Development of Cenozoic deep-sea benthic foraminiferal faunas in Antarctic waters

ELLEN THOMAS

Department of Earth and Environmental Sciences, Wesleyan University, Middletown, CT 06457, USA

Abstract: Upper abyssal to lower bathyal benthic foraminifera from Ocean Drilling Program Sites 689 (present water depth 2080 m) and 690 (present water depth 2914 m) on Maud Rise (Antarctica) recorded changes in deep-water characteristics at high southern latitudes during the Cenozoic. The benthic foraminiferal faunas show only minor differences as a result of the difference in water depths between the sites, and changes in faunal composition were coeval. These changes occurred at the early/late Paleocene boundary (± 61.6 Ma), in the latest Paleocene (± 57.5 Ma), in the middle early Eocene (± 55.0 Ma), in the middle middle Eocene (± 46.0 Ma), in the earliest Oligocene (± 36.5 Ma) and in the early middle Miocene (± 14.5 Ma). The faunal change at the end of the Paleocene was the most important and has been recognized world-wide. On Maud Rise, the diversity decreased by 50% and many common species became extinct over a period of less than 20000 years. Diversity increased again during the early Eocene, and reached the same values as in the Paleocene by the middle Eocene. In the middle Eocene the diversity started to decrease, and continued to decrease until the middle Miocene. From the beginning of the middle Miocene until today biosiliceous oozes accumulated and calcareous benthic foraminifera were generally absent, with the exception of part of the late Miocene $(\pm 8.5 - 7.5 \text{ Ma})$ and the Quaternary.

Changes in composition of the benthic foraminiferal faunas over a wide depth range (upper abyssal-lower bathyal) probably indicate periods of major changes in the formational processes of the deep waters in the oceans. The earliest Eocene faunas, living just after the major extinction at the end of the Paleocene, are characterized by low diversity and high relative abundance of small species that probably migrated downslope into the deep waters. These faunas, and to a lesser degree those in the early middle Eocene, are characterized by high relative abundance of biserial and triserial species. In contrast, older and younger faunas have high relative abundances of spiral species. This suggests that bottom waters on Maud Rise were poor in dissolved oxygen in the latest Paleocene through early middle Eocene, and that the major extinction of benthic foraminifera at the end of the Paleocene might have resulted from a decrease in availability of dissolved oxygen as a result of warming of the deep waters. Warming might have been caused by a change in sources of deep waters, possibly as a result of plate-tectonic activity. The overall decrease in diversity from middle Eocene through Miocene probably reflects continual cooling of the deep waters.

Benthic foraminiferal faunas thus indicate that Cenozoic changes in the deep oceanic waters at high latitudes did not consist of gradual progression from Cretaceous circulation to the present-day patterns of formation of deep water: the benthic faunal changes occurred in discrete steps. Benthic faunal composition indicates that deep water most probably formed at high latitudes during the Maastrichtian-early Paleocene, and from the middle Eocene to Recent, with episodes of deep water formation at low latitudes (warm, salty deep water) during the latest Paleocene and early Eocene.

Goals of the research

The Earth's climate and the temperaturestructure of the oceans have changed considerably during the Cenozoic, from a warm climate with equable temperatures in the Cretaceous to the present-day situation with extensive polar ice caps and strong latitudinal and vertical temperature gradients in the oceans (e.g. Douglas & Savin 1975; Savin 1977; Barron 1985). The world may not have been completely ice-free in the Cretaceous (Frakes & Francis 1988), but ice-caps were certainly either absent or much smaller than they presently are (e.g., Frakes 1979; Schnitker 1980; Berger *et al.* 1981). The changes in climate were largest at high latitudes: cooling was of little importance in the tropics, but it was considerable in Antarctica. Beech-type (*Nothofagus*) forests were growing on the Antarctic Peninsula during the Eocene, where vegetation is much more limited today (e.g., Frakes 1979; Mohr in Barker *et al.* 1988;

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Birkenmayer & Zastawniak 1989; Chaloner & Creber 1989). The decrease in polar temperatures during the Cenozoic probably did not occur gradually, but proceeded stepwise (e.g., Kennett 1977; Berger *et al.* 1981; Miller *et al.* 1987*a*).

Polar cooling probably caused major changes in the formation processes of deep waters in the oceans. At present the deep waters of the oceans are all formed at high latitudes, in the Norwegian-Greenland Sea (North Atlantic) and the Weddell Sea (South Atlantic) (e.g. Tolmazin 1985). In those areas the surface waters are very cold, and salinities increase as a result of extensive winter freezing (e.g. Weddell Sea; Foster & Carmack 1976) or through advection of lower latitude surface waters (e.g. Norwegian-Greenland Sea; Worthington 1972). In the absence of large ice caps deep water may still have formed as a result of cooling at high latitudes (e.g. Schnitker 1980, figs 1 & 2; Wilde & Berry, 1982; Manabe & Bryan 1985; Barrera et al. 1987). Alternatively, deep waters might have formed at lower latitudes because of strong evaporation and formation of dense, salty, warm waters (Brass et al. 1982; Prentice & Matthews 1988).

Thus during the Cenozoic the sources of deep waters in the oceans changed considerably, leading to changes in the physical and chemical properties of the deep waters because these are dependent upon the properties of the surface waters in the area of deep-water formation (e.g. Schnitker 1980; Manabe & Brvan 1985). Deepsea benthic foraminiferal faunas are known to reflect changes in deep-water characteristics, and therefore it should be possible to trace major changes in deep water formation by studying changes in faunal composition of these organisms (e.g. Douglas & Woodruff 1981). Study of deep-sea benthic foraminiferal faunas from high latitudes is of particular interest for reconstructing the deep-water formation patterns of the past, because there the environmental changes are expected to have been greatest. Until recently the southernmost sections of Paleogene deep-sea calcareous oozes (containing a record of calcareous deepsea benthic foraminifera) were recovered from the Falkland Plateau area (Dailey 1983). More southerly sites in the Pacific sector of the Southern Oceans and in the Ross Sea do not contain deep-water calcareous sediments older than Oligocene (e.g. Leckie & Webb 1985).

On Ocean Drilling Program Leg 113, Upper Cretaceous through upper Miocene calcareous and mixed siliceous/calcareous biogenic oozes were recovered at two sites on the Maud Rise, constituting the southernmost record of calcareous deep-sea benthic foraminiferal faunas through the Cenozoic. In this paper preliminary data are presented of the changes in benthic foraminiferal faunas through the Cenozoic, with emphasis on the Paleogene.

Material and methods

Ocean Drilling Program (ODP) Sites 689 and 690 were drilled on Maud Rise, Antarctica (Site 689: 64°31.01'S, 03°05.99'E, present water depth 2080 m; Site 690: 65°09.63'S, 01°12.30'E, present water depth 2914 m; Fig. 1; Barker et al. 1988). At both sites siliceous, mixed siliceous-calcareous, and calcareous biogenic oozes were recovered spanning the lowermost Maastrichtian through Pleistocene. Upper Eocene and older sediments are dominantly calcareous, upper Eocene through lower Miocene sediments mixed siliceous-calcareous with increasing amounts of siliceous oozes in younger sediments, and middle Miocene through Pleistocene sediments are dominantly siliceous.

Ages were estimated from the diatom zonation by Burckle & Gersonde and the calcareous nannofossil zonation by Pospichal & Wise in Barker et al. in press, in combination with data on the palaeomagnetic records at the sites (Spiess, in press), and using the time scale of Berggren et al. 1985. At Site 689 there are prominent unconformities in the lower Eocene and Paleocene, at Site 690 the upper Paleocene record is expanded, but there are prominent unconformities in the upper Eocene. Recovery at both sites was very good with only minor core disturbance. Palaeodepths cannot easily be estimated by backtracking (using simple thermal subsidence models) because of the location of the sites on Maud Rise. Maud Rise is an aseismic ridge with basement consisting not of typical mid-ocean ridge basalts (MORBs), but of alkali basalts of the ocean island basalt type (Barker et al. 1988) Depth estimates from benthic foraminiferal faunas for Site 689 suggest a depth of 1000-1500 m in the Paleocene, increasing to 1500-2000 m in the Eocene and later. For 690 estimates are 1500-2000 m in the Paleocene, increasing to more than 2500 m in the Eocene and later (Thomas in Barker et al. 1988).

For a preliminary overview of the material two samples per core (9.6 m) were studied, with additional samples (one per section of 1.5 m) in intervals where faunas showed changes, to a total of 100 samples. Samples of 15 cm^3 were dried at about 75°C, soaked in Calgon, washed



Fig. 1. Location map of Sites drilled at high southern latitudes by the Deep Sea Drilling Project and the Ocean Drilling Program. Sites 689 through 697 were drilled on Leg 113; only at Sites 689 and 690 were Upper Cretaceous through Paleogene calcareous oozes recovered. At most other sites of this leg the oldest sediment recovered was Neogene, with the exception of Sites 692 (the only sediment recovered was Lower Cretaceous), Site 693 where lower Oligocene biosiliceous hemipelagic muds were in contact with upper Albian 'black shales', and Site 696, where Oligocene (?) biosiliceous hemipelagic muds rested on barren glauconitic sands, which lay on upper-middle Eocene inner neritic sediments. Sites 608-704 were drilled on ODP Leg 114.

through sieves with openings of 63 µm, and residues dried at 75°C. Splits were made of such a size that they contained at least 300 specimens. Middle Miocene, most of the upper Miocene, and Pliocene samples consist of radiolarian-diatom oozes and are barren of benthic foraminifera. All other samples contained enough specimens for study. Specimens were picked from the greater than 63 µm size fraction to make sure that small specimens were wellrepresented (Thomas 1985; Schroeder et al. 1987). At least 300 specimens per sample were picked, because rarefaction curves (plots of number-of-species versus number-of-specimens recorded) showed that this number was required to give a good representation of the species in the most diverse samples from the sites. All specimens of benthic foraminifera in the sample splits were picked and mounted in cardboard slides; the counts and a discussion of the taxonomy will be fully presented in Thomas (in

press). The taxonomy is after Morkhoven *et al*. 1986.

Counts were completed on the 100 samples selected, and data are shown in Table 1 and Fig. 2. In addition, benthic foraminifera were picked from samples at intervals of 1.5 m over the whole section and qualitative data on these samples are included in this report; counts, however, are not yet complete.

Results

The faunas of the two sites are similar, with differences in relative abundance of species but overall the same species composition. The faunas resemble coeval lower bathyal to upper abyssal faunas from lower latitudes, as described by Vincent *et al.* (1974), Proto-Decima & Bolli (1978), Schnitker (1979), Tjalsma & Lohmann (1983), Boersma (1984), Wood *et al.* (1985), Miller & Katz (1987b), and Katz & Miller (1988).

285

	Site 690	Site 689	Abundant species-morphology
Assemblage 1: Quaternary and late	nr. of samples: 5 nr. of species: 31–41 e Miocene (8.5–7.5 Ma)	nr. of samples: 3 nr. of species: 21-31	<i>E. exigua</i> -spiral <i>Oridorsalis</i> sppspiral
Assemblage 2: Oligocene-early Mid	nr. of samples: 9 nr. of species: 31–48 ocene (36.5–14.5 Ma)	nr. of samples: 11 nr. of species: 21-46	<i>N. umbonifera</i> -spiral <i>Stilostomella</i> sppcylindrical <i>C. mundulus</i> -spiral
Assemblage 3: late middle Eocene	nr. of samples: 7 nr. of species: 31–57 -late Eocene (46.0–36.5 Ma	nr. of samples: 10 nr. of species: 37–52	<i>N. umbonifera-</i> spiral <i>Stilostomella</i> sppcylindrical <i>B. elongata-</i> buliminid
Assemblage 4: 4a: early middle Eo 4b: late early Eocer	nr. of samples: 5 nr. of species: 40–65 ocene (51.8–46.0 Ma) ne (55.0–51.8 Ma)	nr. of samples: 5 nr. of species: 37–46	N. truempyi-spiral S. eleganta-buliminid B. semicostata-buliminid S. brevispinosa-buliminid
Assemblage 5: early Eocene (57.5-	nr. of samples: 8 nr. of species: 28–49 -55.0 Ma)	nr. of samples: 5 nr. of species: 27-47	<i>S. brevispinosa</i> -buliminid <i>Tappanina selmensis</i> -buliminid <i>B. simplex</i> -buliminid
Assemblage 6: late Paleocene (61.6	nr. of samples: 12 nr. of species: 52–67 5–57.5 Ma)	nr. of samples: 3 nr. of species: 32–70	<i>B. thanetensis</i> -buliminid <i>Gavelinella</i> sppspiral <i>S. brevispinosa</i> -buliminid
Assemblage 7: late Maastrichtian-e	nr. of samples: 7 nr. of species: 58–79 arly Paleocene (68.9–61.61	nr. of samples: 4 nr. of species: 35-50 Ma)	<i>Gavelinella</i> sppspiral <i>O. navarroana</i> -spiral diverse lagenids-cylindrical
Assemblage 8: Maastrichtian (or ol	nr. of samples: 3 nr. of species: 48–62 lder: sedimentary units rest	nr. of samples: 5 nr. of species: 32-52 on basement)	<i>Gavelinella</i> sppspiral <i>Gyroidinoides</i> sppspiral

Table 1. Assemblages at Site 689 and Site 690.

Ages were derived from correlation with the diatom zonation by Gersonde & Burckle and the calcareous nannofossil zonation of Pospichal & Wise in Barker *et al.*, in press, using the time scale of Berggren *et al.* 1985. Cretaceous assemblage 8 is not discussed in detail in this paper.

There is a particularly great resemblance between Eocene–Oligocene faunas from Maud Rise and those from the Eocene of the northern Atlantic (Berggren & Aubert 1976*a*, 1976*b*; Murray 1984) because of the dominance of *Stilostomella* species.

At each site eight assemblages could be recognized, one of which was subdivided into two sub-assemblages (Table 1). The assemblages were distinguished using a combination of data on presence—absence of species with a short range, and relative abundances of the most common or dominant species. Species used to distinguish between assemblages are listed in Table 1, and most are illustrated in Fig. 3.

The transitions between the assemblages are coeval within the resolution of the diatom, calcareous nannofossil and planktonic foraminiferal zonations (Barker *et al.* 1988) and preliminary data on carbon and oxygen isotopic, composition of bulk carbonate (N. J. Shackleton, pers. comm. 1987) and benthic foraminifera (L. D. Stott, pers. comm. 1988), in combination with data on the palaeomagnetic record at the sites (Spiess, in press).

The diversity was higher at the deeper Site 690 at all times (Fig. 2), as was expected because of the commonly observed increase in diversity towards deeper water (e.g. Douglas & Woodruff 1981). There is an overall decrease in diversity during the Cenozoic, but the exception to this overall trend is the high diversity in middle Eocene assemblage 4. The diversity of lower Eocene assemblage 5 is exceptionally low as compared with that of upper Paleocene assemblage 6 and middle Eocene assemblage 4, as a result of the disappearance of many species at the end of the Paleocene. Similar disappearances occurred at the end of the Paleocene at sites in the Caribbean and Atlantic (Tjalsma & Lohmann 1983) and the Pacific (Miller et al. 1987b) and southernmost Atlantic (Katz & Miller 1988). Little detailed information was available on this major extinction event of deep-sea benthic foraminifera because few Paleocene/Eocene boundary sections were re-

CENOZOIC DEEP-SEA BENTHIC FORAMINIFERA



Fig. 2. Comparison of the species diversity and composition of the benthic faunal assemblages at Sites 689 and 690. Each bar indicates the average value for one assemblage (see Table 1 for number of samples in each assemblage). Assemblages are shown from 1 (youngest, see Table 1) on top to oldest (assemblage 8, see Table 1) on the bottom, but they are not spaced according to a linear time scale (see Table 1 and Fig. 4 for ages). 'Spiral species' include trochospiral and planispiral species; 'cylindrical species' include uniserial lagenids and *Stilostomella* spp., and 'buliminid' species include biserial and triserial species. The three groups do not add up to 100% because unilocular and agglutinated taxa were not included.

covered and sedimentation rates were usually low in this interval. At Site 690 the sedimentation rate for the uppermost Paleocene– lowermost Eocene palaeomagnetic Chrons 24 and 25 was about 14.4 m Ma⁻¹; at that site the major part of the faunal change occurred over less than 35 cm (equivalent to about 20 000 years). The diversity remained very low (25–30 species per 300 specimens) for about 260 000 years.

Placement of the Paleocene/Eocene boundary with regard to biostratigraphic zonations is being discussed (Berggren *et al.* 1985; M. P. Aubry *et al.* pers. comm.). Data on the calcareous nannofossil zonation at Site 690 (Pospichal & Wise in press) and the palaeomagnetic record (Spiess in press) are in better agreement with Aubry *et al.* (pers. comm.) than with Berggren *et al.* (1985). At the Maud Rise sites the extinction event of benthic foraminifera occurred in the middle of calcareous nannofossil zone CP8, after the first appearance (FA) of *Discoaster multiradiatus*, and before the FA of

Tribrachiatus bramlettei and the LA of Fasciculithus spp., i.e. before the end of the Paleocene as recognized by Berggren et al. 1985. The last appearance (LA) of the planktonic foraminiferal species Morozovella velascoensis, used to recognize the boundary by Berggren et al. (1985), could not be determined at Site 690 because of the absence of this low-latitude species. The FA of the planktonic foraminiferal taxon Pseudohastigerina spp., used to mark the boundary at higher latitudes, occurs higher in the section than the boundary as defined by the nannofossils (FA of T. bramlettei). Tjalsma & Lohmann (1984) placed the extinction at the end of planktonic foraminiferal Zone P5 in the uppermost Paleocene, whereas Miller et al. (1987b) placed it within or at the end of planktonic foraminiferal Zone P6a (the Paleocene/ Eocene boundary as defined in Berggren et al. 1985). At Site 690 the distinction between zones P5 and P6a is difficult to make because of the absence of marker species at high latitudes, which makes recognition of these planktonic



Fig. 3. The scale bar at (13) corresponds to 10 μm, all other scale bars correspond to 100 μm. (1) *Epistominella exigua*, side view; sample 690B-1H-1,0-2 cm. (2) *Nuttallides umbonifera*, side view; sample 690B-4H,CC. Note the traces of dissolution in the corrugation of the surface of the test. (3) *Stilostomella subspinosa*; sample 690B-12H-6,45-47 cm. (4) *Bulimina elongata*; sample 690B-12H-4,41-45 cm. (5) *Bulimina semicostata*; sample 690B-12H,CC. (6) *Siphogenerinoides eleganta*; sample 690B-12H,CC. (7) *Siphogenerinoides brevispinosa*; sample 690B-18H-4,40-44 cm. (8) *Tappanina selmensis*; sample 690C-15X,CC. (10a) *Bulimina thanetensis*; sample 690C-12X-2,40-42 cm. (10) *Gyroidinoides quadrata*; sample 690C-15X,CC. (10a) dorsal view; (10b) ventral view. (11) *Stensiona beccariifornis*; sample 690C-15X,CC. (11a) dorsal view; (11b) ventral view. (12) *Aragonia aragonensis*; sample 689B-22X,CC. (13) *Bulimina simplex*; sample 690B-13H-3,40-42 cm. (14) *Coryphostoma incrassata*; sample 690C-15X,CC.

foraminiferal zones impossible.

The extinction of benthic taxa occurred exactly during a major decrease in the δ^{13} Cvalues and δ^{18} O values of bulk carbonate and benthic foraminifera (Shackleton, pers. comm. 1987; Stott, pers. comm. 1988). These isotopic changes have been correlated with the Paleocene/Eocene boundary (Shackleton 1986; Miller *et al.* 1987*b*), but data from the highsedimentation rate section at Site 690 suggest that the isotopic changes occurred during the latest Paleocene, and definitely before the Paleocene/Eocene boundary as defined by Aubry *et al.* (pers. comm.)

Concise overviews of changes in composition of benthic foraminiferal faunas are difficult to give, because faunas are very diverse and many species need to be discussed to give a complete picture of faunal events. The most distinctive species in the assemblages are listed in Table 1 and shown in Fig. 3.

In general, assemblages 8 through 6 (Maastrichtian–Paleocene) have much in common, as do assemblages 3 through 1 (Oligocene–Recent). There are large differences in faunal composition of the older assemblages 6 through 8 and the younger assemblages 1 through 3, but these two groups of assemblages have strong similarities as to the morphology of the dominant taxa (see below). Assemblages 4 (early–middle Eocene) and especially 5 (earliest Eocene), however, strongly differ from both older and younger faunas (Fig. 2).

The three oldest assemblages (covering Maastrichtian through Paleocene) are very diverse and usually dominated by trochospiral and planispiral species. They contain many large, heavily calcified species, with Stensioina beccariiformis, the Nuttallides truempyi group, Gyroidinoides spp., Gavelinella spp., Alabamina creta, and Pullenia spp. as the most common trochospiral and planispiral species, and diverse lagenids and small agglutinated forms as common constituents. There are fluctuations in faunal composition in all these assemblages, with varying amounts of biserial and triserial taxa ('buliminid' species). In assemblage 8 the biserial/triserial group consists mainly of Coryphostoma incrassata and Praebulimina reussi with Reussella szajnochae in some samples. In assemblage 7 the 'buliminid' group consists of Coryphostoma spp. with rare P. reussi. In assemblage 6 Bulimina thanetensis, Rectobulimina carpentierae and Siphogenerinoides brevispinosa are the dominant buliminids. There are minor faunal changes at the Cretaceous/Tertiary boundary within assemblage 7 (Thomas 1988), but no major faunal

turnover occurred in the benthic foraminiferal faunas, in agreement with Tjalsma & Lohmann (1983), Dailey (1983), and Widmark & Malmgren (1988).

Assemblage 5, present after the major extinction at the end of the Paleocene, differs considerably from the older assemblages in the following ways: the faunas are less diverse, dominated by 'buliminid' species, and contain predominantly small, thin-walled forms. There are no indications that the decrease in diversity resulted from dissolution. A similar decrease in size of benthic taxa at the end of the Paleocene was noted by Boersma (1984). There is little fluctuation from sample to sample in the relative abundance of spiral as compared with 'buliminid' species. Of the spiral species present, Nuttallides truempyi occurs in most samples but constitutes less than 10% of the fauna. Other spiral species are rare, with the exception of Abyssamina quadrata, Clinapertina spp., and small specimens of Anomalinoides spissiformis and Nonion havanense. The most common 'buliminid' forms are Tappanina selmensis, Siphogenerinoides brevispinosa, small, smoothwalled Bulimina species such as B. simplex and B. trihedra, small Bolivinoides species, and in a few samples Aragonia aragonensis. The fauna has a low diversity, partially caused by the absence or rare occurrence of lagenids. The big difference between assemblages 6 and 5 is the loss of the many common spiral species, which had existed for a long time and had given the older assemblages their overall character. Species such as Stensioina beccariiformis, Alabamina creta, Pullenia coryelli and Gavelinella spp. rapidly (within 20000 years) disappeared from the fauna, in addition to the rare large biserial species Bolivinoides delicatulus.

From the base of the Eocene the diversity increases upwards (through the middle Eocene), and assemblage 4 is once again very diverse, with large, heavily calcified species, and common, diverse lagenids. In the spiral species group *N. truempyi* is common, as are *Gyroidinoides* spp., and *Oridorsalis umbonatus*; in all samples of assemblage 4a the large species *Bulimina semicostata* is common (4-35%), in addition to *Siphogenerinoides eleganta*. Assemblage 4b is transitional between 5 and 4a, with common *S. eleganta*, and *S. brevispinosa*, but rare *B. semicostata*.

Assemblage 3 (middle-late Eocene) forms a transitional assemblage between the highdiversity assemblage 4 and the lower-diversity younger assemblages. Faunal changes taking place during this transition have been described from many areas (Tjalsma & Lohmann 1983; Corliss & Keigwin 1986). The diverse lagenid species (uniserial and lenticulinid) gradually decreased in relative abundance during the middle Eocene (assemblage 3), and disappeared at the end of the Eocene. In assemblage 3 there are once again fluctuations in relative abundance of spiral and 'buliminid' species, with *Bulimina elongata* as the dominant buliminid. Assemblages 2 and 3 contain few lagenids, and common to abundant *Nuttallides umbonifera* (with common *N. truempyi* in the lower part of assemblage 3 at Site 690), *Oridorsalis umbonatus*, *Pullenia* spp., and *Gyroidinoides* spp. as spiral species. In addition, *Stilostomella* spp. are very common to abundant (15–45%).

Assemblage 1 has a composition similar to that of assemblage 2, with the addition of *Epistominella exigua*, and the disappearance of *Stilostomella* spp. at Site 690, the very strong decrease in relative abundance of *Stilostomella* spp. at Site 689, and overall decrease in diversity.

Assemblages 1 through 3 have lower diversities than assemblages 6 through 8, and contain more small, smooth, thin-walled species. In this group of assemblages, as in the older group of assemblages 6 through 8, there are fluctuations in relative abundance, with triserial/biserial species common in some samples. In assemblage 3 the triserial/biserial group ('buliminid' species) consists mainly of the small, smooth-walled species *Bulimina elongata*, in assemblage 2 of *Bolivina* spp., *Uvigerina* spp., and *Turrilina alsatica*, and in assemblage 1 of *Bolivina decussata* and *Fursenkoina* species.

In conclusion, we see relatively long-lived assemblages of deep-sea benthic foraminifera in the Paleocene and older sediments, and in the upper middle Eocene and younger sediments at Maud Rise. These long-lived assemblages are characterized by the dominance of spiral species, with fluctuations in relative abundance of species of a triserial-biserial group. The species in the latter group tend to have shorter ranges than the spiral species. In contrast, there were short-lived assemblages in the early through early middle Eocene. These assemblages are characterized by high relative abundances of 'buliminid' species, and are very different from both younger and older faunas because of the low relative abundance of spiral species.

First and last appearances of deep-sea benthic foraminiferal species can probably not be used to correlate over large distances; the easily recognized species *Bulimina semicostata*, for instance, has a much shorter range at Sites 689 and 690 (limited to assemblage 4) than in the rest of the Atlantic Ocean (Tjalsma & Lohmann 1983; Morkhoven *et al.* 1986). Periods of faunal change in deep-sea benthic foraminifera, however, can probably be correlated well from one basin to another: the boundaries between the faunal assemblages at Sites 689 and 690 appear to be well-correlated with the zonal boundaries of the proposed deep-sea benthic foraminiferal zones (Berggren & Miller, in press), although specific first and last appearances are not synchronous (see also Thomas 1986).

Discussion

To evaluate the environmental significance of changes in deep-sea benthic foraminiferal assemblages, the faunal records were compared with the records of carbon and oxygen isotopic values for bulk carbonate and benthic foraminifera for several sites on the Walvis Ridge-Rio Grande Rise, southern Atlantic Ocean (Shackleton 1987; Fig. 3). Data on the isotopic record for the Maud Rise sites have not yet been published, but major features of isotopic records are similar at different places in the oceans (e.g. Berger et al. 1981; Miller et al. 1987a), and the record at the sites on Maud Rise is in its major features similar to that collected at other sites (N. J. Shackleton, pers. comm. 1987; L. D. Stott, pers. comm. 1988; Kennett & Stott 1988).

The isotopic records from the Walvis Ridge sites show the major features of the global record: the oxygen isotopic curve shows a decrease in bottom water temperature and surface water temperature just after the Eocene/ Oligocene boundary (e.g. Keigwin & Corliss 1986), highest temperatures of bottom waters during the middle Eocene with a strong decrease during the middle Eocene, and an increase in bottom water temperatures during the latest Paleocene/earliest Eocene (Oberhaensli 1986; Oberhaensli & Toumarkine 1985). The temperature difference between deep and surface waters was lowest in the early to early middle Eocene. The carbon isotope record of the surface waters shows a major positive excursion during the late Paleocene (see Miller & Fairbanks 1985, and Shackleton 1987, for a discussion of the Cenozoic carbon isotope record). Carbon isotopic values during the Late Cretaceous were about as high as values during the late Paleocene (Zachos & Arthur 1986).

Shackleton (1987, Fig. 4) suggested that the major decrease in δ^{13} C at the end of the Paleocene resulted from a drop in primary productivity. During a collapse of primary productivity, however, carbon isotopic ratios of



Fig. 4. Paleogene benthic foraminiferal assemblages plotted against the time scale of Berggren *et al.* 1985, and compared with the oxygen and carbon isotope records for sites on the Walvis Ridge (Shackleton 1987). The carbon isotope record and the oxygen isotope record on the right are for bulk-carbonate; the oxygen isotope record on the left is for benthic foraminifera. Data on benthic foraminifera can be used to derive estimates of bottom water temperature, but the bulk record cannot be used to estimate the temperature of the surface waters, because the 'vital effect' of the organisms forming the bulk carbonate is not known. The difference between bulk and benthic record does give an estimate of changes in the difference in temperature of deep and bottom waters.

deep-sea benthic foraminifera should become heavier while the ratios in bulk carbonate (mainly consisting of surface-dwellers) should become lighter, as was observed in many sections across the Cretaceous/Tertiary boundary (Zachos & Arthur 1986). Curves of carbon isotopic ratios of bulk carbonate and benthic foraminifera for the uppermost Paleocene, however, are parallel (Miller *et al.* 1987*b*), indicating a change in δ^{13} C of mean ocean water (probably as a result of changes in the input or output ratio of organic carbon to carbonate carbon; Miller & Fairbanks 1985).

There is agreement in timing of changes in deep-sea benthic foraminiferal assemblages and global isotopic changes, but the exact relation cannot yet be established because the isotopic record from Sites 689 and 690 is not yet available. Ocean-wide faunal events in the middle Miocene, for instance, generally predated the middle Miocene oxygen isotopic shift (Thomas & Vincent 1987; Miller & Katz 1987b; Berggren & Miller, in press). The boundary between assemblages 2 and 3 appears to be coeval with

this major decrease in temperature and probably an increase in ice volume (e.g. Corliss & Keigwin 1986; Miller et al. 1987a), but there is a short hiatus in the records across this boundary at the Maud Rise sites making a precise correlation impossible. The boundary between assemblages 3 and 4 and the more gradual changes within assemblage 3 occur during a long-term decrease in bottom water temperature (see Corliss & Keigwin 1986, fig. 5). The short-lived assemblages 4b and 5 occur during a period of maximum bottom water temperatures and minimum differences in temperature between deep and surface waters. The major extinction at the end of the Paleocene (assemblages 5 and 6) occurred at the same time as a major decrease in δ^{13} C and an increase in temperature. The boundary between assemblages 6 and 7 occurred during a strong increase in δ^{13} C, but no large change in temperature.

Deep-sea benthic foraminifera are conservative organisms with long ranges, living in a conservative environment (e.g. Boltovskoy 1987). Many deep-sea species have cosmopolitan distributions (e.g. Douglas & Woodruff, 1981) and the Paleogene faunas at Sites 689 and 690 are similar to coeval faunas described from sites at high northern latitudes (Murray 1984; Berggren & Aubert 1976a, b) and at lower latitudes throughout the Caribbean and South Atlantic (Tjalsma & Lohmann 1983), the New Jersey continental margin (Miller & Katz 1987a), the Bay of Biscay (Schnitker 1979; Miller et al. 1984), Barbados (Wood et al. 1985), and the central Pacific Ocean (Miller et al. 1987b). The short-lived assemblages characterized by the presence of several species with ranges of a few millions of years indicate a period of unusual variability in the deep oceans (Wilde & Berry 1982). The major extinction event at the end of the Paleocene is especially remarkable: during other extinctions in deepsea benthic foraminifera, the extinction process appears to have had a duration of millions of years (Miller & Katz 1987b; Thomas 1985, 1986; Thomas & Vincent 1987) as opposed to the estimate in this study of less than 20000 years for the Paleocene event in this paper. The species that became extinct at this time were almost all survivors from the Cretaceous, and had survived the collapse of primary productivity at the Cretaceous/Tertiary boundary (Zachos & Arthur 1986).

During the Cretaceous/Tertiary boundary extinction planktonic taxa were very severely affected, which probably means that this was mainly a disturbance of the surface of the Earth with only secondary effects felt at greater depths in the oceans (Thomas 1988). The extinction event at the end of the Paleocene, a period characterized by few extinctions overall (Raup & Sepkoski 1986), must thus probably be seen as an event rooted in the deep waters of the oceans. Present biology of deep-sea benthic foraminifera is not well known, and thus it is difficult to evaluate the meaning of fluctuations in species composition. Corliss (1985) and Corliss & Chen (1988), however, suggest that the morphology of the tests of benthic foraminifera reflects the microhabitat in which the organisms live. Specifically, Corliss & Chen (1988) suggest that many trochospiral species have an epifaunal way of living, whereas biserial and triserial species live infaunally; these authors show that faunas dominated by infaunal species are associated with relatively high organic carbon contents of the sediments, whereas epifaunal species live in microhabitats with lower amount of organic carbon. Similarly, Lutze & Coulbourn (1984) and Bernard (1988) found that biserial/triserial species are typical of high organic carbon or low O₂ contents, and Caralp (1984) and Sen Gupta

et al. (1981) demonstrated that high percentages of triserial and biserial species in benthic foraminiferal faunas reflect high primary productivity in the surface waters.

Using the morphology of recent taxa as a guide, it appears that the group of spiral taxa is indicative of what we call 'normal bottom water conditions' in the present oceans, i.e., well-oxygenated water with fairly low levels of organic carbon. The 'buliminid' species, on the other hand, may indicate lower levels of oxygen (although by no means anoxic waters; see also Lutze & Coulbourn 1984) and possibly a higher supply of nutrients. This explanation suggests that the faunal fluctuations within assemblages 8 through 6 as well as in assemblages 3 through 1 indicate fluctuating primary planktonic productivity, resulting in fluctuating levels of nutrients.

The species adapted to 'normal' (i.e., welloxygenated and low in nutrients) waters have very long ranges; possibly such species could survive the collapse of the surface productivity at the end of the Cretaceous because they were well-adapted to low nutrient levels. The few species becoming extinct at Sites 689 and 690 at the end of the Cretaceous (e.g., *Coryphostoma incrassata* and *Bolivinoides draco*) belong to the 'buliminid' group thought to indicate a high level of nutrient supply, and these species probably could not survive this strong drop in their food supply.

The lack of a large extinction event of deepsea benthic foraminifera, the extinction process Tertiary boundary at Sites 689 and 690 suggests that these organisms were well-suited to survive strong fluctuations in primary productivity. However, those species that survived the end of the Cretaceous were strongly affected by events at the end of the Paleocene, and many of them became extinct; therefore the author concludes that the extinction at the end of the Paleocene was not caused by a change in surface productivity. It seems more probable that the extinction of benthic faunas was caused by changes in the deep waters, probably in bottom water chemistry. Such a change in chemistry could well be caused by a switch of the sources of deep waters.

Miller *et al.* (1987b) suggested that deep waters were formed at the poles at least for some time during the late Paleocene, in agreement with Barrera *et al.* (1987), but that waters might have formed at lower latitudes later on. These authors place the change in circulation to deep-water sources at lower latitudes in the early Eocene, but indicate that the change might have occurred at the Paleocene/Eocene boundary (Miller et al. 1987b, fig. 6b). More recent data (Katz & Miller 1988; Miller & Katz 1988) on material recovered from ODP Sites 698-702 (Fig. 1) suggest that the Southern Oceans were filled with nutrient-depleted bottom water during the late Paleocene and early Eocene, but that there might have been an interval of reduction or shutdown of bottom water formation in the Southern Oceans at the time of the extinction of deep-sea benthic foraminifera. A change from formation of deep waters somewhere close to Sites 689 and 690 to deep-water formation at lower latitudes would explain the changes in the benthic faunas. The faunas had been able to adapt to fluctuations in productivity over a long period, but could not handle an overall change in bottom water characteristics to warmer deep waters with less oxygen. If deep waters formed in the Weddell Sea region then deep waters over Maud Rise would be 'young', cold and well-oxygenated even in the absence of large ice caps. In contrast, deep waters formed at low latitudes from warm, salty water with a high density as a result of evaporation (Brass et al. 1982; Wilde & Berry 1982) would be not only lower in oxygen content because of the higher temperature, but also old, and thus even lower in oxygen-content and higher in nutrients by the time that they arrived at the Maud Rise sites.

Such deep waters would be unsuitable for the faunas dominated by epifaunal species, but 'buliminid'-dominated faunas with a high abundance of small species (assemblage 5) might be expected to do well. These deep waters from another source region might bring with them juvenile mobile stages of benthic foraminifera (Berggren & Aubert 1975). The fact that the major extinction of deep-sea benthic foraminifera at the end of the Paleocene occurred at many sites in all oceans, and the short time scale (less than 20000 years) imply a major change in circulation as the cause of the event.

The change in deep-water source might have resulted from a global increase in temperature (Owen & Rea 1985; Barron 1987), which caused stronger evaporation in low-latitude basins. It might also have been caused by changes in plate tectonic arrangements: at the end of the Paleocene large changes in plate arrangement occurred as a result of the collision of India and the Asiatic land mass (Williams 1986), as well as in the North Atlantic (Berggren & Schnitker 1985). These two possibilities might have been related: plate tectonic activity could have resulted in warmer climates because of high production of CO_2 at mid oceanic ridge systems (Owen & Rea 1985). Barron (1985), however, denies that plate tectonic rearrangement and the resultant circulation changes could have caused the warm and very equable Eocene climate (Shackleton & Boersma 1984; Boersma *et al.* 1987).

Deep-sea benthic faunal compositions suggest that warm salty bottom waters formed during the late Paleocene through early Eocene only, in disagreement with the conclusion by Prentice & Matthews (1988) that low-latitude production of such waters dominated the thermohaline circulation during the Tertiary. More detailed research is necessary to determine whether the formation of such waters occurred continuously during the late Paleocene and early Eocene, or whether there were several short periods (less than 1 million years) of formation of warm, salty bottom water during that time interval. The deep-sea benthic foraminiferal faunas indicate that formation of warm, salty deep water probably stopped at some time in the middle Eocene, a period characterized by a very long-term decrease in temperature (Keigwin & Corliss 1986; Boersma et al. 1987) and global faunal changes in the deep-sea benthic assemblages. The benthic faunal changes from assemblage 4 to assemblage 3 and within assemblage 3 might reflect such a change in bottom water sources. These faunal changes were not as rapid as the latest Paleocene extinction, suggesting that these circulation changes were more gradual or possibly occurred in several steps. The overall decrease in diversity from the middle Eocene onwards probably reflects continuing cooling of the deep waters. The faunas also show the decrease in availability of CaCO₃ (colder waters will take up more CO_2 from the atmosphere), reflected in decrease in size and wall-thickness of the benthic faunas. The end of the Eocene is marked by the disappearance of the last species of Bulimina that is common at Sites 689 and 690, B. elongata. The fauna in the earliest Oligocene (assemblage 2) strongly resembles younger faunas (assemblage 1), which differ by lower diversities, and especially by the decrease in relative abundance of Stilostomella spp. at the end of the early Miocene (similar to the situation in equatorial Pacific sites; Thomas & Vincent 1987).

Conclusions

(1) Cenozoic deep-sea benthic foraminiferal faunas reflect changes in the physicochemical character of the deep waters and thus reflect processes of deep-water formation.

(2) Changes occurred at the early/late Paleocene boundary, in the latest Paleocene, in the early Eocene, in the earliest middle Eocene,

in the middle middle Eocene, in the earliest Oligocene, and in the middle Miocene.

(3) Benthic foraminiferal assemblages indicate that deep-water formation in the early and early middle Eocene was very different from the periods before and after that. Possibly deep water during this period formed by evaporation at low latitudes ('warm saline bottom water'), whereas deep water formed at high latitudes earlier and later.

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(4) Many benthic foraminiferal species do not appear to have globally synchronous first and last appearances, but periods of faunal change appear to be synchronous.

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