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Biogeography of the Late Paleocene Benthic Foraminiferal Extinction

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ABSTRACT
During the Late Paleocene Thermal Maximum (LPTM) benthic foraminifera at middle bathyal and greater depths suffered extinction of 30–50% of species during a few thousand years. Extinction was less severe at neritic to upper bathyal depths, where temporary changes in faunal composition prevailed. Preextinction deep-sea faunas were cosmopolitan and diverse, and contained heavily calcified species. Immediate postextinction faunas were more variable geographically, exhibited low diversity, and were dominated by thin-walled calcareous or agglutinated taxa, possibly because $CaCO_3$ dissolution increased globally from neritic to abyssal depths just before the extinction. These assemblages were dominated either by long-lived taxa such as *Nuttallides truempyi* or by buliminid taxa, the latter accompanied by agglutinants in some areas.

Faunas dominated by *N. truempyi* were common in the South Atlantic and at lower bathyal through upper abyssal depth in the Indian Ocean, and might indicate oligotrophic conditions as well as increased corrosiveness. Buliminid-dominated faunas might indicate high rates of deposition of organic matter or low-oxygen conditions. Such faunas were common globally along continental margins, and locally co-occurred with sedimentologic or planktonic faunal indicators of high productivity. In the bathyal central Pacific, however, buliminid-dominated faunas co-occurred with planktonic faunas suggesting oligotrophy, and they could reflect low-oxygen conditions resulting from sluggish ocean circulation, oxidation of dissociated methane hydrates, or warming of bathyal–abyssal waters caused by a change in deep-sea circulation. Alternatively, they could indicate that the fraction of organic matter reaching the seafloor increased as a result of decreased oceanic oxygenation. The latest Paleocene benthic extinction thus was complex, and factors such as changes in deep-sea circulation, increased $CaCO_3$ corrosiveness, increased temperatures, decreased oxygenation, and changes in the patterns of high productivity may have contributed to its severity.

Environmental Setting

The late Paleocene and early Eocene were the warmest epochs of the Cenozoic Era; polar ice caps were almost certainly absent, and shallow seas covered large parts of all continents. During these epochs, major changes occurred in global climate and in the carbon cycle on scales of millions to thousands of years. Long-term warming of the deep oceans started in the mid-Paleocene Epoch (Miller et al. 1987a; Shackleton 1987; Kennett and Stott 1990; Zachos et al. 1992, 1993; Seto 1995). Warm-water pelagic marine organisms penetrated to polar latitudes by the end of the Paleocene Epoch (Stott and Kennett 1990; Premoli Silva and Boersma 1984; Boersma et al. 1987; Aubry 1992; Berggren 1992). Thermophilic vertebrates occurred in the Arctic (Estes and Hutchison 1980; McKenna 1980; Markwick 1994), with vegetation and soil types indicating warm climates (Kemp 1978; Nilsen and Kerr 1978; Wolfe 1994; Basinger et al. 1994; Manum 1994). Clay mineral associations in oceanic sediments at high to midlatitudes indicate high humidity and intense chemical weathering (Antarctic, Robert and Kennett 1992; New Jersey margin, Gibson et al. 1993; New Zealand, Kaiho et al. 1996). Oxygen isotope data suggest that latitudinal temperature gradients were very shallow (Shackleton and Boersma 1981; Stott et al. 1990; Barrera and Huber 1991; Zachos et al. 1994; Bralower et al. 1995a, 1995b; Lu and Keller 1995b).

Rates of species origination and diversity were high for terrestrial vertebrates and flora (Hooker 1991; Collinson 1983; Rea et al. 1990; Wing et al. 1991, 1995; Maas et al. 1995), as well as for pelagic oceanic organisms (Romein 1979; Boersma et al. 1987; Boersma and Premoli Silva 1991; Corfield and Shackleton 1988; McGowran 1991; Aubry 1992; Berggren 1992; Corfield 1993; Kelly et al. 1996). The late Paleocene and earliest Eocene epochs thus constitute a time of major innovation of the biosphere (Briggs 1995).

The unusual warmth of these epochs has been commonly explained by high atmospheric $p\mathrm{CO}_2$ concentrations, probably caused by plate tectonic processes such as massive volcanism in the North Atlantic Volcanic Province during initial opening of the North Atlantic, decarbonation of limestone or oxidation of organic-rich sediments during the beginning of the India–Asia continental collision, and high hydrothermal activity along midoceanic ridges (see Thomas and Shackleton 1996 for a review). Proxy data for atmospheric $p\mathrm{CO}_2$ levels tentatively support higher values than today (Cerling 1991; Freeman and Hayes 1992), although this remains debatable (Stott 1992). Climate modeling indicates that at such CO_2 levels tropical temperatures would be much higher than deduced from oxygen isotope data, and mechanisms for highly increased heat transport from low to high latitudes at the low latitudinal temperature gradients remain unexplained (Sloan et al. 1995; Sloan and Rea 1995).

In the latest Paleocene Epoch the world warmed even more for a short time (Kennett and Stott 1991; Pak and Miller 1992; Thomas and Shackleton 1996), which has been named the Late Paleocene Thermal Maximum (LPTM; Zachos et al. 1993). This event occurred within paleomagnetic Chron C24r, in nannofossil Biochron NP9 (= Biochron CP8), and before the last appearance datum (LAD) of the planktonic foraminifer *Morozovella velascoensis* (Aubry et al. 1996; Berggren and Aubry 1996). Oxygen isotope data indicate that intermediate to deep ocean waters globally warmed by 4 to 6° C over less than a few thousand years (Kennett and Stott 1991; Thomas and Shackleton 1996), but tropical to subtropical surface to neritic temperatures remained constant (Stott 1992; Bralower et al. 1995a, 1995b; Lu and Keller 1995b; Schmitz et al. 1996). This rapid warming of the deep ocean has been explained by a change in deep- to intermediate-water circulation, during which the dominant sources of deep and intermediate waters shifted from high to subtropical latitudes (Kennett and Stott 1991; Pak and Miller 1992; Thomas and Shackleton 1996).

Coeval with this short-term warming was a shift in carbon isotope values by about $-2‰$ in surface and deep waters of all oceans (Kennett and Stott 1991; Pak and Miller 1992; Lu and Keller 1993, 1995a, 1995b; Canudo et al. 1995; Aubry et al. 1996; Thomas and Shackleton 1996; Schmitz et al. 1996), superimposed on a long-term decrease in values that started in the middle Paleocene Epoch (Shackleton and Hall 1984; Shackleton 1986, 1987; Corfield et al. 1991; Corfield and Cartlidge 1992; Corfield 1995). An isotope excursion similar in magnitude and estimated duration occurred in the tooth enamel of herbivores and in carbonate concretions on land (Koch et al. 1992, 1995; Stott et al. 1996), and in terrestrial-derived organic matter in a New Zealand marine section (Kaiho et al. 1996). The whole atmospheric–oceanic reservoir thus underwent a rapid, negative shift in carbon isotope values during the LPTM, the duration of which has been estimated at between 50 kyr (Thomas and Shackleton 1996) and 200 kyr (Kennett and Stott 1991).

Mass balance equations show that this carbon isotope excursion was so large that it probably could not have been caused by transfer of terrestrial biomass into the ocean–atmosphere system or by eruption of volcanogenic CO_2; it was so rapid that it probably could not have been caused by a change in deposition or erosion rates of carbon in carbonate as compared to carbon in organic matter (see Thomas and Shackleton 1996, for a review). This leaves few explanations open, and recently it has been speculated that this unusual, negative carbon isotope excursion could have been caused by massive dissociation of (isotopically extremely light) oceanic methane hydrates as a result of the deep-ocean warming (Dickens et al. 1995; Kaiho et al. 1996).

Benthic Foraminifera

The latest Paleocene benthic foraminiferal extinction has been described from land sections and at oceanic drill sites, at depths ranging from outer neritic to abyssal (appendices 12.1 and 12.2; figure 12.1). This extinction was rapid; it affected benthic foraminiferal faunas catastrophically worldwide, and it occurred during or close to the beginning of the LPTM and the negative excursion in carbon isotopes, just before the Paleocene/Eocene Epoch boundary as most commonly defined (Thomas 1989, 1990b; Stott and Kennett 1990; Nomura 1991 in combination with Seto et al. 1991; Pak and Miller 1992; Bralower et al. 1995a, 1995b; Canudo et al. 1995 in combination with Ortiz 1995; Aubry et al. 1996; Thomas and Shackleton 1996; Kaiho et al. 1996).

This major break in deep-sea benthic foraminiferal faunas occurred between the Paleocene and Eocene epochs if viewed at coarse timescales, whereas planktonic foraminifera underwent a major extinction at the end of the Cretaceous Period (Cushman 1946; Beckmann 1960; von Hillebrandt 1962). After the late Paleocene

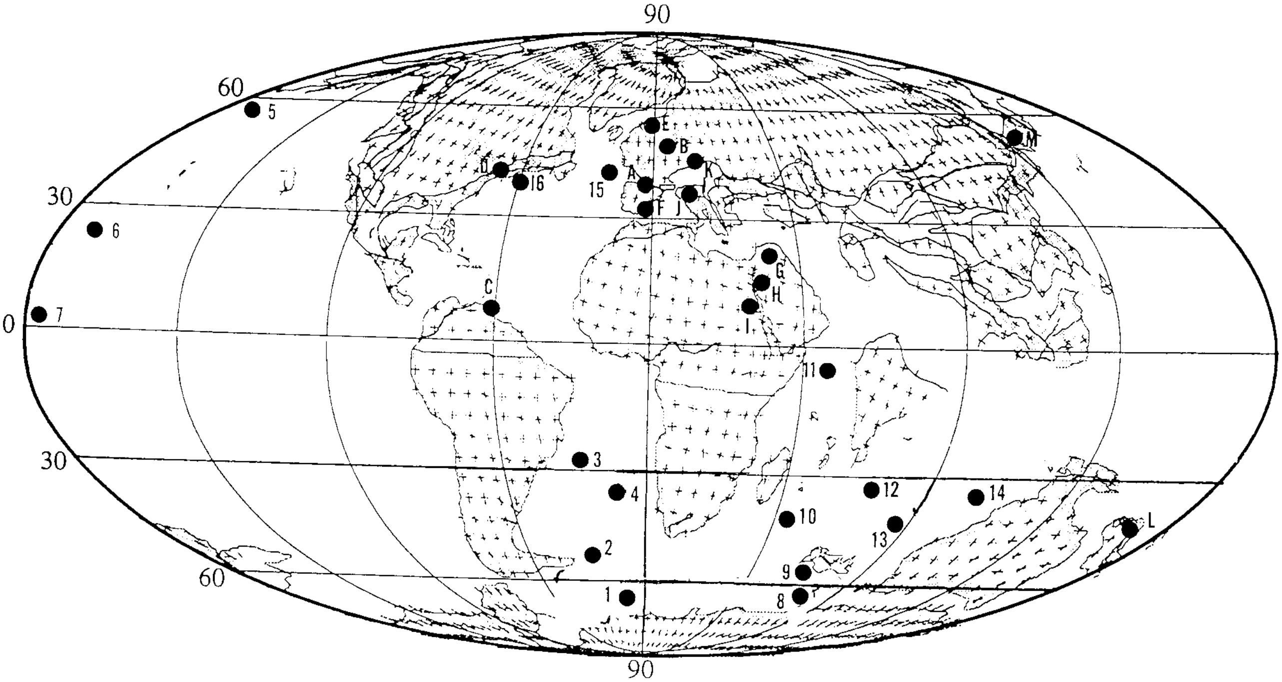

Figure 12.1 Location of drilling sites and land sections as described in appendices 12.1 and 12.2: numbers (drill sites) and letters (land sections) identify locations in the appendices.
The paleogeography of the continents in the late Paleocene Epoch is after Zachos et al. (1994).

benthic extinction faunas were predominantly of low diversity throughout the bathyal and abyssal regions of the oceans, whereas coeval planktonic organisms showed high rates of species turnover, high rates of species origination, and high diversity (Shackleton et al. 1985; Boersma et al. 1987; Corfield and Shackleton 1988; Boersma and Premoli Silva 1991; Hallock et al. 1991; Aubry 1992; Corfield and Cartlidge 1991; Corfield 1993; Lu and Keller 1993, 1995a, 1995b; Kelly et al. 1996). Major extinctions of planktonic and benthic organisms in the oceans thus appear to have been decoupled (e.g., Thomas 1990b; Kaiho 1994b).

The rapidity of the extinction makes it difficult to compare immediate postextinction faunas at different locations, especially because many sections contain unconformities in the interval straddling the extinction (Aubry et al. 1996). Only for high-resolution data sets can we know that postextinction faunas were indeed coeval, because we can compare faunas that co-occurred with the short-term negative carbon isotope event. Faunal comparisons may be more difficult because of differences in taxonomic concepts of different authors and because of the difference in size fraction being studied, varying between 63 and 150 µm in most cases (appendices 12.1 and 12.2).

High-resolution faunal data and carbon isotope analyses are available from Ocean Drilling Program (ODP) Sites 689 and 690 (Weddell Sea; Thomas and Shackleton 1996), South Atlantic (Walvis Ridge) Deep Sea Drilling Project (DSDP) Sites 525 and 527 (Thomas and Shackleton 1996), and equatorial Pacific ODP Site 865 (Bralower et al. 1995a, 1995b; Thomas unpublished data). Detailed data are also available for the Zumaya and Caravaca land sections in Spain (Canudo et al. 1995; Ortiz 1995) and for the Tawanui section in New Zealand (Kaiho et al. 1993, 1996). The short-term carbon isotope anomaly has been recognized in neritic Egyptian sections (Schmitz et al. 1996), but benthic foraminiferal data have not yet been published at high resolution (Speijer 1994; Speijer et al. 1996a, 1996b). Isotope records for ODP Site 738 registered the $\delta^{13}C$ excursion (Lu and Keller 1993), but only limited data on the benthic faunas are available (Nomura and Kennett, personal communication 1995; Thomas, unpublished data). Faunal data for equatorial Pacific DSDP Site 577 and Bay of Biscay DSDP Site 401 (Pak and Miller 1992) probably do not cover the time interval directly after the extinction because the magnitude of the $\delta^{13}C$ anomaly is much smaller at these sites than at others, suggesting that its minimum value (and thus the details of the benthic foraminiferal extinction) occurred between samples.

Most authors concluded that a change in deep-water circulation played a major role in the extinction, that most of the deep to intermediate waters of all oceans formed at least for some time at subtropical latitudes, and that decreased levels of deep-sea oxygenation resulting from the increased temperature of these waters were a causal factor (e.g., Miller et al. 1987b; Thomas 1989, 1990b, 1992; Katz and Miller 1991; Pak and Miller 1992, 1995; Kaiho 1991, 1994b; Nomura 1991; Coccioni et al. 1994; Ortiz 1995; Speijer et al. 1996b). Others, however, suggested that the patterns of faunal extinction vary geographically and that their complexity cannot be explained by decreased oxygenation only (e.g., Nomura 1991; Coccioni et al. 1994; Thomas and Shackleton 1996).

In this chapter, I first explore postextinction benthic foraminiferal faunal patterns following the extinction using high-resolution data from the sites mentioned above. Then I use literature data (figure 12.1, appendices 12.1 and 12.2) to try to evaluate oceanic environmental changes between late Paleocene and early Eocene times, to determine the biogeographic pattern of the extinction, and to speculate on its possible causes.

Methods

Sample Preparation and Stratigraphic Framework for High-Resolution Study

In this chapter new data are presented from ODP Site 865, and a few additional samples from ODP Sites 689 and 690 and DSDP Site 527 (figures 12.2 and 12.3), as compared to data in Thomas and Shackleton (1996). Samples for benthic foraminiferal faunal and isotope analysis were taken from DSDP Site 527 (Walvis Ridge, South Atlantic), ODP Sites 689 and 690 (Maud Rise, Weddell Sea), and ODP Site 865 (equatorial Pacific). They were dried overnight at 50° C and weighed, then soaked overnight in distilled water. Most samples disaggregated readily and could be washed over a 63-μm screen. Benthic foraminifera for faunal analysis were picked from the >63 μm size fraction, following Thomas (1990a). All specimens were picked and mounted in cardboard slides. All samples contained sufficient specimens for analysis (>250). Taxonomy is as in Thomas (1990a) and Thomas and Shackleton (1996), and largely follows van Morkhoven et al. (1986). The species richness was used to calculate species richness in a sample of 100 specimens using rarefaction (Sanders 1968).

I use the integrated magnetobiochronologic framework of Berggren et al. (1995), which is based on the geomagnetic polarity timescale of Cande and Kent (1992) and modified by Cande and Kent (1995). For ODP Site 690, I use the biostratigraphic interpretation of Aubry et al. (1996), giving an age of 55.5 Ma to the benthic extinction event and 55 Ma to the NP9/NP10 biochronal boundary. I derive numerical ages for ODP Site 690 assuming constant sedimentation rates between the benthic extinction and the NP9/NP10 zonal boundary, and between the benthic extinction and the top of Chron C25. For samples from DSDP Sites 525 and 527 and ODP Sites 689 and 865 I assign numerical ages according to Berggren et al. (1995) to datum levels in Thomas et al. (1990), Shackleton et al. (1984), and Bralower et al. (1995b). Finally, I revise the numerical ages at these four sites until the benthic foraminiferal carbon isotope curves agree with that for ODP Site 690 (Thomas and Shackleton 1996) in order to correct optimally for varying sedimentation rates, especially for the dissolution zone at Sites 525 and 527 and for the interval with very low sedimentation rates just above the extinction at Site 865.

Selection of Literature Data Sources

Appendices 12.1 (DSDP and ODP sites) and 12.2 (land sections) list sites for which data are available that straddle the extinction level; hence only a few sites from Tjalsma and Lohmann (1983) are included (figure 12.1). Data on sections in the Norwegian–Greenland Sea and Labrador Sea were not included because in many of the sections sedimentation probably started after the extinction event (Hulsbos et al. 1989; Kaminski et al. 1989). Data on agglutinated faunas were mostly not included, even though they suggest that changes occurred in agglutinated faunas at the end of the Paleocene Epoch (e.g., Geroch and Novak 1984; Kuhnt and Kaminski 1990; Kaminski et al. 1996), because exact data and precise correlations are difficult in the absence of carbonate and thus of isotope data. Data from the North Sea region are included because detailed stratigraphic data are available (Gradstein et al. 1994).

Few papers on neritic faunas are included because benthic faunas at these depths are more geographically variable and planktonic zonation is commonly difficult; therefore, it is not possible to determine whether observed faunal change can indeed be correlated to the late Paleocene extinction in the deep sea. For instance, papers on neritic to brackish water Paleogene faunas from the northern North Atlantic were not included (Berggren 1974a; Murray 1989). Data on neritic sections in Egypt (Speijer 1994; Speijer et al. 1996a,b) were included because detailed carbon isotope data are available (Charisi and Schmitz 1995; Schmitz et al. 1996). Data from Spain (Molina et al. 1992; Ortiz and McDougall 1991) were tentatively included because planktonic foraminiferal data suggest that benthic extinctions were at least close in time to the extinction in the deep sea. Data from coastal New Jersey were tentatively

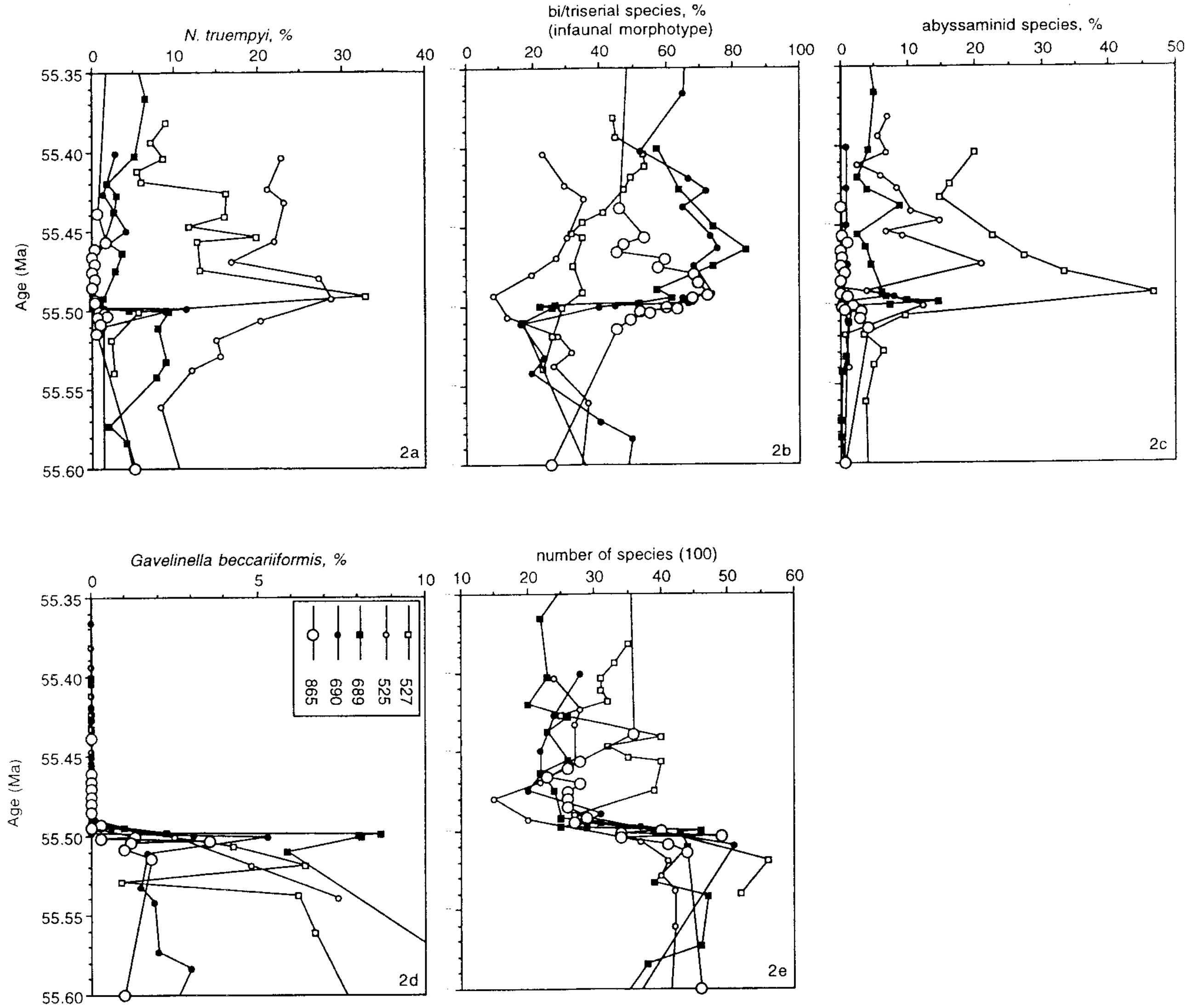

Figure 12.2 Comparison of the species richness and relative abundance of significant taxa at the time of the late Paleocene benthic foraminiferal extinction. See text for derivation of the age model.

Data for DSDP Sites 525 and 527 and ODP Sites 689 and 690 after Thomas and Shackleton (1996), with the addition of a few data points for Sites 527, 689, and 690; data for ODP Site 865 have not yet been published.

included (Olsson and Wise 1987; Gibson et al. 1993; Gibson and Bybell 1994) because the clay mineral record at these sites may be a means of correlation to ODP Site 690 (Robert and Kennett 1994).

Results

High-Resolution Studies

At ODP Sites 689 (paleodepth 1100 m) and 690 (1900 m), DSDP Sites 525 (1600 m) and 527 (3400 m), and ODP Site 865 (1300–1500 m) benthic foraminiferal diversity dropped precipitously at the extinction level, with 35 to 50% of species becoming extinct (figures 12.2 and 12.3). This percentage is a minimum estimate because several nodosariid species are rare, so their ranges cannot be determined with accuracy. Some nodosariids are absent in the interval corresponding to the LPTM, but reappear higher in the section at varying levels throughout the lower Eocene section.

At both Walvis Ridge sites the extinction occurs just above the base of a level with severe dissolution, although benthic foraminifera were well preserved; planktonic foraminifera show severe dissolution and fragmentation (Thomas and Shackleton 1996). No lowering of the $CaCO_3$ percentage of the sediment occurred at Sites 689 and 865, but faunas at these sites show more etching and are less well preserved just above the

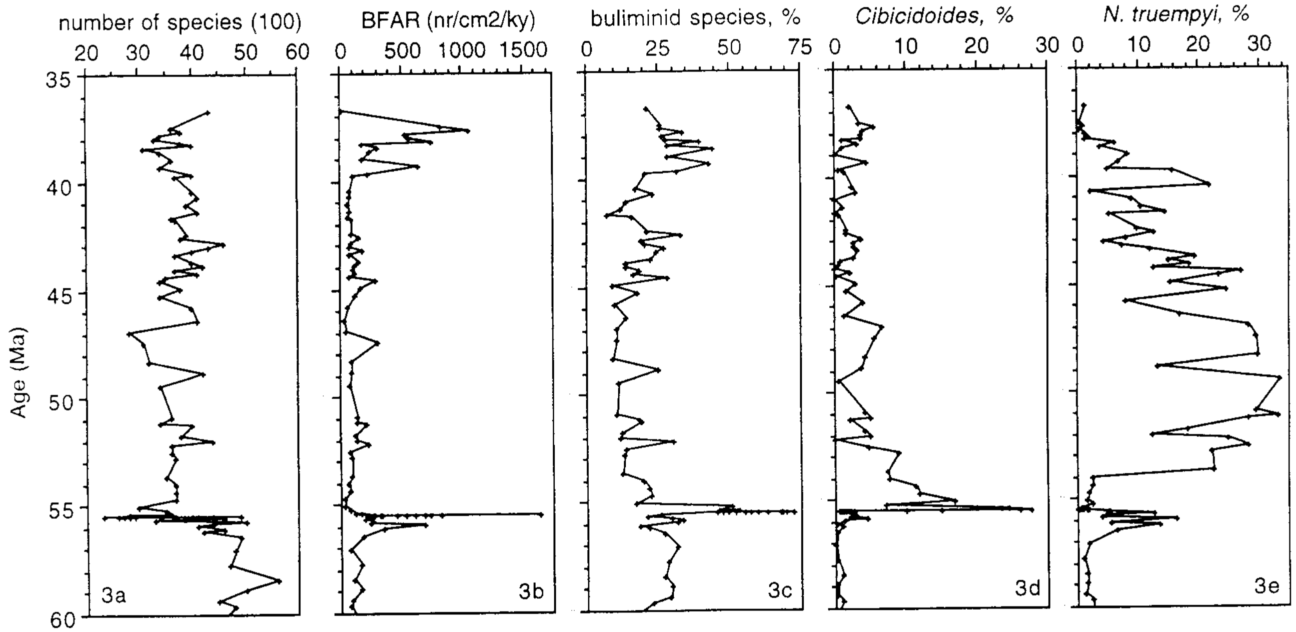

Figure 12.3 (a) Species richness at 100 specimens, (b) benthic foraminiferal accumulation rates (BFAR), and relative abundances of (c) buliminid taxa, (d) *Cibicidoides* spp., and (e) *Nuttallides truempyi* at equatorial Pacific Site 865.
Numerical ages according to Cande and Kent (1995); age model after Bralower et al. (1995a, 1995b).

extinction level. At Site 690 similar slight dissolution occurs in the faunas, and $CaCO_3$ values decrease just below the extinction level (O'Connell 1990; Thomas 1992).

At all sites, *Gavelinella beccariiformis* has its uppermost occurrence at the extinction level of several other taxa (see below). Our data confirm the observation by Katz and Miller (1991) that this species is most common at higher-latitude sites; it never reaches abundances higher than about 5% at equatorial Pacific Site 865. Other species that have their highest occurrence at this level include several large agglutinated species with calcareous cement (*Dorothia oxycona, Tritaxia havanensis,* and *Tritaxia paleocenica*) and calcareous species such as *Aragonia velascoensis, Bolivinoides delicatulus, Bulimina midwayensis, Bulimina thanetenis, Neoflabellina reticulata, Neoeponides hillebrandti, Neoeponides lunata,* and *Pullenia coryelli.*

Immediately above the extinction level, specimens are smaller and have thinner walls than below, even specimens of species that straddle the extinction interval (e.g., *Oridorsalis umbonatus* and *Nuttallides truempyi*). At ODP Sites 689 and 865 the change to smaller and thinner-walled taxa occurs a few centimeters below the highest occurrence of *G. beccariiformis*, possibly because of bioturbation. *Tappanina selmensis* and *Aragonia aragonensis* are at all sites more common above the extinction level than below (as also observed by Boersma 1984b; Speijer 1994), but their relative abundances vary strongly between sites. *Tappanina selmensis* reaches up to 40% at the Maud Rise sites, up to 15% at the Walvis Ridge sites, and up to 25% at Pacific Site 865. At all sites, peak occurrences of *T. selmensis* occur directly above the extinction level, whereas those of *A. aragonensis* occur at the top of the LPTM interval.

Despite these similarities, postextinction faunas are most notable for the major differences between sites, especially in the abundance patterns of buliminid species, *Nuttallides truempyi, Oridorsalis umbonatus, Cibicidoides* spp., and abyssaminid species (Thomas and Shackleton 1996; appendix 12.1). The postextinction faunas differ much more from site to site than the preextinction faunas, which are comparable to Velasco-type faunas at all five sites (see also Berggren and Aubert 1975; Kaiho 1988). These postextinction faunal differences cannot be completely attributed to the presence of stratigraphic gaps and comparison of noncoeval faunas, because faunas at all five sites were coeval with the short-term carbonate isotope excursion. Data were collected by one researcher, so there is homogeneity in the database with regard to taxonomic concepts and size fraction. Postextinction faunas differ more by geographic region than by depth; faunas from the two Walvis Ridge sites and the two Maud Rise sites are quite similar despite large differences in depth.

At the Walvis Ridge sites, postextinction faunas are dominated by *N. truempyi, O. umbonatus,* and abyssaminid species; the latter are especially abundant at the deepest site (figure 12.2). Abyssaminids (*Abyssamina poagi*, *Abyssamina quadrata*, and *Clinapertina planispira*) increase in relative abundance postextinction at Maud Rise, but much less than at the Walvis Ridge sites. At Pacific Site 865 these species have very low abundances throughout, with a slight further decrease at the extinction level. *Nuttallides truempyi* declines strongly in relative abundance at and just above the extinction level at the Maud Rise sites as well as at Site 865, in strong contrast with the situation in the South Atlantic. At the Walvis Ridge sites the postextinction *N. truempyi* specimens are smaller and have thinner walls than preextinction specimens, but are much more numerous than in preextinction faunas.

At the extinction level the relative abundance of the buliminid species group decreases at Site 527, does not change at Site 525, but increases strongly at both Maud Rise sites and Site 865 (figure 12.2). Above the extinction level this group is dominated by small species such as *T. selmensis*, *Bolivinoides* sp. cf. *B. decorata*, and *Bulimina simplex*. At the Maud Rise sites *Siphogenerinoides brevispinosa* is common (up to 40%) across the extinction level, at the Walvis Ridge sites it is much less common (up to 15%), and at Site 865 its abundance is similar to that at Walvis Ridge, but the species has its highest occurrence at the extinction level. *Bulimina semicostata* is abundant at Pacific Site 865 just above the extinction level, then decreases in abundance but remains present throughout the lower and middle Eocene Series. At the Maud Rise sites this species appears only in Zone NP12 (51–52 Ma, Berggren et al. 1995). In the lowermost postextinction specimens of *B. semicostata* at Site 865 the costae on the lower part of the test, typical for this species, are unusually thin and the specimens are small; possibly the species originated at this time from a noncostate, trihedral *Bulimina* species.

At Site 865 the predominance of buliminid species appears to have lasted for a shorter time than at the Maud Rise sites. At this site the interval of buliminid dominance is only 15 cm thick, representing about 10 kyr in our age model, whereas it is about 500 cm thick, representing about 100 kyr, at the Maud Rise sites. Above the buliminid-dominated interval at this site faunas are dominated by *Cibicidoides* spp. up to a level in Zone NP11 (zonal assignment in Bralower et al. 1995b; 52.85–53.61 Ma in Berggren et al. 1995; figure 12.3), where the relative abundance of *N. truempyi* increases to 12–25%. At none of the other sites is there an interval dominated by *Cibicidoides* species (up to 30%). The taxonomy of these *Cibicidoides* species is still under investigation; they resemble large, flat shallow-water European species such as *C. proprius* (Brotzen 1948).

A detailed record of planktonic foraminifera and isotopes is available from southern Indian Ocean ODP Site 738 (Lu and Keller 1993), but the benthic foraminiferal record is limited. Immediate postextinction faunas are very poorly preserved because the extinction occurs within a layer with very strong dissolution. I observed very common small, buliminid species (including *T. selmensis* and *B. simplex*) just above the extinction level, suggesting that the faunal patterns at this site resemble those at Maud Rise.

Detailed data on faunas with age control by the LPTM carbon isotope excursion are available for the Zumaya and Caravaca sections in Spain (Canudo et al. 1995; Ortiz 1995; appendix 12.2). In both sections strong dissolution occurs at the extinction level, as indicated by the presence of dark gray, laminated shales. Faunas just above the extinction level of *G. beccariiformis* are dominated by the agglutinated species *Haplophragmoides retrosepta*. At Zumaya, above the dissolution interval there is a thin interval with common *Bulimina tuxpamensis* (*Bulimina* spp. Assemblage); higher *N. truempyi* is dominant. At Caravaca *N. truempyi* is not as common as at Zumaya, and it is accompanied by *Anomalinoides capitatus* and *Oridorsalis umbonatus*. The *Bulimina* spp. Assemblage may have persisted somewhat longer at the somewhat shallower Caravaca section than at Zumaya, but for this part of the section age control is not as precise, and short-term changes in sedimentation rates may obscure the pattern.

In the Tawanui Section (New Zealand; Kaiho et al. 1993, 1996; appendix 12.2) the benthic extinction occurs in laminated, dark gray, organic carbon-rich shales. Age control is provided by recognition of the LPTM $\delta^{13}C$ excursion in terrestrial organic matter. Within a 4-cm interval directly above the highest occurrence of *G. beccariiformis* faunas are dominated by *Bulimina tuxpamensis* and *Praeglobobulimina pupoides*. Above the *Bulimina* spp. Assemblage there is an ~80-cm-thick interval with very strong dissolution, in which faunas are dominated by agglutinant taxa (*Rhabdammina* spp., *Conotrochammina depressa*, and *Reophax regularis*). Higher in the section faunas are more diverse, with common *Cibicidoides* spp., *Anomalinoides* spp., and *B. tuxpamensis*.

We can conclude from these high-resolution studies that postextinction faunas are characterized by low diversity, and that geographic differences cannot be attributed to insufficient age control, differing taxonomic concepts, or differing size fractions studied. With this in mind, we can try to evaluate the lower-resolution data available in the literature.

Literature Data

Beckmann (1960) was the first author to recognize the importance of the benthic foraminiferal extinction at the end of the Paleocene Epoch, based on his study of the bathyal Lizard Springs Formation (Trinidad). His data (as given in Bolli et al. 1994) show a very strong increase in highest occurrences as well as a decrease in lowest occurrences of benthic foraminifera in the upper Paleocene *Morozovella velascoensis* Zone, close to the Paleocene/Eocene Series boundary (Bolli et al. 1994). Benthic foraminiferal faunas in the overlying zone have a much lower diversity. There are more last appearances of agglutinated, nodosariid, and rotaliid taxa than of buliminid taxa (figure 12.4). Another early recognition of the importance of a late Paleocene benthic foraminiferal extinction event was by von Hillebrandt (1962), who noticed a strong drop in diversity of benthic foraminiferal faunas toward the top of his *M. velascoensis* Zone (Zone F) in the Reichenhall–Salzburg Basin (figure 12.5). In these sections, however, rotaliid taxa appeared to be the more common survivors.

The importance of the benthic foraminiferal extinction was recognized by many later authors (appendices 12.1 and 12.2) in studies of land sections as well as of DSDP and ODP sites in all oceans. High-resolution studies demonstrate that the extinction was a very short-term event, so comparison of faunal events between sites is problematic for data that are so disparate in chronologic resolution, age control, taxonomic concept, and size fraction studied, as presented in the appendices. However, some overall conclusions can be drawn from these data, especially in combination with the high-resolution data.

In the first place, the extinction was severe at middle bathyal through abyssal depth, with extinction of species ranging between 30 and 50%. At upper bathyal through neritic depths the extinctions were much less severe, but faunal composition changes were highly significant. These compositional changes were temporary and many species returned to the sites (Speijer 1994; Gibson and Bybell 1994).

Second, preextinction Paleocene faunas were remarkably cosmopolitan, extending over a wide depth range (Brotzen 1948; Berggren 1974a, 1974b; Berggren and Aubert 1975). The latter authors distinguished a continental shelf fauna (Midway-type) and a lower continental slope and abyssal plain fauna (Velasco-type),

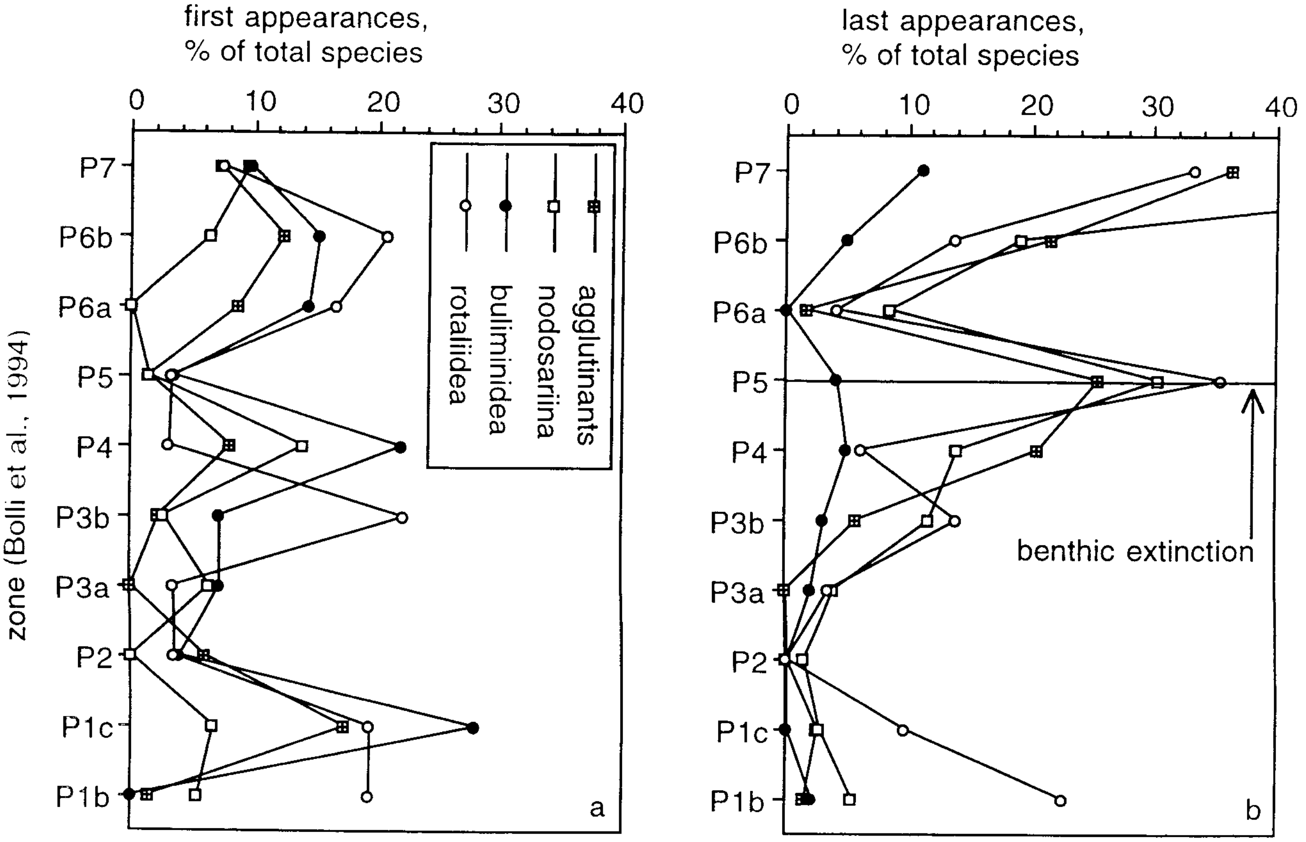

Figure 12.4 (a) Lowest and (b) highest occurrences of species belonging to the four most important groups of taxa as a percentage of the total number of species in the Lizard Spring Formation, Trinidad (Beckmann 1960; Bolli et al. 1994). The horizontal line shows the level of the benthic extinction.

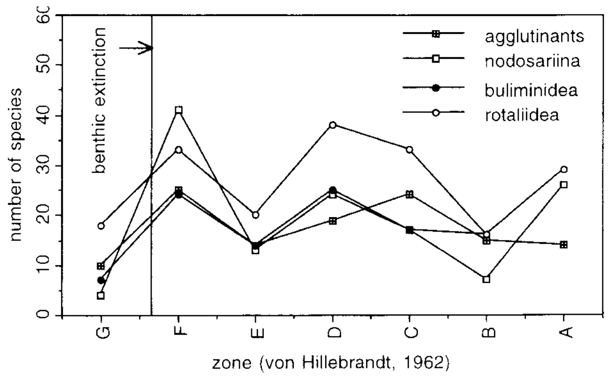

Figure 12.5 Numbers of species of the four most important groups of species in the Reichenhall–Salzburg Basin (von Hillebrandt 1962). The vertical line shows the level of the benthic extinction.

although several species (e.g., *Bulimina midwayensis* and *Coryphostoma midwayensis*) occur in both faunas (e.g., Kaiho 1988, 1991; Nomura 1991; Kaiho et al. 1993; Speijer 1994; Coccioni et al. 1994). The Midway fauna typically contains more *Cibicidoides* and especially *Anomalinoides* species, whereas the Velasco fauna has *A. velascoensis*, *Gyroidinoides* spp., *N. truempyi*, and agglutinant taxa such as *Dorothia oxycona*, *Gaudryina laevigata*, *Tritaxia havanensis*, and *Tritaxia paleocenica*. The common species *N. truempyi* generally is considered typical for the Velasco fauna (below about 500 m). *Tappanina selmensis* occurs from the shelf (about 100 m) down to abyssal depths, but is rare in bathyal–abyssal faunas below the level of the extinction. Both Midway and Velasco faunas are characterized by extremely high diversities, the occurrence of many rare taxa (especially nodosariids), and thick-walled calcareous taxa.

Third, there were geographic differences in faunal assemblages in spite of the cosmopolitan occurrence of many species. *Gavelinella beccariiformis*, for instance, appears to be more common at high-latitude than low-latitude sites (Katz and Miller 1991), although it was also common in the Tethys (Speijer 1994). *Aragonia velascoensis* is extremely rare at both Maud Rise sites, whereas *S. brevispinosa* is abundant at these sites, but shows large fluctuations in relative abundance (Thomas 1990a, 1990b). The geographic differences have not been well evaluated; the availability of more oceanic drill sites in depth transects would help in separating depth from geographic effects, and in distinguishing Paleocene biogeographic provinces, possibly similar to those in the latest Cretaceous Period (Widmark 1995).

Fourth, this high degree of faunal cosmopolitanism ended with the late Paleocene extinction (Kaiho 1988; Thomas 1992; Thomas and Shackleton 1996). This apparent difference in provinciality between late Paleocene and early Eocene faunas might be thought to result at least partly from the lack of a monograph on the early Eocene benthic foraminiferal taxonomy comparable to that of Berggren and Aubert (1975) for the late Paleocene Epoch, so that there are greater differences in taxonomic concepts between authors. This cannot be the full explanation, however, because greater differences between early Eocene faunas from different locations have been observed in faunas studied by one investigator (Tjalsma and Lohmann 1983; Kaiho 1988; Katz and Miller 1991).

Finally, postextinction faunas were of low diversity and high dominance, in stark contrast with the highly diverse, low-dominance preextinction faunas. The postextinction community thus has a structure typical for faunas affected by a major environmental perturbance (e.g., Pearson and Rosenberg 1978). In these perturbed communities the species *T. selmensis* and *A. aragonensis* are common to abundant everywhere below shelf depths (appendices 12.1 and 12.2; Boersma 1984a).

Otherwise, few faunal observations are valid on a worldwide basis. The postextinction pattern as seen by Tjalsma and Lohmann (1983) and Katz and Miller (1991), i.e., dominance by *N. truempyi* with survivor species such as *O. umbonatus*, appears to be typical for the South Atlantic and possibly Gulf of Mexico; abyssaminid taxa are common below about 2500 m in this type of assemblage. Thomas (1990a, 1990b) suggested that this association might be seen only in studies using the large size fraction (>150 μm) because many of the buliminid taxa are small. High-resolution data in Thomas and Shackleton (1996) and this chapter (figure 12.2) show that this is incorrect, and that faunas are dominated by *N. truempyi* and abyssaminids even though the >63-μm fraction is studied, as was also observed by Müller-Merz and Oberhänsli (1991).

Patterns in the North Atlantic are more variable. Most North Atlantic data are from the Goban Spur–Bay of Biscay Sites, and postextinction faunas vary from buliminid dominated to *N. truempyi* dominated. Possibly, the two types of faunas can be differentiated by depth: Buliminid-dominated faunas appear to occur at middle bathyal and shallower bathyal depths (DSDP Sites 548, 549; Reynolds 1992; Boltovskoy et al. 1992), whereas *N. truempyi*–dominated faunas occur at lower bathyal through abyssal sites (Schnitker 1979; Pak and Miller 1992; appendix 12.1). All these sites, however, show increased dissolution and occurrence of unconformities in the lower Eocene stratigraphic record, which makes faunal comparisons more difficult (Aubry et al. 1996).

Bathyal land sections close to the Bay of Biscay (Coccioni et al. 1995; Ortiz 1995) show buliminid-dominated postextinction faunas, although the pattern is complicated by the occurrence of agglutinated faunas in an interval of severe dissolution. In New Jersey margin DSDP Site 605 *N. truempyi*–dominated faunas occur above the extinction level (Hulsbos 1987; Thomas unpublished data). Shelf faunas (Olsson and Wise 1987; Gibson et al. 1993) in the region show common *Epistominella*, *Pulsiphonina*, and *Turrilina*, and cannot easily be compared to the deeper faunas; coastal sections generally have unconformities at the extinction level (Gibson and Bybell 1994). The postextinction faunas from Trinidad are buliminid dominated (Beckmann 1960; Bolli et al. 1994).

In conclusion, we can speculate that the northern Atlantic abyssal to lower bathyal faunas were similar to South Atlantic faunas (*N. truempyi*–dominated), whereas they were buliminid dominated in the upper- to mid-bathyal reaches. We cannot be certain, however, that we are indeed comparing coeval faunas because dissolution and unconformities are common.

The bathyal faunas in the North Sea (depths 750–1000 m) were dominated by noncalcareous agglutinated taxa through the late Paleocene and early Eocene epochs (Charnock and Jones 1990; Gradstein et al. 1994). These agglutinated taxa underwent a period of severe extinction close to the Paleocene/Eocene Epoch boundary, after which extremely impoverished, low-diversity, agglutinant faunas remained (e.g., Charnock and Jones 1990; King 1989; Gradstein et al. 1994). Direct postextinction sediments indicate strong $CaCO_3$ corrosiveness and dysoxic to anoxic conditions (Charnock and Jones 1990; Schroeder 1992). At somewhat shallower levels (100–500 m) calcareous taxa (including *G. beccariiformis*) were present during the Paleocene Epoch (King 1989). These faunas were replaced by extremely low-diversity agglutinated faunas similar to those from deeper regions. The timing of the disappearance of the calcareous taxa is difficult to establish because of the biostratigraphic complexity of the North Sea region (Gradstein et al. 1994; Berggren and Aubry 1996). The local North Sea disappearance of *G. beccariiformis* probably did not predate the global extinction of *G. beccariiformis* at the LPTM by very much time because it can be correlated to the lower part of dinoflagellate Zone D5 (King 1989), which has been correlated to just below the middle part of nannofossil Zone NP9. Palynological studies indicate the occurrence of a peak warm period somewhere in dinoflagellate Zone D5 (thus Zone NP9; Schroeder 1992), which might possibly be correlated to the LPTM in mid-Biochron NP9 (Aubry et al. 1996).

Tethyan faunas are known from land sections only (appendix 12.2). Sections in the eastern Tethys (Speijer 1994) from a depth range of 500–1000 m show postextinction faunas with common *N. truempyi*, *Anomalinoides* species, and *Cibicidoides*. Shallower faunas (100–300 m) contain more buliminids, but on the shelf *Cibicidoides* spp. and especially *Anomalinoides aegyptiacus* dominate. Sections in Spain (Ortiz 1995) and Italy (Braga et al. 1975; Di Napoli et al. 1970; 500–1500 m depth) show strongly increased percentages of buliminids above the extinction level, including *Bulimina semicostata*. Faunas from the Reichenhall–Salzburg Basin (von Hillebrandt 1962; 200–800 m) show increased abundance of rotaliid taxa, but detailed stratigraphy is not available from these sections. We can conclude tentatively that western Tethys faunas were similar to North Atlantic faunas from the same depth.

In the Indian Ocean, no simple faunal pattern can be extracted, particularly because many DSDP and ODP sites have records with poor recovery and unconformities. Faunas at some lower bathyal–abyssal sites (appendix 12.1) seem to resemble South Atlantic faunas (*N. truempyi*–dominated), but abyssaminids are much less common or absent, possibly because no lower abyssal sites are available. Other taxa in the postextinction faunas are mostly long-term survivors such as *O. umbonatus*, although *B. semicostata* may be present above the extinction level. Faunas at upper and middle bathyal sites (appendix 12.1) have very different postextinction faunas, dominated by *Lenticulina* species (Mackensen and Berggren 1992) or by *Anomalinoides* species (similar to faunas in the eastern Tethys; Speijer 1994). Such faunas dominated by *Anomalinoides* species have been interpreted as indicating low-oxygen conditions or high productivity (Speijer et al. 1996b; Nomura and Kennett, personal communication 1995). At all these sites, however, core recovery was poor and the existence of the LPTM $\delta^{13}C$ excursion has not been fully documented. High-latitude ODP Site 738 (1350 m), however, where the carbon isotope excursion is present (Lu and Keller 1993), has the buliminid-dominated pattern of the Maud Rise sites.

Data on the Pacific Ocean are available from few sites only at bathyal depths. Northern Pacific ODP Site 883 (Pak and Miller 1995; 1000–2000 m) has a poor upper Paleocene record and an unconformity, but its postextinction faunas appear to be of the *N. truempyi*–dominated type. Faunas at DSDP Site 577 (Pak and Miller 1992; Kaiho in press; 1800–2100 m) have common *Bulimina semicostata* above the extinction level, although buliminid percentages are much lower than at Site 865. At this site, however, a 0.5-m section in the critical interval was not recovered (between Cores 9 and 10 in Hole 577), and the section probably contains unconformities (Aubry, personal communication 1995). Sites 577 and 865 (described above) thus have buliminid-dominated faunas. Land sections in Japan and New Zealand (500–1500 m; Kaiho 1988; Kaiho et al. 1993,

1996) show buliminid-dominated faunas, although complicated by dissolution intervals with agglutinated taxa.

Data on the neritic faunas do not indicate a relationship between the benthic extinction (thus the LPTM) and changes in sea level. The extinction event occurred during the second order supercycle TA2 of Haq et al. (1987), and might have been coeval with part of short-term third-order cycle 2.3, in mid-nannofossil Biochron NP9. Speijer (1994) and Speijer et al. (1996b) did not observe significant sea-level effects in neritic sections in Egypt. European and North American sections have many unconformities in their upper Paleocene–lower Eocene stratigraphic record (e.g., Olsson and Wise 1992; Gibson and Bybell 1994; Berggren and Aubry 1996), suggesting that sea level was relatively low at the time. In the northern Spanish sections the benthic extinction event has been correlated to a lowstand (Pujalte et al. 1995). It has been proposed, however, that sea-level trends in the North Atlantic reflected the development and collapse of the Iceland Plume under the North Atlantic Volcanic Province, and thus were regional rather than global (Nadin and Kusznir 1995).

Discussion and Speculation on $CaCO_3$ Dissolution, Productivity, and O_2 Levels

$CaCO_3$ Dissolution

The global data set on the benthic foraminiferal extinction event is incomplete and requires high-resolution studies to describe in detail the events that occurred during the LPTM. Data are needed from sites located on depth transects in order to discriminate between depth and geographic effects. Most information is from sites at lower bathyal depths (figure 12.6a), with few data from abyssal depths. Geographically, most data are from the North and South Atlantic oceans. Coverage in the Pacific Ocean is extremely poor, data being available only from middle to lower bathyal depths (figure 12.6b). Coverage is slightly better for the Indian Ocean, but recovery is poor at many sites. In addition, taxonomic concepts for the postextinction faunas, specifically for *Bulimina* spp., *Cibicidoides* spp., and *Anomalinoides* spp., needs to be uniformized between researchers before global patterns can be established with any degree of confidence.

Combining lithological and paleontological data in this incomplete set, however, suggests that a remarkable global episode of carbonate dissolution occurred at least partially coeval with the LPTM (figure 12.7). In the North Sea region calcareous species occurred only in the shallowest neritic areas of the time (King 1989; Gradstein et al. 1994). This severe dissolution has commonly been attributed to local factors such as basin restriction, which certainly may have contributed, but the severe dissolution occurred synchronously with worldwide dissolution. In the eastern Tethys (Egypt), Speijer (1994) observed dissolution layers over a wide depth range, Benjamini (1992) reported such layers from the north central Negev (Israel), and Berggren and Aubry (1996) from the Khieu River section in Georgia (NW Caucasus). Similar dissolution intervals occur in land sections in Spain (Tethys and Atlantic sides; Coccioni et al. 1994; Canudo et al. 1995).

Dissolution is more difficult to trace in DSDP and ODP sites than in land sections because poor recovery is a problem. A thin layer (<50 cm) of sediment may not be recovered, and therefore many sites are listed as "no data" in figure 12.7 and appendix 12.1. We cannot be sure of the full geographic and bathymetric extent of carbonate dissolution, but it was extensive in and around the Atlantic Ocean, as well as at least in parts of the Indian Ocean, along the Tethys margin, and along the Pacific margins. We have no data on the Pacific deep basin floors, which were probably below the CCD during most of the Paleocene and Eocene epochs (e.g., as shown by red clays in Core LL44-GPC 3, Rea 1994). We cannot be sure about the exact timing of the initiation of this increased dissolution, but it may have started slightly before the LPTM (Thomas 1992; Thomas and Shackleton 1996; Kaiho et al. 1996).

The occurrence of such widespread $CaCO_3$ dissolution during a period of warming is unexpected because rising temperatures alone would result in decreased solubility of calcite (e.g., Broecker and Peng 1984). Therefore, the occurrence of widespread dissolution strongly indicates massive addition of carbon to the ocean–atmosphere reservoir, and the pattern of dissolution (more severe around the Atlantic, less in the Pacific) resembles that predicted to result from massive burning of fossil fuel and deforestation (e.g., Walker and Kasting 1992). The occurrence of the extremely negative carbon isotope anomaly in this interval of dissolution suggests that the added mass of carbon must have been isotopically unusually light. The amount of biosphere-derived organic carbon needed to cause such a large isotopic anomaly would have to be reflected in widespread destruction of land biomass, which does not agree with paleontological evidence (Thomas and Shackleton 1996). Therefore, widespread carbonate dissolution associated with the $\delta^{13}C$ excursion supports the speculation that dissociation of methane hydrates (and their oxidation of methane to CO_2) may have been involved (Dickens et al. 1995; Kaiho et al. 1996). This speculation implies that the temperature increase of the deep waters preceded the carbon isotope excursion slightly, in agreement with Thomas and Shackleton (1996).

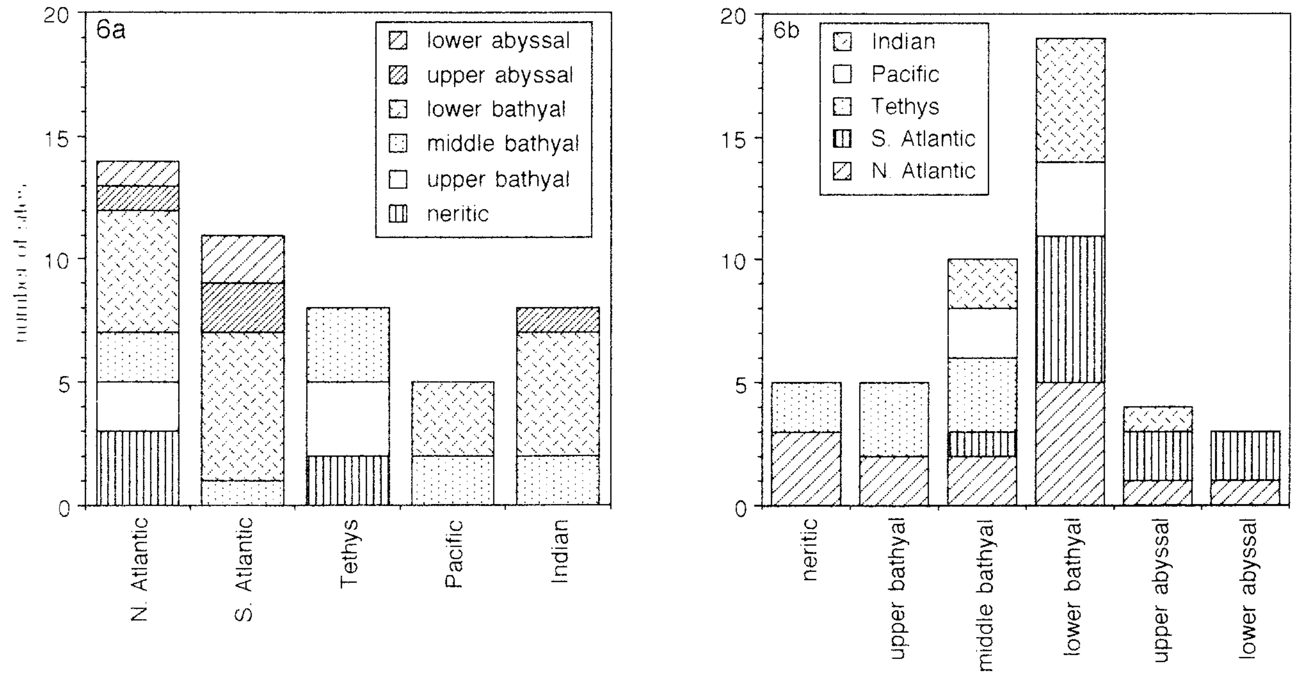

Figure 12.6 Distribution of sites listed in appendices 12.1 and 12.2 according to (a) depth and (b) geographic location.

The depth categories are after van Morkhoven et al. (1986): neritic, 0–200 m; upper bathyal, 200–600 m; middle bathyal, 600–1000 m; lower bathyal, 1000–2000 m; upper abyssal, 2000–3000 m; lower abyssal, >3000 m. Plotted was the midpoint of the paleodepth range for each site, as estimated by the authors of the original papers and given in appendices 12.1 and 12.2.

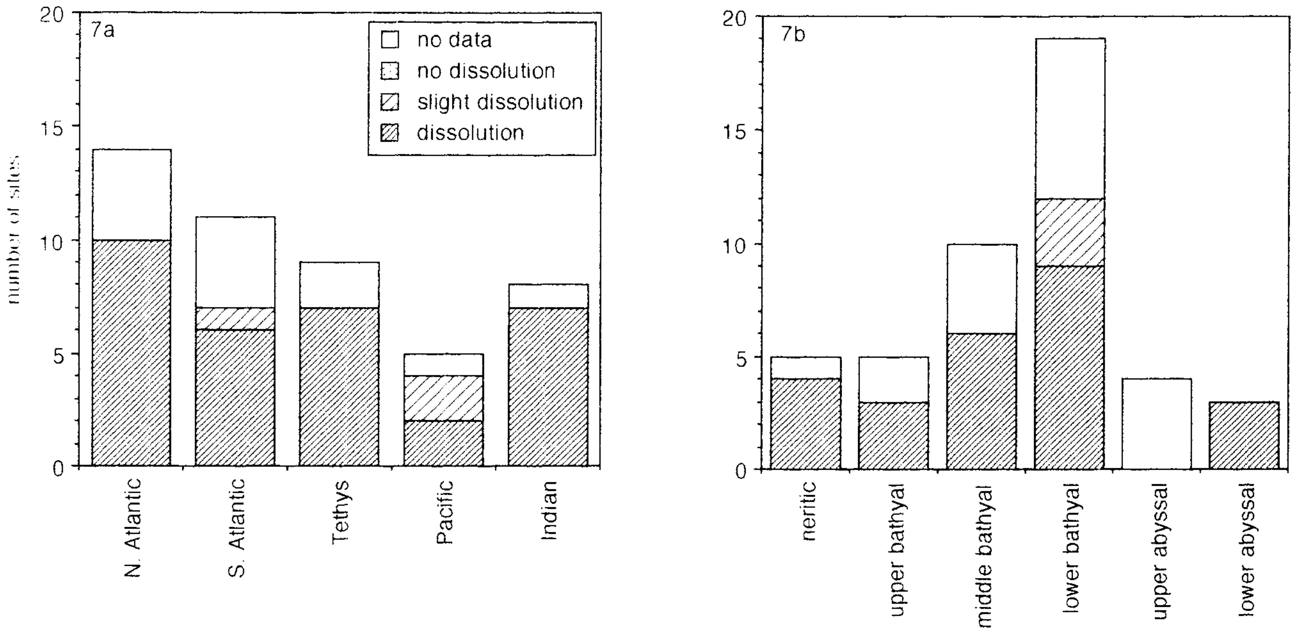

Figure 12.7 Occurrence of dissolution across the interval of the benthic foraminiferal extinction by (a) depth and (b) geographic location: sites listed in appendices 12.1 and 12.2, depth categories as in figure 12.6.

Dissolution: decrease in $CaCO_3$ content of the sediment by 30% or more: occurrence of black or dark gray, laminated shales. Slight dissolution: increased dissolution and etching of microfaunas, but no clear sedimentary evidence.

Such an increase of the ocean–atmosphere carbon reservoir is in contradiction with Stott's interpretation (1992) of data on the carbon isotopic composition of organic matter in foraminiferal tests, although such data cannot be easily interpreted (Goericke and Fry 1994; Hinga et al. 1994). Stott's data (1992) might be explained by many factors, such as species-specific effects, diagenetic effects, effects of varying temperature, or salinity. More problematic for the methane hydrate hypothesis might be the precise timing and sequence of events during the LPTM; dissolution appears to have preceded the $\delta^{13}C$ anomaly.

Dissolved Oxygen Levels and Productivity

What caused the benthic foraminiferal extinction, and what can explain the biogeographic patterns observed? This is a difficult question to answer because there is no agreement on the interpretation of Recent benthic faunas (see e.g., Gooday 1994, Schnitker 1994, for reviews). There is no modern analog for faunas dominated by *N. truempyi* because this species became extinct in the late Eocene Epoch. Its modern relative, *Nuttallides umbonifera*, is common to abundant in $CaCO_3$-corrosive waters, and specifically in Antarctic bottom water (e.g., Bremer and Lohmann 1982; Schmiedl 1995). Others, however, have described *N. umbonifera* as a typically oligotrophic species (Loubere 1991, 1994; Gooday 1993, 1994). Possibly, the waters in which *N. umbonifera* is common are $CaCO_3$ corrosive because of the presence of abundant dissolved CO_2 derived from oxidation of organic matter, leaving little food for benthic faunas, thus combining oligotrophy and corrosiveness. Some support for the view that *N. truempyi* may have been an oligotrophic indicator may be seen in its Eocene distribution pattern: This species had its highest abundance during the middle Eocene Epoch (e.g., figure 12.3; Kaminski et al. 1989; Berggren and Miller 1989; Miller et al. 1992). It then declined in abundance and became extinct during the late Eocene Epoch, at a time when global productivity may have increased considerably (e.g., Hallock 1987; Hallock et al. 1991; Aubry 1992; Brasier 1995; Thomas and Gooday 1996).

In the Recent oceans, low-diversity faunas dominated by small, thin-walled specimens belonging to the buliminid group commonly occur in low-oxygen environments (e.g., Boltovskoy et al. 1991; Sen Gupta and Machain-Castillo 1994; Kaiho 1994a). Such environments usually occur below a well-developed oxygen minimum zone, where oxygen levels are low because of enhanced productivity and oxidation of organic matter, and where $CaCO_3$ dissolution may be severe because of the high concentrations of dissolved CO_2 resulting from this oxidation (e.g., Mullins et al. 1985; Hermelin and Shimmield 1990; Levin et al. 1991; Schmiedl 1995; Wishner et al. 1995). There is considerable discussion whether such benthic faunas reflect the low oxygen levels or the high food supplies (e.g., Corliss et al. 1986; Linke and Lutze 1993; Miao and Thunell 1993; Loubere 1994; Rathburn and Corliss 1994; Jorissen et al. 1995). Recent species of *Bulimina* are particularly common in areas with high rates of deposition of nondegraded organic matter (Corliss and Chen 1988; Caralp 1989; Corliss 1991; Mackensen et al. 1993). Additional factors of importance might be the lack of metazoan predators under low-oxygen conditions (Wishner et al. 1995), and some thin-walled taxa have been described as being opportunistic taxa rather than directly linked to high productivity or low oxygen (Alve 1994; Gooday 1994).

We thus cannot determine from the benthic faunas alone whether the buliminid-dominated postextinction faunas primarily reflect low-oxygen conditions, high-productivity conditions, stressed conditions, or high $CaCO_3$ corrosiveness. Similarly, we cannot determine whether the *N. truempyi*–dominated fauna reflects the occurrence of $CaCO_3$-corrosive waters or low productivity. We need to consider evidence from co-occurring planktonic organisms and sedimentary and isotopic evidence in order to evaluate the most probable causes for the extinction, and compare data on dissolution with those on benthic faunas (figures 12.7 and 12.8).

It appears probable that the occurrence of small and thin-walled benthic foraminifera following the benthic extinction primarily reflects increased $CaCO_3$ corrosiveness of deep waters because both dissolution and thin-walled tests occurred at almost all locations (figure 12.7), and the association of thin-walled tests with corrosive waters is well documented (Boltovskoy et al. 1991). Proxies for high productivity or lower dissolved oxygen levels are not as common as for dissolution, and thus neither can be seen as the dominant factor controlling the occurrence of the thin-walled taxa (figure 12.8). In addition, ostracodes, which are complex metazoans, became thin-walled during the LPTM at ODP Site 689 at the same time as the benthic foraminifera (protistans) did. Ostracodes have been shown to form such "degraded" tests in hydrochemical regimes unfavorable to biomineralization, i.e., in $CaCO_3$-corrosive waters (Steineck and Thomas 1996).

Increased corrosiveness thus probably played a role in the extinction. It has been hypothesized that the benthic foraminiferal extinction was largely caused by decreased levels of dissolved oxygen (Thomas 1989), and a parallel has been established with the Cretaceous anoxic oceanic events, although of lesser intensity (Kaiho 1994b). The LPTM benthic extinction occurred

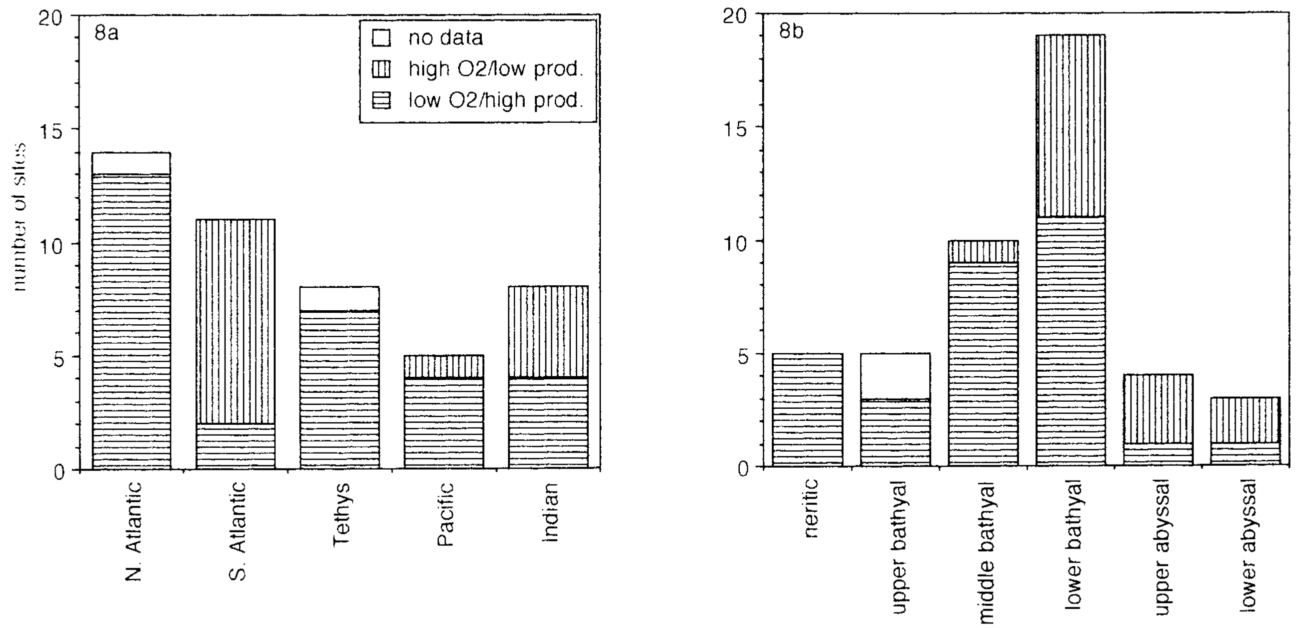

Figure 12.8 Occurrence of benthic faunas suggesting either low-oxygen conditions or increased productivity by (a) depth and (b) geographic location; sites listed in appendices 12.1 and 12.2, depth categories as in figure 12.6.

during rapid warming of the deep waters, possibly caused by a switch to dominant formation at subtropical latitudes of warm and saline deep to intermediate waters (e.g., Thomas 1989; Kennett and Stott 1991; Pak and Miller 1992, 1995). Warmer deep waters can be predicted to have a lower oxygen content because of the strong decrease in solubility of oxygen at higher temperatures (Thomas 1989, 1990a; Kaiho 1991). If the speculation about dissociation of methane hydrates is correct (Dickens et al. 1995; Kaiho et al. 1996), oxidation of these compounds would have used large amounts of oxygen and thus have contributed to the creation of low-oxygen environments. There is no agreement between the distribution of dissolution and that of low-oxygen conditions and/or high productivity with regard to depth and paleogeography (figures 12.7b and 12.8b).

The buliminid-dominated faunas, however, did not occur globally. Faunas indicating either high productivity or low oxygen contents were most common in the North Atlantic over a wide range of depths (with possible exception of abyssal sites), along Tethys, along the Antarctic continent, in the central Pacific, and at upper to middle bathyal depths in the Indian Ocean (figure 12.8). Faunas dominated by *N. truempyi* were common in the South Atlantic, and occurred in the northernmost Pacific and at middle to lower bathyal depths in the Indian Ocean. It is difficult to interpret such patterns because of the small number of localities to compare: The North Atlantic DSDP sites, for instance, are all close to the continents (Bay of Biscay, New Jersey margin), whereas the South Atlantic sites are mainly along oceanic ridges and rise (figures 12.1 and 12.6; appendix 12.1). We thus cannot determine whether the differences in distribution patterns between the North and the South Atlantic are true geographic differences between deep waters in these basins, or the differences between open ocean and margin. The lack of indications that South Atlantic waters were especially low in oxygen content, however, may suggest that warm and saline waters did not dominantly flow from subtropical regions of Tethys into the Atlantic. If Tethys functioned as a source area, the more probable region of outflow was the eastern Tethys, in agreement with carbon isotope data (Seto 1995). On the other hand, agglutinated benthic foraminiferal assemblages do support a Tethys–Atlantic connection (Kaminski et al. 1996).

It remains that faunal patterns were not globally the same, and, consequently, decreased oxygen content as a result of global deep-water warming does not fully explain the faunal changes and the benthic extinction. Thomas and Shackleton (1996) used carbon isotope data to interpret the postextinction, buliminid-dominated faunas at the Maud Rise sites as indicative of a high rate of supply of organic matter to the seafloor. This hypothesis appears to be in contradiction with the view that the Paleocene long-term carbon isotope record reflects a decrease in productivity (e.g., Shackleton et al. 1985; Shackleton 1986; Corfield and Shackleton 1988; Corfield and Cartlidge 1992; Corfield 1995), a view that is in agreement with biogeographical patterns of planktonic microfossils (e.g., Hallock 1987; Boersma et al. 1987; Hallock et al. 1991; Ottens and Nederbragt 1992; Brasier 1995). Theoretically, one would expect extremely low productivity during the LPTM, when temperature gradients were shallow, so that wind velocities over the equatorial regions were very low and upwelling and nutrient supply to the surface waters were almost null (chapter 9). In addition, benthic foraminifera have higher metabolic rates at higher temperatures and increased temperatures thus lead to oligotrophy.

Thomas and Shackleton (1996), however, argued that global productivity might have declined, but that the carbon isotope records at the Maud Rise sites suggested increased local upwelling, and thus possibly enhanced local productivity. Along other continental margins productivity might have also increased during the LPTM, possibly caused by changed patterns of upwelling as a result of changing patterns of deep-intermediate water circulation. High abundances of chiloguembelinid planktonic foraminifera in lowermost Eocene sediments in the Bay of Biscay and along the New Jersey margin have been interpreted as indicating increased local productivity and an expanded oxygen minimum zone (Saint-Marc 1991a, 1991b; Pardo et al. 1997). Productivity may also have increased locally in the eastern Tethys, where typically a "flood of radiolarians" occurs in the dissolution layer (Benjamini 1992; Berggren and Aubry 1996). At Indian Ocean Sites 738, 752, and 762 the abundance of chiloguembelinid planktonic foraminifera also increases above the extinction level (Nomura and Kennett, personal communication 1995). In other eastern Tethys sections, however, benthic faunas suggest low-oxygen conditions as well as increased productivity (Speijer et al. 1996b).

Local increased productivity during the LPTM in spite of the decreased temperature gradients could have resulted from an increased influx of nutrients from the continents. An increased abundance of kaolinite in the sediments deposited during the LPTM indicates enhanced precipitation and chemical weathering around the world (e.g., Robert and Kennett 1994; Gibson et al. 1993; Kaiho et al. 1996), in agreement with climate modeling (chapter 9). The higher rainfall could have led to increased runoff and nutrient supply to coastal waters; the increased influx of fresh water could also have increased water stratification and caused local shelf or slope anoxia (Malone 1991; van der Zwaan and Jorissen 1991).

Increased productivity cannot be seen as the cause of all occurrences of buliminid-dominated faunas: at equatorial Pacific ODP Site 865 planktonic foraminiferal faunas and coccolithophorids indicative of extreme oligotrophy occur in the same samples as buliminid-dominated benthic faunas (Kelly et al. 1996). At such sites the faunas probably reflect low-oxygen conditions in the water column. Such low-oxygen waters in the bathyal open Pacific may have resulted from the high temperatures (e.g., Thomas 1990a; Kennett and Stott 1991), their formation possibly exacerbated by sluggish circulation due to the extremely low temperature gradients. It may also be possible, however, that the buliminid-dominated faunas reflect the input of a larger proportion of organic matter on the seafloor under lower oxygen conditions, as supported by the strong increase in benthic foraminiferal accumulation rates at the level of extinction at Site 865 (figure 12.3; Herguera and Berger 1991).

The peak abundance in buliminid species at ODP Site 865 is just below a peak abundance of *Cibicidoides* species that was not observed at other sites. The *Cibicidoides* specimens resemble the Recent species *C. wuellerstorfi*, which lives on elevated supports above the sediment–water interface and is most common in regions with active bottom currents (Linke and Lutze 1993). If the earliest Eocene *Cibicidoides* had a similar habitat, its high abundance might indicate increased bottom current activity and winnowing, as also indicated by increased percentages of material in the >63-μm size fraction, low accumulation rates, and intensive reworking of planktonic foraminifera (Kelly et al. 1996).

The widespread occurrence of the *N. truempyi*–abyssaminid faunas can be tentatively explained as reflecting increased corrosiveness of bottom waters, as shown by the occurrence of widespread $CaCO_3$ dissolution (figure 12.6). These faunas, however, might also reflect an overall decline in open-ocean productivity during the LPTM. The pattern observed by Tjalsma and Lohmann (1983), that *N. truempyi*–dominated faunas migrated to shallower depths in the oceans during the late Paleocene Epoch, could be explained by the hypothesis that organic matter derived from the surface waters became exhausted at shallower and shallower levels in the oceans because of the declining productivity, as also suggested by agglutinated microfaunas (Kaminski et al. 1996). This pattern was not global, and was not observed, for instance, at Falkland Plateau Sites 698–702 (Katz and Miller 1991).

The question remains open concerning the significance of faunas containing common to abundant *Tappanina selmensis*, a species that occurs in postextinction faunas worldwide over a large depth range but was common only at neritic to upper bathyal depths before the extinction. Although it might be seen as a part of the buliminid-dominated faunas, this is not a satisfactory explanation because the species occurs in *N. truempyi*–

dominated assemblages as well. At ODP Site 689 it is most abundant together with an ostracode fauna dominated by taxa related to the present-day propontocyprids (Steineck and Thomas 1996). Propontocyprids are opportunistic forms that live dominantly in neritic environments. They are confined in the deep sea to wood-based and hydrothermal vent communities that form in transient, food-rich environments. I therefore suggest that *T. selmensis*, originally described from shallow-water regions, was likewise an opportunistic taxon rather than a low-oxygen indicator, similar to modern taxa such as *Stainforthia fusiformis* (Alve 1994).

In conclusion, I suggest that the latest Paleocene benthic foraminiferal extinction was a complex phenomenon. Factors that contributed to the extinction may have been the global increase in $CaCO_3$ corrosiveness and the global decrease in oxygenation of neritic through abyssal waters as a result of increased temperatures. The average oceanic productivity may have declined, but sluggish circulation and low oxygenation could have led to the sequestering of organic matter in the deep sea. The upwelling of such nutrient-enriched deep waters, possibly in combination with an increase in nutrient-carrying runoff along continental margins, may have caused increased local productivity, leading to the expansion of the trophic resource continuum, i.e., the occurrence of highly oligotrophic as well as highly eutrophic conditions (Hallock 1987; Hallock et al. 1991). Benthic faunas can then be seen as reflecting both extremes, with the buliminid-dominated faunas at the eutrophic end, the *N. truempyi*–dominated faunas at the oligotrophic end, with patterns complicated by the occurrence of opportunistic taxa such as *Tappanina selmensis*.

During the LPTM, benthic foraminiferal faunas at middle bathyal and greater depths exhibited high rates of extinction (30 to 50% of species), whereas at upper bathyal through neritic depths extinction was less severe and faunas showed significant but temporary changes in species composition.

After the extinction deep-sea benthic foraminiferal faunas were typical for perturbed communities (low-diversity, high-dominance). Strong $CaCO_3$ dissolution occurred worldwide, resulting in thin-walled faunas; this dissolution might have resulted from the addition of carbon to the atmosphere–ocean system through dissociation of methane hydrates.

Two widely occurring postextinction assemblages at bathyal through abyssal depths are *N. truempyi*–dominated and buliminid–dominated. In regions where both assemblages occurred, the *N. truempyi*–dominated assemblage lived deeper (lower bathyal–abyssal).

Productivity may have decreased globally during the LPTM, but this effect could have been counteracted locally by lower oxygen levels in the water column, resulting in delivery of a larger fraction of organic matter to the seafloor. Productivity may have increased along continental margins as a result of increased continental runoff and upwelling of nutrient-enriched deep waters.

Speculatively, *N. truempyi*–dominated faunas may be seen as indicators of highly oligotrophic conditions on the seafloor, and buliminid-dominated faunas as indicators of eutrophic conditions. The occurrence of both faunas after the extinction suggests an expansion of the trophic resource continuum.

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Appendix 12.1

	Site	Location	Reference	Depth	Resolution	LPTM δ^{13}C	Size	Recovery/ Unconformity
South Atlantic								
1.1	ODP 689	Weddell Sea	Thomas 1990a; Thomas and Shackleton 1996	1100	High	Yes	>63	Medium unconformity
1.2	ODP 690	Weddell Sea	Thomas 1990a; Thomas and Shackleton 1996	1900	High	Yes	>63	Good
2.1	ODP 698	Falklands Plateau	Katz and Miller 1991	800–900	Low	No	>150	Poor
2.2	ODP 702	Falklands Plateau	Katz and Miller, 1991	1700–1800	Low	No	>150	Poor
2.3	ODP 700	Falklands Plateau	Katz and Miller 1991	2250–2600	Low	No	>150	Poor
2.4	DSDP 329	Falklands Plateau	Tjalsma 1977; Tjalsma and Lohmann 1983	1740–1745	Low	No	>150	Medium
3.1	DSDP 20C	Mid-Atlantic Ridge, west	Tjalsma and Lohmann 1983; Müller-Merz and Oberhänsli 1991	2275–3000	Low	No	>150, >63	Poor
3.2	DSDP 516	Rio Grande Rise	Dailey 1983; Tjalsma 1983; Boltovskoy et al. 1995	1000–2000	Low	No	>150, >150, >63	Good
4.1	DSDP 524	Walvis Ridge	Clark and Wright 1984; Hsu et al. 1984; Parker et al. 1984	3500–4000	Low	No	>150	Poor
4.2	DSDP 525	Walvis Ridge,	Thomas and Shackleton 1996; Boersma 1984; Boltovskoy and Boltovskoy 1989	1600	High	Yes	>63	Poor/LPTM in core
4.3	DSDP 527	Walvis Ridge,	Thomas and Shackleton 1996; Boersma 1984	3400	High	Yes	>63	Poor/LPTM in core
Pacific Ocean								
5	ODP 883	North Pacific	Pak and Miller 1995	1000–2000	Low	No	>150	Poor/ unconformity
6	DSDP 577	Subtropical North Pacific	Miller et al. 1987b; Pak and Miller 1992; Kaiho in press	1800–2100	High/ medium	Partim	>150	Good/gap unconformity
7	ODP 865	Equatorial Pacific	Bralower et al. 1995a,b; Thomas, unpublished data, this chapter	1300–1500	High	Yes	>63	Good/ unconformity?

Appendix 12.1

-Extinction	Postextinction/ Short-Term	Postextinction/ Long-Term	Low O2/ High Productivity	Dissolution
ccariiformis, B. midwayensis, uempyi, B. thanetensis, ponides spp., *S. brevispinosa*	*T. selmensis, B. simplex, A. aragonensis, S. brevispinosa*	Buliminids (*B. semicostata*), *S. eleganta, N. truempyi, O. umbonatus*	Yes	Slight
ccariiformis, R. carpentierae, anetensis, N. truempyi	*T. selmensis, B. simplex,* abyssaminids, *S. brevispinosa*	Buliminids (*B. semicostata*), *S. eleganta, N. truempyi*	Yes	Yes
ccariiformis, Cibicidoides spp., *ryelli, buliminids*		*Cibicidoides* spp., *N. truempyi, O. umbonatus*	No?	Yes
ccariiformis, Gyroidinoides spp., *idoides* spp.		*N. truempyi,* buliminids, *Lenticulina* spp., *O. umbonatus*	No?	?
ccariiformis, P. coryelli, lascoensis, Neoeponides spp.		Abyssaminids, *Cibicidoides* spp., buliminids, *N. truempyi*	No?	?
eccariiformis, P. coryelli, utinants, *Gyroidinoides* spp.	Abyssaminids, *N. truempyi, A. aragonensis*	*N. truempyi, O. umbonatus, T. selmensis, A. aragonensis, B. semicostata*	No?	?
eccariiformis, buliminids, *cidoides* spp., agglutinants	Abyssaminids, *N. truempyi, A. aragonensis*	Abyssaminids, *N. truempyi, A. aragonensis,* buliminids	No?	?
eccariiformis, P. coryelli, elascoensis, S. brevispinosa, elicatulus, N. truempyi	?	*N. truempyi, O. umbonatus, A. aragonensis, P. prolixa*	No?	Yes
beccariiformis, Neoeponides spp., utinants	?	*N. truempyi,* abyssaminids, *B. trihedra, T. selmensis*	Yes	Yes?
beccariiformis, N. truempyi, glutinants, *Neoeponides* spp., *icidoides* spp.	*N. truempyi,* abyssaminids, *T. selmensis, A. aragonensis*	*N. truempyi,* buliminids, *Cibicidoides* spp.	No	Yes
beccariiformis, A. velascoensis, truempyi, B. thanetensis	*N. truempyi,* abyssaminids, *T. selmensis*	*N. truempyi,* buliminids, *Cibicidoides* spp.	No	Yes
beccariiformis, B. midwayensis, gglutinants, *P. coryelli*	?	*N. truempyi, A. aragonensis,* abyssaminids	No?	?
beccariiformis, P. coryelli, velascoensis, B. midwayensis	? *T. selmensis, A. aragonensis, Neoeponides* spp.	*N. truempyi,* buliminids	Yes	Slight
beccariiformis, A. velascoensis, semicribratus, agglutinants	*T. selmensis, B. semicostata*	*Cibicidoides* spp. *N. truempyi,* buliminids (*B. semicostata*)	Yes	Slight

Appendix 12.1 *(continued)*

	Site	Location	Reference	Depth	Resolution	LPTM $\delta^{13}C$	Size	Recovery/ Unconformity
Indian Ocean								
8.1	ODP 747	Kerguelen	Mackensen and Berggren 1992	2000–3000	Low	No	>150	good/ unconformity
8.2	ODP 748	Kerguelen	Mackensen and Berggren 1992	600–2000	Low	No	>150	Poor
9	ODP 738	Kerguelen	Lu and Keller 1993; Nomura and Kennett personal communication; Thomas unpublished data	1350	High	Yes	>150, >63	poor/ LPTM in core
10	DSDP 245	South Madagascar Basin	Sigal 1974	600–1000	Low	No	>150	Poor
11	DSDP 237	Mascaren Plateau	Vincent and Brün 1974	600–2500	Low	No	>150	Poor
12	DSDP 215	Ninetyeast Ridge	McGowran 1974; Hovan and Rea 1992	600–2500	Low	No	>150	Good/LPTM not in core?
13	ODP 752	Kerguelen	Nomura 1991; Nomura and Kennett personal communication	500–1000	High/ medium	Partim	>150	Poor
14	ODP 762	Eastern Indian Ocean	Nomura and Kennett personal communication; Thomas unpublished data; Thomas et al. 1992	1000–1500	High/ medium	Partim	>150, >63	Poor/ disturbed
North Atlantic								
15.1	DSDP 549	Bay of Biscay/ Goban Spur	Reynolds 1992; Berggren and Aubry 1996	600–1500	Low	Yes/no benthics	>150	Good/ unconformity
15.2	DSDP 401	Bay of Biscay	Pak and Miller 1992; Schnitker 1979; Saint Marc 1991a, 1991b; Pardo et al. in press	1800	High/ medium	Partim/ no/ no yes	>150	Good/ unconformity
15.3	DSDP 400A	Bay of Biscay	Schnitker 1979	3100–4200	Low	No	>150	Poor
15.4	DSDP 548	Goban Spur/ Bay of Biscay	Boltovskoy et al. 1992	600–2000	Medium	No	>63	good/post
16	DSDP 605	New Jersey margin	Hulsbos 1987; Saint Marc 1987; 1991b; Thomas, unpublished data	1800–2300	Low/high	No	>150, >63	Good/ unconformity

Appendix 12.1 *(continued)*

Pre-Extinction Taxa	Postextinction/ Short-Term	Postextinction/ Long-Term	Low O2/ High Productivity	Dissolution
G. beccariiformis, *Cibicidoides* spp., *P. coryelli*, *N. truempyi*	?	*N. truempyi*, *Cibicidoides* spp., *O. umbonatus*	No?	?
G. beccariiformis, buliminids	?	*Stilostomella* spp., *Lenticulina* spp.	No?	?
G. beccariiformis, *N. truempyi*, *B. thanetensis*, agglutinands	*T. selmensis*, buliminids	*N. truempyi*, buliminids, *Cibicidoides* spp.	Yes	Yes
G. beccariiformis, *A. velascoensis*, *A. welleri*, *B. thanetensis*		? *T. selmensis*, *A. aragonensis*, *N. truempyi*	Yes?	?
G. beccariiformis, *N. truempyi*		*N. truempyi*, *Anomalinoides* spp.	No?	?
G. beccariiformis, *N. truempyi*, agglutinants		*T. selmensis*, *Aragonia* spp.	Yes?	?
G. beccariiformis, *P. coryelli*, *Cibicidoides* spp., *N. truempyi*, buliminids		*N. truempyi*, *Anomalinoides danicus*, *O. umbonatus*	Yes?	?
G. beccariiformis, *N. truempyi*, *Cibicidoides* spp., *B. thanetensis*, *B. delicatulus*	*N. truempyi*, *B. semicostata*, *Cibicidoides* spp., *T. selmensis*	*N. truempyi*, buliminids, *Cibicidoides* spp., *A. aragonensis*, *O. umbonatus*	No	?
G. beccariiformis, agglutinants		Buliminids, *T. selmensis*	Yes?	Yes
G. beccariiformis, *C. hyphalus*, *C. midwayensis*, *B. delicatulus*, *Neoeponides* spp., *Gyroidinoides*	? *N. truemypyi*, abyssaminids, buliminids (*B. semicostata*)	*N. truempyi*, abyssaminids, buliminids, *Cibicidoides* spp.	Yes	Yes
Cibicidoides spp., *N. truempyi*, abyssaminids, *Gyroidinoides* spp.	?	*Cibicidoides* spp., *Aragonia aragonensis*, *Cibicidoides* spp.	Yes	Yes
No data	*T. selmensis*, *S. brevispinosa*, *A. aragonensis*, *B. semicostata*	*N. truempyi*, buliminids, *Cibicidoides* spp.	Yes	Yes
G. beccariiformis, *Cibicidoides* spp., *A. velascoensis*, *B. midwayensis*, *P. coryelli*, agglutinants	? Probably unconformity	*N. truempyi*, *Cibicidoides* spp., abyssaminids, *T. selmensis*, buliminids (*B. semicosta*)	Yes	Yes?

Appendix 12.2

	Country	Section/ Formation	References	Depth	Resolution	LPTM $\delta^{13}C$	Size	Lithology
North Atlantic								
A.1	Spain	Zumaya (Atlantic)	Ortiz 1995; Canudo et al. 1995; Molina et al. 1994; von Hillebrandt 1965	600–1500	High	Yes	>63	Marl, calcarenite turbidites
A.2	Spain	Trabakua Pass, Ermua, west Pyrenees	Coccioni et al. 1994; Orue-Extebarria et al. in press	800–1000	High	No	>100	Limestones/marls
A.3	Spain	Tremp/Campo (Ilerdian stratotype)	Molina et al. 1992; Ortiz and McDougall 1991; von Hillebrandt 1965	?50–500	Low/ medium	No	>150	Marls
B	France	Paris Basin	Le Calvez 1970	10–200	Low	No	>150	Clays/silts
C	Trinidad	Lizard Springs Formation	Beckmann 1960; Bolli et al. 1994	500–1500	Low	No	>150	Marls
D.1	USA	New Jersey; Vincentown Manasquan Formations	Gibson et al. 1993; Gibson and Bybell 1995	50–200	Low	No	>63	Clayey sands/ clays
D.2	USA	New Jersey; Vincentown Manasquan Formations	Olsson and Wise 1987	50–250	Low	No	>150	Silty sands/clays
E.1	NW Europe	North Sea region	King 1989	100–500	Low	No	>150	Sand/clays
E.2	NW Europe	North Sea region	Gradstein et al. 1994	750–1000	Low	No	>150	Sand/clays
Tethys								
F	Spain	Caravaca (Tethys)	Ortiz 1995; Canudo et al. 1995	500–1000	High	Yes	>63	Marls, limestone
G	Israel	Nahal Avdat (Negev)	Speijer 1994	500–700	Low	No	>125	Marls/limestone
H	Egypt	Abu Rudeis = Wadi Nukhl (Sinai)	Speijer 1994	500–700	Low/ medium	No	>125	Marl/limestone
I.1	Egypt	Gebel Aweina	Speijer 1994; Speijer et al. 1996a; Charisi et al. 1995; Schmitz et al. 1996	100–150	Low/ medium	Yes	>125	Marl/limestone
I.2	Egypt	Bir Inglisi = Gebel Duwi	Speijer 1994; Speijer et al. 1996b; Schmitz et al. 1996	50–200	Low/ medium	No/ Yes	>125	Marl/limestone
J.1	Italy	Belluno	Di Napoli et al. 1970	500–1500	Low	No	>150	Marls/scaglias

Appendix 12.2

Pre-Extinction Taxa	Postextinction/ Short-Term	Low O_2/ Postextinction/ Long-Term	High Productivity	Dissolution
G. beccariiformis, Cibicidoides, buliminids, *P. coryelli*	First agglutinants, *O. umbonatus,* then *B. tuxpamensis*	*N. truempyi,* abyssaminids, *O. umbonatus,* buliminids	Yes	Yes
G. beccariiformis, N. truempyi, agglutinants, buliminids, *Anomalinoides welleri*	Rare agglutinants, then small buliminids, *N. truempyi*	*A. dissonata, N. truempyi,* buliminids, *O. umbonatus*	Yes	Yes
A. rubiginosus, Bulimina trigonalis, P. coryelli, agglutinants		*Cibicidoides* spp., *Uvigerina* . spp., *Hanzawaia* spp	?	?
Protelphidium, Pulsiphonina, Cibicidoides, buliminids		Buliminids, *Cibicides suc-, cedens, Bolivina* spp.	Yes?	?
A. velascoensis, B. midwayensis, buliminids, *Cibicidoides* spp.		*N. truempyi, T. selmensis, B. semicostata* (buliminids)	Yes?	?
Gavelinella spp., *Cibicidoides* spp., *Anomalinoides* spp., *Uvigerina*	*T. selmensis, Epistominella* sp.A A., buliminids, *Pseudouvigerina* spp.	*T. selmensis, Pulsiphonina prima, Anomalinoides* spp., *Epistominella*	Yes	Yes
Gavelinella spp., *Anomalinoides* spp., *Cibicidoides* spp.	Agglutinants, *T. selmensis*	*Epistominella* sp., *T. robertsi, N. truempyi*	Yes	Yes
G. beccariiformis, B. midwayensis, Bulimina trigonalis, Cibicidoides	Low-diversity agglutinants	*T. brevispira, Gaudryina hiltermanni,* buliminids	Yes	Yes
Trochammina ruthyenmurrayi, Reticulophragmium paupera, assemblage (agglutinant)	Low-diversity agglutinants	*T. robertsi, R. amplectens, R. intermedia* assemblage (agglutinant)	Yes	Yes
G. beccariiformis, A. velascoensis, P. coryelli, Gyroidinoides spp.	Rare *Haplophragmoides* (barren), *T. selmensis,* buliminids, *A. aragonensis*	Buliminids, *N. truempyi, Anomalinoides* spp.	Yes	Yes
G. beccariiformis, agglutinants, *P. coryelli,* buliminids, *Cibicidoides* spp.		*N. truempyi, Cibicidoides* spp.	Yes?	Yes
G. beccariiformis, agglutinants, *P. coryelli,* buliminids, *Cibicidoides* spp.	(?) *Anomalinoides* spp., vaginulinids, *Stainforthia* spp., buliminids	*T. truempyi, Cibicidoides* spp., *T. selmensis,* buliminids	Yes	Yes
Cibicidoides spp., lagenids, *C. midwayensis, A. avnimelechi*	(?) *B. callahani, Cibicidoides* spp., *A. aragonensis, P. wilcoxensis*	Buliminids, *Cibicidoides* spp., *Anomalinoides* spp.	Yes	Yes
Anomalinoides, spp., *Valvulineria* spp., *Loxostomoides applinae*	*Anomalinoides aegyptaicus, Lenticulina* spp., *L. applinae*	*Valvulineria scrobiculata, Cibicidoides* spp., *Anomalinoides* spp., *B. farafraensis*	*Yes*	*Yes*
Agglutinants, N. truempyi, G. beccariiformis, buliminids, *A. velascoensis, P. coryelli*	? *B. semicostata, B. trinitatensis*	*N. truempyi, Anomalinoides* spp., buliminids	Yes?	?

Appendix 12.2 *(continued)*

	Country	Section/ Formation	References	Depth	Resolution	LPTM $\delta^{13}C$	Size	Lithology
J.2	Italy	Possagno	Braga et al. 1975	500–1500	Low	No	>150	Marls
K	Austria	Reichenhall–Salzburg Basin	von Hillebrandt 1962	200–800	Low	No	>150	Silts/marls
Pacific								
L	New Zealand	Tawanui	Hornibrook et al. 1989; Kaiho et al. 1993, in press	500–1500	High	No	>63	Siltstone, silty limestone
M	Japan	Hokkaido, Tokachi district	Kaiho 1988	500–1000	Low	No	>63	Silty marls

Appendix 12.2 *(continued)*

Pre-Extinction Taxa	Postextinction/ Short-Term	Low O_2/ Postextinction/ Long-Term	High Productivity	Dissolution
G. beccariiformis, N. truempyi, agglutinants, buliminids, *A. velascoensis, P. coryelli*	*N. truempyi, O. umbonatus*	*N. truempyi, B. semicostata,* buliminids	Yes?	Yes
Agglutinants, buliminids, nodosariids, lenticulinids		Agglutinants, *Anomalinoides rubiginosus*	?	?
G. beccariiformis, agglutinants, *C. midwayensis, A. rubiginosus*	First: *B. tuxpamensis,* agglutinants Second: agglutinants only	*Cibicidoides* spp., *O. umbonatus,* agglutinants	Yes	Yes
A. welleri, agglutinants, *B. midwayensis*		Agglutinants, buliminids	Yes	Yes