig. 7). The three signals of test-size variations are rather tentative at this point, but do suggest possible evolutionary

changes or/and phenotype variation, which could in turn be driven by dynamic oceanography.

Coiling ratios.—Many previous investigations of planktonic foraminifera have linked coiling directions and environmental conditions. One of the best known historic examples of biased coiling is the occurrence of sinistral-dominated populations of *Neogloboquadrina pachyderma* in cold polar waters (e.g., Kennett 1968, 1976; Hemleben et al. 1989). More recent observations (e.g., Naidu and Malmgren 1996) also suggested a link between sinistral *N. pachyderma* and high-productivity, upwelled waters. Similarly, left-coiled *Globigerina bulloides* dominates high- and temperate-latitude Southern Ocean (Malmgren and Kennett 1976) as well as fertile, upwelled surface waters (Naidu and Malmgren 1996).

Norris and Nishi (2001) believed that, in each Paleogene planktonic foraminiferal radiation, the clade-founding species developed biased coiling, which was then maintained by their descendants. Heritability of coiling suggested that it could be genetically determined. Based on genetic evidence, Darling et al. (2006) concluded that sinistral and dextral ge-

notypes of *Neogloboquadrina pachyderma* are in fact different species. Thus, it appears that although associated with environmental implications, coiling direction may be in fact in large part genetically related and associated with much larger than previously anticipated genetic diversity among planktonic foraminifera.

In Hole 747A, the *Neogloboquadrina continuosa* populations are uniformly 80–90% sinistral throughout Interval D, where they dominate the large test planktonic assemblage. In other portions of the succession, too few *Neogloboquadrina* specimens are found to investigate its coiling direction. On the other hand, *Globigerina bulloides* populations are randomly (~50% sinistral) coiled throughout the Middle Miocene section of ODP Hole 747A. No coiling direction changes in *G. bulloides* are found even across the MMS. Likewise, Gonera et al. (2003) reported no coiling changes in their Middle Miocene *G. bulloides* assemblages from the Central Paratethys (southern Poland) despite sea-water temperature variations recorded by $\delta^{18}O$ variations. Both the results of Gonera et al. (2003) and the data discussed above seem to support the possibility that random (proportionate) coiling persisted in *G. bulloides* throughout the Neogene. This was also suggested for most globigerinids by Brunner and Kroon (1988).

Coiling directions were also investigated among Neogene globorotalids (e.g., Scott et al. 1990; Scott 1995; Majewski 2002). As already mentioned, Norris and Nishi (2001) noted a tendency for species with random coiling to survive mass extinctions and a rarity of reversion from biased to random coiling. This predisposition may suggest a rather opportunistic character in randomly coiled species. Thus, the brief tendency towards random coiling among the two globorotalid plexi after the MMS (Fig. 3) may reflect a minor extinction or temporal reduction of highly specialized species in favor of those more opportunistic taxa. The *Globorotalia praescitula* form, which becomes reestablished after the hiatus (13.2–12.5 Ma), during Interval E, is strongly sinistral-dominated and definitely smaller in test-size than its pre-MMCT relatives. Its well defined, fixed morphology suggests rather low genetic diversity and a high level of environmental specialization of this late Middle Miocene foraminifer.

Gross assemblage transitions between 15.0 and 12.2 Ma

Foraminiferal abundances in the upper water column are determined by several often interacting environmental factors. They may include SST and salinity, depth and shape of the thermocline, marine eutrophication, and seasonality (Pfuhl and Shackleton 2004). Four distinct assemblage transitions are found within the ODP Hole 747A planktonic foraminiferal record across the MMCT. Their stratigraphic positions are indicated on Fig. 2.

First faunal transition between Intervals A and B (14.5–14.4 Ma). —This transition is expressed by a sharp reduction in encrusted *Globorotalia amuria*, which dominates the *Glo-*
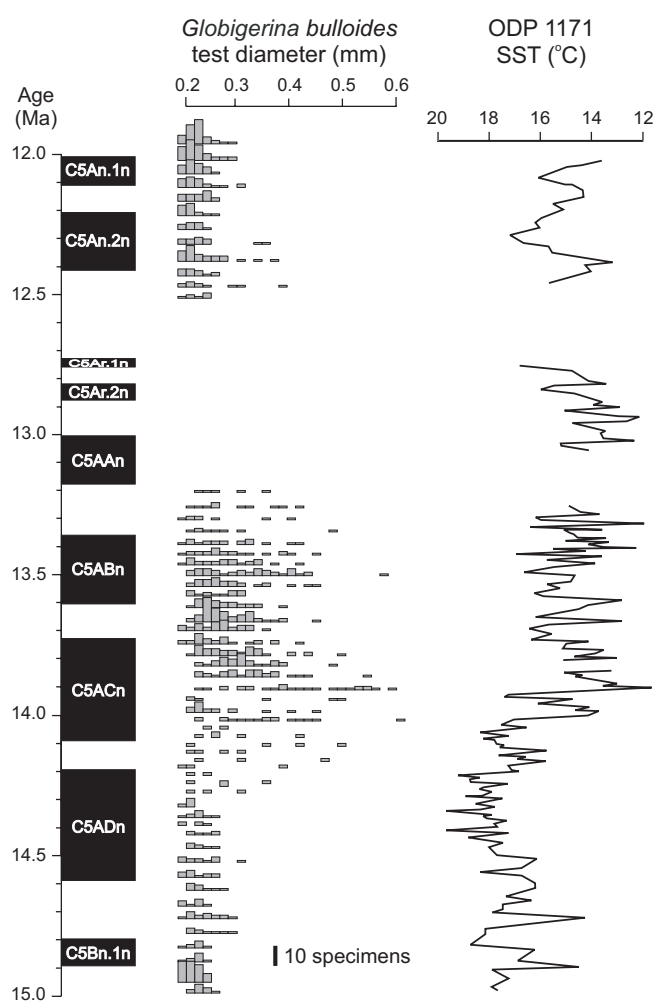

Fig. 11. Comparison of test-size variations in *Globigerina bulloides* at ODP 747A and sea surface temperature (SST) at ODP Site 1171 (Shevenell et al. 2004) between 15.0 and 12.2 Ma.

borotalia zealandica plexus almost completely, from 15–20% of the total assemblage practically throughout Interval A to just ~5% in early Interval B (Fig. 3). Across the same Interval, a considerable increase in the *Globorotalia miozea*-rich *Globorotalia praescitula* plexus is noted from 30–50% in Interval A to 60–70% in early Interval B. This well defined change is accompanied by a less pronounced and not as well time constrained reduction in *Globigerina bulloides*, *Globoturborotalita* sp. (Fig. 6) large fraction *Globigerinita juvenilis–Globigerinita glutinata* s.l. (Fig. 9), and an increase in *Globoturborotalita woodi* (Fig. 7).

The decline in *Globoturborotalita* sp. and large fraction *Globigerinita juvenilis–Globigerinita glutinata* s.l. suggests less favorable conditions (cooler and/or a different pattern/degree of seasonality) during Interval B. Moreover, the notable reduction in *Globigerina bulloides* may indicate the lowest primary productivity during early Interval B, as Recent *G. bulloides* frequencies are also believed to reflect high food availability and not only the temperature (Reynolds and Thunell 1985). Verducci et al. (2007) show a significant cooling; however, Shevenell et al. (2004) indicated a SST rise at ~14.45 Ma. On the other hand, Majewski and Bohaty (2010) interpreted increased seasonality with cooler early-spring and/or late-fall temperatures starting from 14.35 Ma, but heralded as early as ~14.45 Ma by *G. bulloides* δ^{18}O values occasionally exceeding those of *Globorotalia praescitula* (Fig. 2). It appears that the reduction in the *Globorotalia zealandica* plexus, so typical for earlier Mid-Miocene Warmth (Majewski 2002), in favor of the *G. praescitula* plexus between Intervals A and B could be one further result of this environmental change.

Second faunal transition in the middle of Interval B (14.3–14.2 Ma).—This is marked by an increase in the *Globorotalia zealandica* plexus by ~10%, and more notably by the first broad appearance of *Globorotalia* cf. *conica* and non-encrusted *Globorotalia amuria* morphologies, which ended the strong dominance of encrusted *G. amuria* in this lineage (Fig. 3). This change is accompanied by a reduction in *Globigerina bulloides* (Fig. 5) and *Globoturborotalita woodi* and most importantly by an unprecedented increase in both large- and small-fraction *Turborotalita quinqueloba* (Fig. 7).

According to Scott et al. (1990), the New Zealand populations of *Globorotalia amuria* appeared to have had a slightly less northward distribution than *Globorotalia conica*. This could imply warmer water preferences for *Globorotalia* cf. *conica*, which increased considerably between 14.3 and 14.2 Ma. It is known that today only some foraminifera are strictly temperature dependent. Shevenell et al. (2004) and Verducci et al. (2007) show contrasting SST estimates. Thus, it appears that the key to understanding the paleoenvironmental factors that triggered this faunal transition may lie with the sudden increase in large- and small-fraction *Turborotalita quinqueloba*.

As with Recent *Globigerina bulloides*, *Turborotalita quinqueloba* bears symbionts and lives mostly in the photic zone (Hemleben et al. 1989). Both species depend strongly on sea-sonal phytoplankton blooms (Reynolds and Thunell 1985). Therefore, the co-occurrence of very low *G. bulloides* abundances and the unprecedented high abundances of *T. quinqueloba* seems to be inconsistent. The isotopic results of Majewski and Bohaty (2010) suggest an increase in seasonality with cooler early-spring and/or late-fall temperatures between 14.35 and 13.95 Ma. Such environmental change could potentially have impacted abundance of *G. bulloides* and *T. quinqueloba* in opposite ways and create favorable conditions for the increase in morphological diversity within the *Globorotalia zealandica* plexus.

Third faunal transition during Interval C (13.9–13.8 Ma, MMS).—This event involves the most complex faunal change and it affects practically all planktonic taxa at ODP Site 747. During this transition the abundance of the *Globorotalia zealandica* plexus is strongly elevated (20–25%) with increasing *Globorotalia* cf. *conica* and non-encrusted *Globorotalia amuria*, while the *Globorotalia praesitula* plexus gradually declines, which is followed by the last appearance of *Globorotalia miozea* ~13.65 Ma (Fig. 3). During Interval C, an unprecedented increase in the abundance of the *G. bulloides* (~20%) parallels hints of changes in its morphology. *Globoturborotalita woodi* declines greatly, while *Globoturborotalita* sp. (Fig. 6) disappears completely from the record. The rapid increase in *Neogloboquadrina continuosa*, which is the major component of the foraminiferal assemblage during the succeeding Interval D, is probably the most distinct feature of this faunal transition and the entire foraminiferal record at ODP Site 747 between 15.0 and 12.2 Ma (Fig. 7). Between 13.9 and 13.7 Ma, an increase, followed by a decline, in small fraction *Turborotalita quinqueloba*, a decline in *Globigerinita juvenilis–Globigerinita glutinata* s.l., *Globigerinita uvula*, and juvenile *Globorotalia* spp., as well as a strong increase in low trochospiral *Tenuitella–Tenuitellinata* is also noted (Fig. 9).

The numerous changes in foraminiferal abundances, which spread over considerable time, provide a picture of a pronounced and significant faunal transformation, which took place in the Southern Ocean during the MMS. This was the time of a major global cooling that was accompanied by resourcing of deep water production (Woodruff and Savin 1989; Flower and Kennett 1994). At ODP Site 747, these changes were manifested by an increase in benthic and planktonic δ^{18}O ratios by ~1.3‰ on average over ~200 kyr and unprecedented divergence between *Globigerina bulloides* and benthic and *Globorotalia praescitula* δ^{18}O. These changes were interpreted to represent the strong SST cooling by ~7°C at ~14 Ma (Shevenell et al. 2004; Verducci et al. 2007) followed by a possible reduction in niche diversity, indicated by identical δ^{18}O values recorded by *Globigerina bulloides* and *Globorotalia praescitula* (Fig. 2), and the reduction in surface-water salinity by ~2 salinity units that could strengthen stratification of the water column (Majewski and Bohaty 2010).

The SST cooling seems to be mirrored by the apparent increase in *Globigerina bulloides* test-size (Fig. 11). The high

abundances of *G. bulloides*, together with the occurrence of *Turborotalita quinqueloba* between 13.9–13.8 Ma and later during Interval D, may suggest normal levels of primary productivity. However, the first abundant appearance of the "late" morphology among *G. bulloides* suggests the presence of unusual conditions that could accelerate assemblage changes. Both dominant planktonic foraminifera during Interval D (*G. bulloides* and *Neogloboquadrina continuosa*) are potentially tolerant to lower salinity conditions, which points to lower surface-water salinity as the limiting environmental factor for other large foraminifera that declined during Interval D. According to Hilbrecht (1996), Recent *G. bulloides* and *Neogloboquadrina pachyderma* (the modern descendant of *N. continuosa*) both tolerate the global range of oceanic salinities. However, only *N. pachyderma* (sinistral) shows a preference for low salinities, down to and below 34, which could explain the very strong dominance of *N. continuosa* during Interval D. On the other hand, Recent *Globorotalia scitula* (the modern descendant of *Globorotalia paescitula*) does not show considerable abundances in areas where sea surface salinity is less than 35 (Hilbrecht 1996), and this could explain the strong reduction in the *G. praescitula* plexus.

It appears that Interval D, due to the lower SST and salinity, could be characterized by conditions unfavorable for *Globorotalia praescitula* plexus. After the MMS, that cosmopolitan foraminifera could retreated to lower latitudes and returned better adapted after conditions stabilized during Interval E. The *Globorotalia zealandica* plexus, being based primarily in the Southern Ocean, could have nowhere to retreat. It appears that it was forced to adapt to changing conditions. The ODP Hole 747A record may shows such adaptation initiated already by ~14.3 Ma and accelerating at ~13.8 Ma, which was exhibited by the rise of the non-encrusted forms (Fig. 3). It appears that it was at first successful. The non-encrusted *Globorotalia amuria* and *Globorotalia* cf. *conica* morphologies increased between 13.9 and 13.6 Ma. They probably succeeded in colonizing living space freed by the retreating *Globorotalia praescitula* plexus; however, it seems that practically already by ~13.5 Ma the *Globorotalia zealandica* plexus was terminated, while *Globorotalia praescitula* returned some time before 12.5 Ma to replace *Neogloboquadrina continuosa*.

The best time-restricted mass-occurrence of planktonic foraminifera in the record is that of *Neogloboquadrina continuosa* during the entire Interval D. *Neogloboquadrina continuosa* populations begin to dominate foraminiferal assemblages at ~13.7 Ma, after the end of the third foraminiferal assemblage transition. The extremely rapid increase and high dominance of the assemblage (up to 88% of large and 30% of small fractions), followed by a decline at ~13.2 Ma (Fig. 7) suggests the opportunistic nature of this success. *Neogloboquadrina continuosa* was present a long time before and after their mass occurrences between 13.7 and 13.2 Ma, but it could reach high abundances only after the MMS decline in other planktonic foraminifera, and it could not compete with the new- and better-adapted fauna after 12.5 Ma. Therefore, it appears that it was possible for *N. continuosa* to take over owing to the unusual conditions of the low-salinity and cool surface water and reduced competition. Verducci et al. (2009) linked the increase of neogloboquadrinids after the MMS with colder and fresher Antarctic water moving northward, beyond the ODP Hole 747A, which stays in agreement with the postulated cooling and freshening of upper-water as the primary factors facilitating the *N. continuosa* increase between 13.7 and 13.2 Ma.

The change among microperforate planktonic foraminifera between 13.9 and 13.8 Ma is also quite remarkable (Fig. 9). The replacement of a large portion of *Globigerinita juvenilis*–*Globigerinita glutinata* s.l., by low-trochospiral *Tenuitella*–*Tenuitellinata*, including numerous *Tenuitella jamesi*, seems to be a direct response to the cooling and/or freshening of surface waters. This contention is supported by the fact that Recent *G. glutinata* is most abundant in tropical and subtropical environments and prefers warm waters with a strong thermocline and a deep mixed layer (Thunell and Reynolds 1984; Reynolds and Thunell 1985), while *T. jamesi* seems to be rather typical for the Middle Miocene Southern Ocean. It may appear unclear why cool-water *Globigerinita uvula* (Boltovskoy 1969; Li et al. 1992) disappears for most of rather cool conditions during Interval D but the reason for its absence may be the lowering of surface-water salinity.

Fourth faunal transition between Intervals D and E (~13.2–12.5 Ma).—This faunal transition is second in scale only to the MMS faunal transition; however, its magnitude is expanded by the hiatus between 13.2 and 12.5 Ma. The stratigraphic gap is highlighted in the record by ephemeral occurrences of *Globorotalia* cf. *conica* and *Globoturborotalita woodi* (Figs. 3, 7). *Globoturborotalita woodi* is extremely rare already after 13.7 Ma and its significant presence at the hiatus may be due to condensation or reworking of this robust foraminifer. The faunal transition is well manifested among large fraction tests by replacement of the *Neogloboquadrina continuosa* dominated assemblage (Fig. 7) by the *Globorotalia praescitula*–*Globigerina bulloides* assemblage (Figs. 3, 6). Both newly established populations of *Globorotalia praescitula* and *Globigerina bulloides* show well constrained morphologies, much different from the pre-MMS fauna. During the same interval, large increases in small fraction *Turborotalita quinqueloba* are also noted, together with a complete disappearance of *Tenuitella jamesi*, combined with a sharp decline in all low trochospiral *Tenuitella*–*Tenuitellinata* in favor of *Globigerinita juvenilis*–*Globigerinita glutinata* sensu lato and *Globigerinita uvula* (Fig. 9).

The assemblage change in microperforate foraminifera at the hiatus may appear to be incoherent. On one hand, the disappearance of the presumably cold-water and/or opportunistic *Tenuitella jamesi* is accompanied by the reduction in low-trochospiral *Tenuitella*–*Tenuitellinata* and increase in warm-water *T. juvenilis*–*Globigerinita glutinata* s.l., but on the other, the cold water *Globigerinita uvula* increases (Fig. 9). These faunal trends, however, may be at least in part

due to the surface-water salinity reversing to normal levels. Moreover, Recent *Globigerinita glutinata* is regarded as a cosmopolitan species (Boltovskoy 1969), and although it prefers warm waters with a strong thermocline, it can also thrive in nutrient-rich upwelling areas (Thunell and Reynolds 1984; Reynolds and Thunell 1985).

The Verducci et al. (2007) data seem to indicate a ~2°C SST rise across the hiatus. Steadily increasing *Globigerina bulloides* abundance and high numbers of *Turborotalita quinqueloba* may suggest normal or elevated productivity after 12.5 Ma. Although still little is known about the ecology of *G. scitula*, the extant descendant of *Globorotalia praescitula*, in the North Pacific it seems to respond to high productivity in a similar manner as *G. bulloides* (Reynolds and Thunell 1985), but rather during episodes with moderate organic matter fluxes and well-mixed water-column (Kuroyanagi et al. 2008). Therefore, the replacement of *Neogloboquadrina continuosa* by *Globorotalia praescitula*, and its dominance together with *G. bulloides* of the large fraction assemblage, seems to be possibly driven by the return to normal upper-water salinity, and normal or elevated productivity.

It appears that the morphological restrictions within *Globigerina bulloides* and the *Globorotalia praescitula* plexus during Interval E may indicate an evolutionary development of new forms. Schmidt et al. (2004) suggested that macroevolutionary development of large test-size was facilitated during conditions indicative of a broad range of niches available for colonization. The size reduction in *G. bulloides* (Fig. 6) as well as that in the *G. praescitula* plexus, and the tendency of the latter towards strongly biased coiling (Fig. 3), could be due to survival and/or development of few, highly specialized phenotypes within these two taxa in response to the SST drop ~14 Ma (Verducci et al. 2007), followed by possible reduction in niche diversity during MMS, and the reduction in surface salinity for at least 600 kyr (Majewski and Bohaty 2010).

Conclusions

This micropaleontological study of the 15.0–12.2 Ma interval of ODP Hole 747A reveals a record of the demise of the pre- and the genesis of the post-MMCT planktonic foraminiferal assemblage (Fig. 2). It was a complex process, triggered by major changes in the Southern Ocean environment.

The first two foraminiferal transitions in the record, before the MMS, affect only limited number of taxa, and do not lead to large-scale assemblage modification. In fact, these are subtle, minor changes within an essentially pre-MMCT planktonic foraminiferal fauna and do not entail its termination. They could be both related to environmental perturbations due to the increased seasonality with cooler early-spring and/or late autumn temperatures predominantly between 14.35 and 13.95 Ma. The first faunal transition (14.5–14.4 Ma) is marked by the sharp decline in the deeper-water dwelling *Globorotalia amuria* (strongly dominating the *Globorotalia zealandica* plexus) in favor of the *Globorotalia praescitula*

plexus. It was probably triggered by episodically increased seasonality starting as early as ~14.45 Ma. The second faunal transition (14.3–14.2 Ma) is delineated by recovery and diversification within the *Globorotalia zealandica* plexus and the sudden appearance of large-test *Turborotalita quinqueloba* that could suggest strongly seasonal phytoplankton blooms in conjunction with cooler early-spring and/or late autumn temperatures.

In contrast, the third faunal transition across the MMS (13.9–13.8 Ma) affects almost all planktonic foraminifera, leading to major assemblage reconstruction. Oceanographic changes were initiated by a reduction in the SST by ~7°C, which is mirrored by the apparent increase in *Globigerina bulloides* test-size. After the dramatic cooling, a possible reduction in niche diversity and at least 600 kyr of decreased sea-surface salinity ensued. All these factors lead to the dismembering of the pre-MMCT assemblage and the decline of the large, thick-walled forms belonging to the two globorotalid plexi, *Globoturborotalita woodi*, and *Globigerina praebulloides*-like *G. bulloides*. Taxa that survive pass the MMS, either disappear shortly after (*Globorotalia zealandica* plexus) or undergo a severe evolutionary modification (*Globorotalia praescitula* plexus, *G. bulloides*). The replacement of a large number of the high trochospiral microperforate *Globigerinita juvenilis–Globigerinita glutinata* s.l., by low-trochospiral *Tenuitella–Tenuitellinata*, including numerous *Tenuitella jamesi*, reflects the perturbations accompanying the MMS as well.

The environmental changes during the MMS are followed by the prevalence of opportunistic *Neogloboquadrina continuosa*. Dominance of this assemblage over planktonic foraminiferal assemblages (13.7–13.2 Ma) marks the transitional period between the termination of the pre-MMCT assemblage on one side and the establishment of the post-MMCT assemblage on the other, characterized most of all by at least a 600 ky reduction in surface water salinity starting at the beginning of the MMS. During 13.9–13.2 Ma, several planktonic foraminiferal events took place, which gradually shaped the post-MMCT planktonic foraminiferal assemblage.

The non-encrusted *Globorotalia amuria* and *Globorotalia* cf. *conica* forms of the *Globorotalia zealandica* plexus initially increase between 13.9 and 13.7 Ma. They probably succeed in colonizing living space vacated by the retreating *Globorotalia praescitula* plexus. However at ~13.5 Ma, the *Globorotalia zealandica* plexus declines completely. Similarly, *Globorotalia miozea* of the *G. praescitula* plexus disappears at ~13.65 Ma. Moreover, the tendencies towards random coiling among the *G. zealandica* plexus at ~13.65 Ma and *G. praescitula* plexus at 13.6–13.5 Ma probably also reflect some minor extinctions or temporal reductions in highly specialized species in favor of the more opportunistic. Finally, the decline in *Neogloboquadrina continuosa* begins with the appearance of its non-encrusted individuals at ~13.2 Ma.

A minor SST rise and return to normal salinity conditions after ~12.5 Ma accompany the presence of the new, post-MMCT, late Middle Miocene foraminiferal assemblage. It is

exhibited by the return of *Globigerina bulloides* and *Globorotalia praescitula*, which are definitely smaller in test-size, and in the case of *G. praescitula* more strongly sinistral-biased, than their pre-MMS ancestors. These well-defined, fixed morphologies suggest low genetic diversity and marked establishment of new forms, which were better adapted for taking advantage of the Southern Ocean than *Neogloboquadrina continuosa*. The assemblage change among smaller foraminifera is accompanied by the disappearance of presumably cold-water and/or opportunistic *Tenuitella jamesi* near the hiatus (13.2–12.5 Ma). This event marks the reduction in low-trochospiral *Tenuitella–Tenuitellinata* and an increase in cosmopolitan, warm-water but also high-productivity *Globigerinita juvenilis–Globigerinita glutinata* s.l., cold-water *Globigerinita uvula*, and high-productivity *Turborotalita quinqueloba*.

The microperforate foraminifera show relatively few morphological changes between 15.0 and 12.2 Ma. This is probably due to their small size and morphological conservatism, as they were near surface dwellers and had to be strongly affected by temperature and salinity changes. In fact, assemblage changes among the microperforate taxa seem to herald the large foraminiferal changes during the MMS and ~13.2 Ma.

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Appendix 1

List of planktonic foraminiferal species noted from the Middle Miocene section investigated.

Globigerina bulloides D'Orbigny, 1826

Globigerinita glutinata (Egger, 1893)

Globigerinita juvenilis (Bolli, 1957)

Globigerinita boweni Brönnimann and Resig, 1971

Globigerinita uvula (Ehrenberg, 1861)

Globorotalia praescitula (Blow, 1959)

Globorotalia miozea Finlay, 1939

Globorotalia zealandica Hornibrook, 1958

Globorotalia conica Jenkins, 1960

Globorotalia amuria Scott, Bishop, and Burt, 1990

Globorotalia sp.

Globoturborotalita woodi (Jenkins, 1960)

Globoturborotalita sp.

Neogloboquadrina continuosa (Blow, 1959)

Tenuitella clemenciae (Bermúdez, 1961)

Tenuitella jamesi Li, Radford, and Banner, 1992

Tenuitellinata pseudoedita (Subbotina, 1960)

Tenuitellinata selleyi Li, Radford, and Banner, 1992

Turborotalita quinqueloba (Natland, 1938)