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# Cretaceous/Paleogene boundary bathyal paleo-environments in the central North Pacific (DSDP Site 465), the Northwestern Atlantic (ODP Site 1049), the Gulf of Mexico and the Tethys: The benthic foraminiferal record

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## Abstract

Uppermost Maastrichtian benthic foraminiferal assemblages (>63 μm) are diverse, indicating mesotrophic conditions in lower bathyal DSDP Hole 465A (Hess Rise, central North Pacific), in 4 lower bathyal land sections in central-East and Northeastern Mexico, and in the upper to middle bathyal Agost section (Tethys area, Southeastern Spain). They indicate more eutrophic conditions in lower bathyal ODP Hole 1049C (Blake Nose, Northwestern Atlantic). Benthic foraminifers did not suffer significant extinction at the K/Pg boundary, but diversity and heterogeneity of the assemblages and the percentage of infaunal morphogroups decreased drastically in all sections, with the exception of DSDP Hole 465A where the percentage of infaunal taxa increased. These faunal changes probably reflect the effect on the benthic faunas of a widespread decrease in the food supply to the sea floor, as a result of the collapse of primary productivity at the K/Pg boundary. The decrease in food supply apparently affected the benthic faunas least at more eutrophic NW Atlantic ODP Site 1049 and at Pacific DSDP Site 465, which is distal from the impact site of the K/Pg bolide on the Yucatan Peninsula. At these sites the faunas recovered within the *Parvulorugoglobigerina eugubina* Biozone (~100 ky), although diversity and heterogeneity remained low through the early Danian, possibly indicating environmental stress. This stress might be related to a high or fluctuating food supply by primary producers that could not easily be used by the benthos, such as various bloom species of dinoflagellates. Benthic assemblages recovered more slowly (~300 ky) in the Mexican and Spanish sections. Low oxygen conditions after the K/Pg boundary could be inferred from the benthic assemblages at Agost (Southeastern Spain) only. A short episode of hypoxia, however, may be obscured at Pacific DSDP Hole 465A by drilling disturbance, and in the Mexican sections and Hole 1049C by incomplete sections due to downslope transport. Benthic foraminiferal assemblages thus appear to have been affected by the collapse of

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primary productivity at the K/Pg boundary to a different extent in different regions, and took different lengths of time for their recovery after the boundary.

*Keywords:* DSDP Hole 465A; ODP Hole 1049C; K/Pg boundary; benthic foraminifers; paleoenvironments; paleoproductivity

## 1. Introduction

Upper Cretaceous through lower Paleogene sections have been investigated intensively because one of the largest mass extinctions of the Phanerozoic occurred at the Cretaceous/Paleogene (K/Pg) boundary. Hypotheses regarding the cause(s) of the extinction and the nature of the paleoenvironmental and biotic turnover at that time are still under debate. Most authors accept that a bolide impact (Alvarez et al., 1980; Smit and Hertogen, 1980) on the Yucatan peninsula (e.g., Smit et al., 1992, 1996) was the main cause of the catastrophic mass extinctions, and that the anomalous concentrations of iridium, shocked quartz and microspherules in K/Pg boundary sediments reflect that impact (e.g., Alvarez et al., 1982). Some researchers, however, argue that the extinctions were not sudden but stepwise, starting in the Maastrichtian (e.g., Keller, 1989a,b, 2003), and linked at least in part to multiple impacts (Keller et al., 2003).

In contrast to many other biota, benthic foraminifers did not suffer significant extinction at the end of the Cretaceous (see Culver, 2003, for a review). Their assemblages show temporal faunal restructuring, which has been related to the collapse of the pelagic food web, which delivers food to the benthos (e.g., Thomas, 1990a,b; Widmark and Malmgren, 1992; Coccioni et al., 1993; Kuhnt and Kaminski, 1993; Speijer and Van der Zwaan, 1996; D'Hondt et al., 1998; Peryt et al., 1997, 2002; Culver, 2003). Decreased delivery of organic matter to the sea floor as the result of the extinction of pellet-producing zooplankton rather than decreased productivity might also have affected the benthos (D'Hondt et al., 1998), although the role of pellet production as compared to that of coagulation of particles is still debated (e.g., Jackson, 2001).

Benthic foraminifers are proxies for nutrient supply as well as for oxygenation at the sea floor, and thus constitute an important tool to reconstruct paleoenvironmental changes at the K/Pg boundary. Information from benthic foraminifers is particularly valuable in order to evaluate K/Pg extinction hypotheses that argue for widespread oceanic anoxia (e.g., Kajiwara and Kaiho, 1992; Kaiho et al., 1999). Widespread anoxia (as contrasted with hypoxia) almost certainly did not occur at the end of the Cretaceous: if it had, deep-sea benthic foraminifers would have shown significant extinction, which they do not (e.g., Culver, 2003). In order to evaluate whether hypoxic conditions were widespread, benthic foraminiferal evidence may be useful, in combination with geochemical evidence.

We must be careful with the interpretation of benthic foraminiferal evidence, however, because present faunas may not be analogs of Cretaceous through Paleogene faunas living in a 'greenhouse world' (Thomas et al., 2000), and parameters such as test morphology may not always be easy to interpret in terms of paleoenvironment (e.g., Buzas et al., 1993). It has been well-documented for recent faunas that the BFOI (Benthic Foraminiferal Oxygen Index) as defined by Kaiho (1994a,b, 1999) using morphotypes of calcareous benthic foraminifers gives no good estimate of dissolved oxygen values, but is influenced by some combination of oxygen values and food supply (e.g., Jorissen et al., 1995, 1998; Morigi et al., 2001; see also review by Gooday, 2003). We use the relative abundance of morphotypes indicating infaunal taxa as an overall indicator of delivery of food to the sea floor (as described, for example, in the review by Gooday, 2003).

The benthic foraminiferal faunal turnover across the K/Pg boundary has been described from many locations worldwide (Culver, 2003), but analyses by different authors are difficult to compare in detail because of taxonomic problems and because different authors routinely study different size fractions (from >250 to >63 μm). In addition, sections close to the impact site are usually incomplete as a result of mass wasting processes, submarine landslides and extensive slumps related to the destabilization of the continental margins at the time of the impact at Chicxulub (e.g., Bralower et al., 1998; Klaus et al., 2000; Soria et al., 2001). A comparison between the faunas in these sections and more continuous K/Pg sections more distal to the impact site is thus needed to obtain a more complete record of the faunal and paleoenvironmental turnover at the K/Pg boundary.

In this paper we compare quantitative data on Upper Cretaceous and lower Paleogene benthic foraminiferal assemblages from DSDP Site 465 (central North Pacific; paleolatitude 16°N, paleodepth ∼1500 m) with published data obtained by the same authors (thus constant taxonomy) and on the same size fraction (>63 μm) in four Mexican sections (Gulf of Mexico area; Alegret and Thomas, 2001; Alegret et al., 2001a,b, 2002a,b; Arz et al., 2001a; Alegret, 2003), at ODP Site 1049 on Blake Nose (Northwestern Atlantic; Alegret and Thomas, 2004) and in the Agost section (Southeastern Spain, Tethys area; Alegret et al., 2003). The Pacific site represents a location distal from the end Cretaceous impact in the largest ocean basin of the world.

## 2. Materials and methods

### *2.1. Sections*

#### *2.1.1. DSDP hole 465A, Southern Hess Rise (central North Pacific)*

Upper Cretaceous through lower Paleogene sediments were recovered at Deep Sea Drilling Project Site 465 (Core 465A-3) on the Southern Hess Rise in the central North Pacific (33°49.23′N and 178°55.14′E; Fig. 1; Thiede et al., 1981). The site has been above the local CCD since its formation, and benthic and planktic foraminifers are well preserved in homogeneous calcareous nannofossil and foraminiferal oozes. The rotary drilling process deformed the recovered sediments, and the K/Pg boundary occurs within an about 20- to 30-cm-thick zone in which Danian and Maastrichtian sediments are deformed and mixed, but can still be recognized because of their color differences (Kyte et al., 1980; Thiede et al., 1981). This mixed interval contains fragments of a 3-mm-thick, pyrite-bearing, dark grey clay layer with high concentrations of iridium and other siderophiles. This broken-up clay layer was deposited under reducing conditions (i.e., anoxia) according to Kyte et al. (1980). In contrast, Boersma (1981) and Widmark and Malmgren (1992) saw no evidence for anoxia or hypoxia in the benthic foraminiferal assemblages (>125 μm; 12 Cretaceous samples, 5 Danian samples), which indicated a lower bathyal paleodepth of about 1500 m, but their sampling may have been at too low a resolution to resolve a short-lived event.

We studied 6 samples from the uppermost 2.5 m of the Maastrichtian, and 12 samples from the lower 4 m of the Danian (Fig. 2) from DSDP Hole 465A. Samples are spaced at 5 to 10 cm intervals just above the K/Pg boundary, and at 30 to 50 cm intervals below and well above it. For biostratigraphical control, we follow Boersma (1981), who identified the planktic

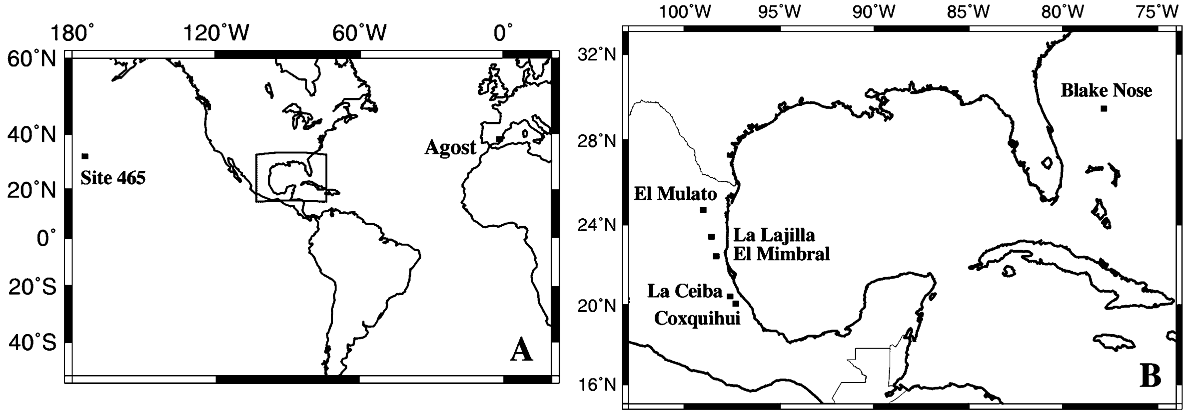

Fig. 1. Location of the studied sections. (A) DSDP Hole 465A (Southern Hess Rise) and Agost (Southeastern Spain); (B) Mexican sections and NW Atlantic ODP Hole 1049C (Blake Nose).

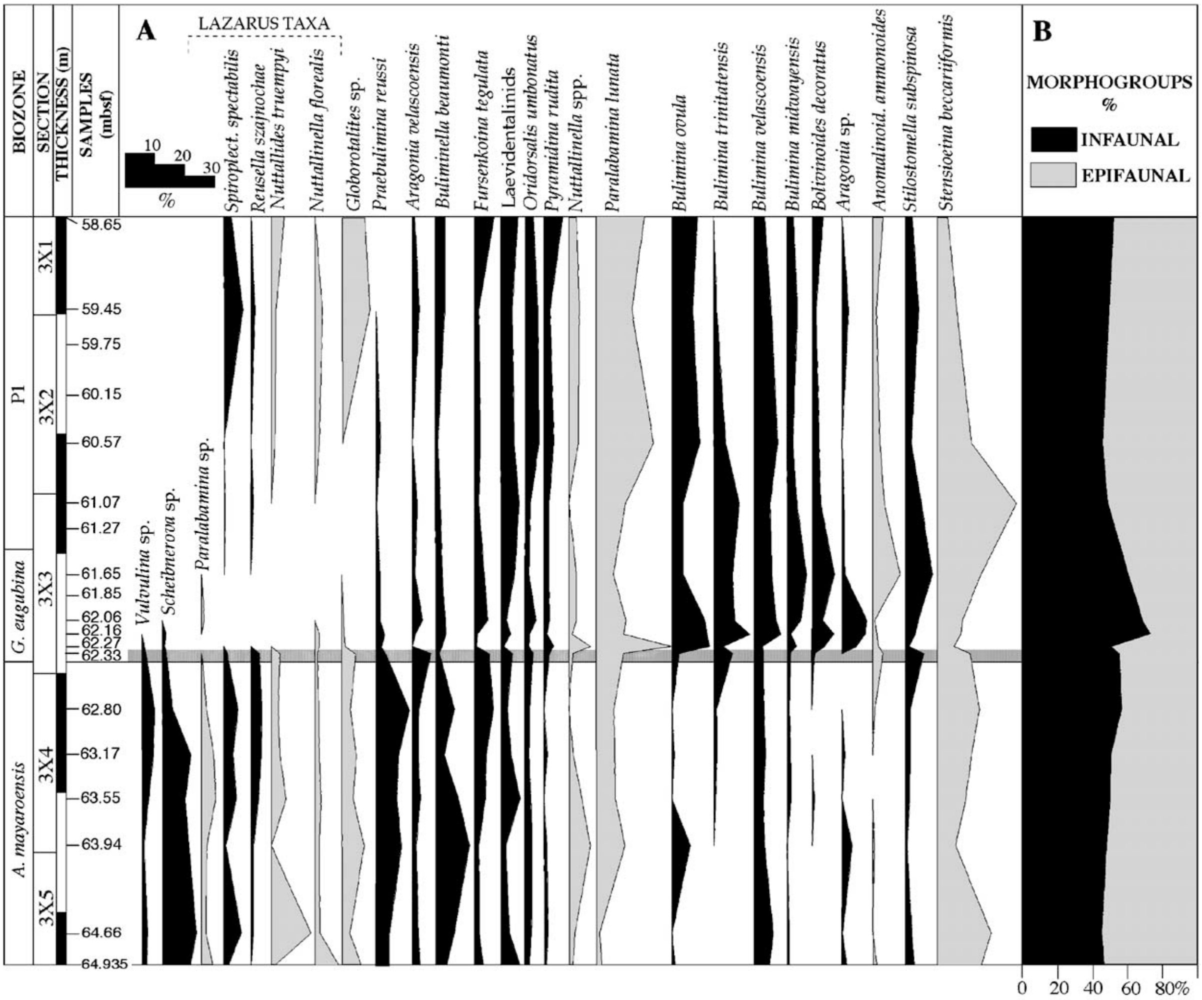

Fig. 2. Upper Maastrichtian and lower Danian benthic foraminifers from DSDP Hole 465A (Southern Hess Rise). (A) Percentages of the most abundant benthic foraminiferal species; (B) relative abundance of infaunal and epifaunal morphogroups. The grey zone at the basal Danian corresponds to the "mixed layer".

foraminiferal *Abathomphalus mayaroensis* Biozone in the Maastrichtian, and the Danian "*Globigerina*" (=*Parvulorugoglobigerina*) *eugubina* and P1 Zones.

### 2.1.2. The Mexican sections

Upper Maastrichtian and lower Danian benthic foraminifers in four Mexican sections (Fig. 1) were described by Alegret and Thomas (2001), and Alegret et al. (2001a,b, 2002a,b). Two of these sections are in Northeastern Mexico (Tamaulipas State): El Mulato (24°54′N, 98°57′W) and La Lajilla (23°40′N, 98°44′W). Two sections are in central-East Mexico (Veracruz State): La Ceiba (20°19.8′N, 97°41′W) and Coxquihui (20°19.5′N, 97°52.5′W). Upper Cretaceous and lower Paleogene sediments consist of the marly Upper Cretaceous Méndez Formation and the marly lower Paleogene Velasco Formation, with an intercalated clastic unit ranging in thickness from 1 to 2 m.

The interval studied in each section depends on the exposure of the outcrops, and ranges from 1.6 to 5 m of Maastrichtian sediments (Méndez Formation), from 3 to 6 m of Danian sediments (clastic unit and Velasco Formation). Samples in the Mexican sections were picked at 1 to 10 dm intervals well below and above the K/Pg boundary, with closer sampling (cm intervals) close to the boundary, i.e., just below and above the clastic unit, from which several samples were also analyzed. The biostratigraphy of these sections, based on planktic foraminifers, has been documented by Arz et al. (2001a,b) and Alegret et al. (2001a,b, 2002b). Not all biozones are represented in all sections, and there is an unconformity above the clastic unit at La Ceiba (upper part of the *Guembelitria cretacea* Biozone, the *Pv. eugubina* Biozone, and almost the whole *Parasubbotina pseudobulloides* Biozone; Arenillas et al., 2002).

The composition of benthic foraminiferal assemblages, the low abundance of macrofauna and the high abundance of planktic foraminifers indicate that the Méndez and Velasco Formations were deposited at depths in the upper part of the lower bathyal zone (~1000 m) in the La Lajilla and El Mulato sections, and in the lower part of the lower bathyal zone (~1500 m depth) at La Ceiba and Coxquihui (Alegret et al., 2001a, 2002a,b; Alegret, 2003). The clastic unit contains coarse-grained siliciclastic sediments, muddy pebbles, and neritic, benthic and planktic foraminifers that were transported from shallow waters into the bathyal zone, probably because of destabilization of the continental margins at the time of the impact at Chicxulub (e.g., Smit et al., 1992, 1996; Soria et al., 2001; Alegret et al., 2002b).

### 2.1.3. ODP Hole 1049C, Blake Nose (Northwestern Atlantic)

The K/Pg boundary at ODP Site 1049 on Blake Nose (Northwestern Atlantic; 30°08.5370′N and 76°06.7271′W; paleolatitude 30°N; Fig. 1) is at the base of a spherule-bed intercalated between the uppermost Maastrichtian and the lowermost Danian pelagic foraminiferal and nannofossil oozes; paleontological, sedimentological and geochemical information on this layer has been presented by Huber et al. (2002), Norris et al. (1999), Klaus et al. (2000), and Martínez-Ruiz et al. (2001). The spherule-bed is overlain by a 3-mm-thick limonitic layer enriched in Ir and a 7-cm-thick dark clay layer with reworked foraminifers (e.g., Norris et al., 1998). Above this level there is a 15-cm-thick white mud layer overlain by a grey-green ooze with abundant Danian foraminifers.

Biostratigraphic information is from Norris et al. (1999) and Huber et al. (2002), who identified the upper part of the *A. mayaroensis* Biozone, and the Danian Pα and P1a Zones. We included the spherule-bed into the P0 Biozone, following Arenillas et al. (2002).

A late Maastrichtian paleodepth of about 2500 m was derived from backtracking (Frank and Arthur, 1999; D'Hondt and Arthur, 2002), but according to Alegret and Thomas (2004) this method is not valid because the site is not on oceanic basement. ODP Site 1049 was a re-drill of Deep Sea Drilling Project (DSDP) Site 390, for which a paleodepth of 600–1600 m was derived from benthic foraminiferal assemblages in the site chapter (Benson and Sheridan, 1978), 1000–1200 m by Widmark and Speijer (1997). According to Alegret and Thomas (2004), deposition occurred at lower bathyal depths (1500–1600 m), whereas the spherule-bed contains elements reworked and transported from shallow areas.

Benthic foraminiferal assemblages from the K/Pg interval in Hole 1049C were described by Alegret and Thomas (2004), who used 30 samples from sections 1049C-8X-1 to 8X-5 (106.21–113.59 mbsf), comprising the upper 52 cm of the Maastrichtian and the lower 7 m of the Danian. Samples are spaced at 4 to 25 cm intervals in the Maastrichtian, at 1 to 10 cm intervals in the lowermost Danian, and at 20 to 80 cm intervals in upper section 8X-5 and sections 8X-4 to 8X-1.

### 2.1.4. Agost (Southeastern Spain, Tethys Region)

The K/Pg boundary at Agost (Betic Cordilleras, Southeastern Spain; Fig. 1) is within the Cenomanian to Eocene Quipar–Jorquera Formation, which consists of pelagic grey marls with abundant microfossils. The boundary is marked by a sharp contact between Maastrichtian marls and a 12-cm-thick layer of black clays, with a 2- to 3-mm-thick, red, ferruginous level at its base. This clay layer contains an anomalous concentration in Ir, has a very low $CaCO_3$ content, and a negative shift in bulk $\delta^{13}C$ values as observed in nearby section Caravaca (Smit, 1990; Martínez-Ruiz et al., 1992, 1999). Trace element data indicate that low oxygen conditions prevailed during the deposition of the black clay layer at Caravaca and Agost (Martínez-Ruiz et al., 1992, 1999). This level is overlain by a 10-cm-thick layer of uniform grey clays, and by 2-dm-thick, tabular bodies of marly limestones, with a 10-cm-thick intercalated layer of calcareous marls. For biostratigraphic control we followed Molina et al. (1996b).

Alegret et al. (2003) studied benthic foraminifers from the upper 6 m of the Maastrichtian and the lowermost 3.5 m of the Danian. Samples are spaced at 1 to 10 cm intervals just above the K/Pg boundary, and at 20 to 100 cm intervals below and well above it. Benthic foraminiferal assemblages indicate an uppermost bathyal depth of deposition during the *A. mayaroensis* and the lower part of the *P. hantkeninoides* Biochrons, with depths increasing to middle bathyal about 2.4 m (about 120–150 ky) below the K/Pg boundary, remaining unchanged through the *Ps. pseudobulloides* Biozone. These authors thus argued for a greater paleodepth than outer neritic-upper bathyal as proposed by Pardo et al. (1996).

### *2.2. Methods of analysis*

All samples were disaggregated in water with diluted $H_2O_2$ and washed through a 63 μm sieve. Quantitative studies were based on representative splits of 300 or more specimens of benthic foraminifers from the $>63$ μm fraction when possible, which were obtained with a modified Otto microsplitter. All specimens were picked, identified, counted and mounted on microslides for a permanent record. Benthic foraminifers were identified at the generic level largely following Loeblich and Tappan (1987) and at the specific level following Alegret and Thomas (2001).

For the samples from Hole 465A we calculated the relative abundances of foraminiferal species (Appendix A), as well as the species richness and the benthic foraminiferal accumulation rate (BFAR, number of foraminifers $cm^{-2}$ $ky^{-1}$). The latter numbers are an estimate because we did not have density values for the exact samples used and thus used those published in the Initial Reports for samples within core 465A-3, which showed little variability (Thiede et al., 1981). To derive sedimentation rates for the Danian and Maastrichtian we used the thickness of the *M. prinsii* Zone and the *Pv. eugubina* Zone as given in Widmark and Malmgren (1992), with estimates of the duration of these zones updated after Shipboard Scientific Party (2004).

As proxies for diversity we calculated the Fisher-α index, the $H(S)$ Shannon–Weaver information function, and the genus richness. High values of $H(S)$ indicate an even distribution of specimens over species; Murray (1991) calls $H(S)$ the index of heterogeneity, with high heterogeneity values indicating high diversity.

We calculated the percentage of buliminid taxa for all the studied sections; a high relative abundance of buliminid taxa has been related to high productivity and a year-round or seasonally fluctuating high delivery of food to the sea floor (e.g., Widmark and Speijer, 1997; Fontanier et al., 2002). Furthermore, the percentage of agglutinated foraminifers was calculated for all the studied sections.

In order to infer probable microhabitat preferences and environmental parameters such as the nutrient supply to the sea-floor or sea water oxygenation (e.g., Bernhard, 1986; Jorissen et al., 1995) we allocated all specimens to infaunal and epifaunal morphogroups following Corliss (1985), Jones and Charnock (1985) and Corliss and Chen (1988). Infaunal species (living at $>1$ cm depth) tend to have tests that are rounded and planispiral or flattened ovoid, flattened tapered, tapered and cylindrical or spherical in shape with pores all over the test, whereas foraminifers with plano-convex, biconvex and rounded trochospiral tests, as well as tubular and coiled flattened tests, have an inferred epifaunal mode of life. Only major changes in percentages of these morphogroups are considered to be significant (e.g., Gooday, 2003). Microhabitats cannot always be predicted correctly; assignments appear to be correct in about 75% of cases (Buzas et al., 1993).

Kaiho (1991, 1992, 1994a) suggested that an oxygenation index could be derived from the relative abundance of different morphotypes of calcareous taxa. Kaiho (1994b, 1999) defined a benthic foraminiferal oxygenation index (BFOI) using data on living foraminifers. We calculated the BFOI for our samples. Kaiho's indices are somewhat differently defined (Kaiho, 1991, 1994b, 1999); we used his 1994b definition. We do not interpret the BFOI values as indicators of oxygenation: it has been documented by several authors that these values indicate some combination of oxygenation and food supply (e.g., Jorissen et al., 1995, 1998; Den Dulk et al., 2000; Morigi et al., 2001; see also review by Gooday, 2003). Av-

Table 1

Palaeoecological indices of benthic foraminifers[a]

| Site/section | Paleodepth | | Fisher-α index | $H(S)$ Shannon–Weaver index | Genus richness | % Agglutinated foraminifers | % Buliminids | % Infaunal morphogroups | BFOI |
|---|---|---|---|---|---|---|---|---|---|
| DSDP Hole 465A (Central N Pacific) | Lower bathyal | Average values P1 (~ *Ps. pseud.*) Zone | 13.2 | 3.2 | 29.2 | 3.4 | 31.3 | 49.1 | 75.7 |
| | | Average values Pv. *eugubina* Zone | 13.4 | 3.21 | 28.6 | 2.6 | 45.8 | 61.4 | 57.1 |
| | | Average values Maastrichtian | 14.7 | 3.24 | 32.3 | 6.7 | 28.8 | 48.4 | 80.9 |
| La Ceiba (Mexico) | Lower bathyal (~1500 m) | Average values *Gl. compressa* Biozone | 15 | 3.1 | 25.4 | 15.5 | 2.2 | 30.9 | 93.1 |
| | | Average values *Ps. pseudob.* Biozone | 14.9 | 3 | 24.9 | 12.1 | 0.9 | 22.5 | 98.2 |
| | | Average values Maastrichtian | 19.5 | 3.1 | 24.1 | 29.8 | 2.7 | 58.5 | 84.1 |
| Coxquihui (Mexico) | Lower bathyal (~1500 m) | Average values *Ps. pseudob.* Biozone | 10.4 | 2.8 | 23.6 | 7.75 | 7.6 | 41 | 89.7 |
| | | Average values *Pv. eugubina* Biozone | 11.2 | 3 | 28.5 | 15.1 | 5.9 | 43.3 | 94 |
| | | Average values *G. cretacea* Biozone | 9.3 | 2.8 | 22.7 | 11.5 | 7.2 | 35.8 | 89.3 |
| | | Average values Maastrichtian | 11.9 | 2.7 | 24.6 | 20.4 | 5.3 | 59.1 | 77.6 |
| La Lajilla (Mexico) | Lower bathyal (~1000 m) | Average values *Ps. pseudob.* Biozone | 21 | 2.8 | 40 | 24.9 | 8.3 | 55.9 | 80.9 |
| | | Average values *Pv. eugubina* Biozone | 18.9 | 2.8 | 35.7 | 25.2 | 7.8 | 66.2 | 67.8 |
| | | Average values *G. cretacea* Biozone | 15.1 | 2.2 | 25.8 | 14.6 | 10.3 | 47.2 | 79.8 |
| | | Average values Maastrichtian | 14.4 | 2.4 | 28.2 | 21.9 | 26.6 | 68.1 | 80.5 |
| El Mulato (Mexico) | Lower bathyal (~1000 m) | Average values *Ps. pseudob.* Biozone | 15.3 | 3.3 | 33 | 19.2 | 6.6 | 47.6 | 85.7 |
| | | Average values *Pv. eugubina* Biozone | 17.2 | 3.6 | 38 | 26.2 | 6.9 | 63.1 | 76.9 |
| | | Average values *G. cretacea* Biozone | 15.4 | 3.2 | 34 | 22.6 | 5.9 | 51.4 | 83.2 |
| | | Average values Maastrichtian | 17.8 | 3.2 | 32 | 28.6 | 18.2 | 73.2 | 72.4 |
| ODP Hole 1049C (NW Atlantic) | Lower bathyal (~1500–1600 m) | Average values *Ps. pseudob.* Biozone | 12 | 2.8 | 26.8 | 0.4 | 48.7 | 75.3 | 34 |
| | | Average values *Pv. eugubina* Biozone | 16.6 | 3.1 | 34.3 | 1.9 | 37.7 | 59.3 | 54.6 |
| | | Average values Maastrichtian | 19.7 | 3.5 | 37.5 | 3.4 | 40.7 | 64 | 59.9 |
| Agost (Spain) | Upper to middle bathyal | Average values *Ps. pseudob.* Biozone | 19.5 | 3.4 | 38.1 | 12.9 | 9.4 | 43.2 | 79.6 |
| | | Average values *Pv. eugubina* Biozone | 21.6 | 3.6 | 37.2 | 12 | 8.7 | 46.2 | 73.4 |
| | | Average values *G. cretacea* Biozone | 16.4 | 3.1 | 25 | 33.6 | 16.4 | 56 | 70.3 |
| | | Average values Maastrichtian | 20.8 | 3.4 | 41.5 | 15.7 | 26.8 | 71 | 71.4 |

[a] Averaged values of Fisher-α diversity index, Shannon–Weaver heterogeneity index $H(S)$, genus richness, relative abundance of agglutinated foraminifers, buliminids and infaunal morphogroups, and benthic foraminiferal oxygenation index (BFOI), calculated for each biozone in Upper Maastrichtian and lower Danian benthic foraminiferal assemblages from DSDP Hole 465A (Southern Hess Rise), the Mexican sections, ODP Hole 1049C (Blake Nose) and Agost (SE Spain).

eraged values of all indices for each biozone are shown in Table 1.

## 3. Results

### 3.1. Benthic foraminiferal assemblages from Hole 465A (Hess Rise, central North Pacific)

Faunas in all samples contain less than 11% agglutinated taxa. Upper Maastrichtian assemblages are highly diverse, containing 40–48 species per sample, belonging to both infaunal and epifaunal morphogroups (Fig. 2). From the bottom of the core to the top of the Maastrichtian part of the section, species richness, genus richness, diversity and heterogeneity of the assemblages appear to increase slightly, while BFAR is stable and low, in most samples 100–200 foraminifers $\mathrm{cm}^{-2}\ \mathrm{ky}^{-1}$ (Fig. 3). Buliminids (e.g., *Bulimina velascoensis*, *Buliminella beaumonti*, *Fursenkoina tegulata*, *Praebulimina reussi*) make up 22–40% of the assemblages (Figs. 2 and 3). The epifaunal

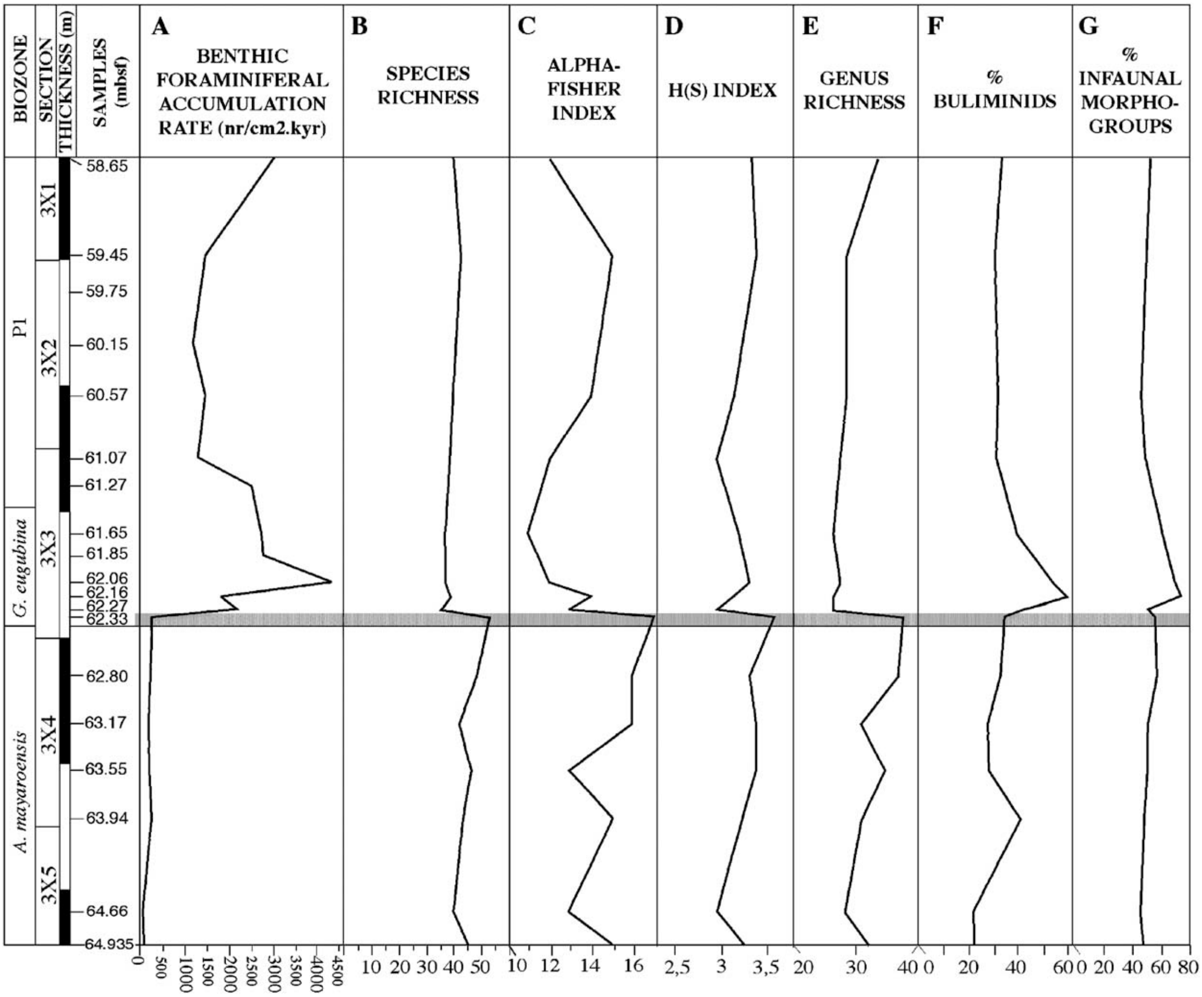

Fig. 3. Benthic foraminiferal indices across the K/Pg boundary at DSDP Hole 465A (Southern Hess Rise). (A) Benthic foraminiferal accumulation rate; (B) number of benthic foraminiferal species per sample; (C) Fisher-α diversity index; (D) $H(S)$ index; (E) genus richness; (F) relative abundance of buliminids; (G) relative abundance of infaunal morphogroups. The grey zone at the basal Danian corresponds to the "mixed layer".

taxa *Paralabamina lunata*, *Scheibnerova* sp. and *Stensioeina beccariiformis* make up 22–29% of the assemblages.

The lowermost Danian *Thoracosphaera* bloom occurs between the top of core 465A and 465A-3X-3, 128 cm (62.27 mbsf), and the highest Maastrichtian nannofossil (probably reworked) was documented in 465A-3X-3, 120 cm (62.18 mbsf) by Thiede et al. (1981). The Ir anomaly is in 465A-3X-3, 115 cm (62.16 mbsf), although single data points (on dark blebs) show a peak at about 465A-3X-3, 125 cm (62.25 mbsf) (Alvarez et al., 1982; Kastner et al., 1984). These data and core photographs indicate that drilling disturbance caused irregular mixing of the sediments in the lower 20–30 cm of section 465A-3X-3. According to Kyte et al. (1980), this zone is at least 20 cm thick, but according to Widmark and Malmgren (1992), it is ~30 cm thick. Detailed observation of the foraminiferal assemblages and the remaining material in our samples suggests that the K/Pg boundary can be placed between samples 465A-3X-3, 132–135 cm (62.33 mbsf) and -3X-3, 126–129 cm (62.27 mbsf), although a few samples higher in the section (up to sample 465A-3X-3, 115–118 cm, 62.16 mbsf) probably contain some Maastrichtian, mixed-in sediment. In the mixed zone, we identified representatives of some benthic foraminiferal taxa (*Dorothia pupa*, *Neoflabellina* sp., *Pyramidina* sp. and *Quadrimorphina allomorphinoides*) that have not been identified in the rest of the studied samples.

Eight benthic foraminiferal species, *Coryphostoma* sp., *Ellipsodimorphina* sp., *Eouvigerina subsculptura*, *Globulina prisca*, *Guttulina* sp., *Gyroidinoides globosus*, *Osangularia cordieriana* and *Vulvulina* sp. have their uppermost occurrence at the K/Pg boundary (where they make up 8.3% of the specimens) or in the “mixed zone” above it (5.6–3.0% of the assemblages). Two species, *Scheibnerova* sp. and *Spiroplectammina excolata*, have their uppermost occurrence in 465A-3X-3, 115–118 cm. Several species (including *Nuttallides truempyi*, *Spiroplectammina spectabilis* and *Reussella szajnochae*) temporally disappeared at the K/Pg boundary or in the “mixed zone”, whereas others (*Nuttallinella florealis*) disappeared a few centimeters above the boundary. These taxa reappear in the lowermost Danian (Fig. 2), thus are ‘Lazarus taxa’.

Benthic foraminifers decreased drastically in size just above the K/Pg boundary, as is common for faunas in disturbed ecosystems, and for benthic foraminifers in high-food, low-oxygen as well as carbonate-corrosive conditions. The number of benthic foraminiferal species per sample, as well as genus richness and diversity and heterogeneity of the assemblages also decreased across the K/Pg boundary (Fig. 3). In most samples, the lowermost Danian benthic foraminiferal assemblages contain similar percentages of infaunal (e.g., *Bulimina ovula*) and epifaunal (e.g., *P. lunata*) morphogroups (Fig. 2). There is a peak in relative abundance of the epifaunal species *P. lunata* (25%) in only one sample, the first above the K/Pg boundary (sample 465A-3X-3, 126–129 cm; 62.27 mbsf). Above this peak, in samples 465A-3X-3, 115–118 cm (62.16 mbsf) and 465A-3X-3, 105–108 cm (62.06 mbsf), which correspond to the first half of the *Pv. eugubina* Biozone, the percentage of buliminids increased (*Aragonia* sp., *Bolivinoides decoratus*, *B. ovula*, *Bulimina trinitatensis*, *B. velascoensis*) to 54% of the assemblages (Figs. 2 and 3).

The BFAR increased by almost a factor of 10 in sample 465A-3X-3, 126–129 cm (62.27 mbsf), where there is also the peak in epifaunal species. BFAR increased from Maastrichtian values of ~200 foraminifers $cm^{-2}$ $ky^{-1}$ to maximum values of 4200 foraminifers $cm^{-2}$ $ky^{-1}$ in sample 465A-3X-3, 105–108 cm (62.06 mbsf). Values dropped below values of 1500 foraminifers $cm^{-2}$ $ky^{-1}$ between samples 465A-3X-3, 6–9 cm (61.07 mbsf) and -3X-3, 26–29 cm (61.27 mbsf), and remained far above Maastrichtian values for the rest of the studied section (Fig. 3).

Most Lazarus taxa reappear towards the upper part of the *Pv. eugubina* Biozone and in the lower half of Zone P1; *S. beccariiformis* is abundant during this interval, where it makes up to 25.36% of the assemblages (Fig. 2). Diversity and heterogeneity of the assemblages, however, as well as the genus richness remained low in the lower half of Zone P1 (Fig. 3). The number of benthic foraminiferal species per sample remains almost constant throughout the studied part of the Danian, but other diversity indices gradually increase towards the upper half of Zone P1.

Dominance of the assemblages and the percentage of *S. beccariiformis* decrease towards the top of the section, whereas the relative abundance of the epifaunal taxa *P. lunata* and *Globorotalites* sp. increases (Fig. 2).

### *3.2. Benthic foraminiferal assemblages from the Mexican sections*

A detailed description of changes in the relative abundances of benthic foraminiferal taxa across the K/Pg boundary in the Mexican sections has been published by Alegret et al. (2001a,b, 2002a,b), Arz et al. (2001a) and Alegret (2003). We present new data on the diversity, heterogeneity, genus richness and the percentages of buliminids and agglutinated foraminifers, and compare these values with those at other sites (Figs. 4–10). The pattern of faunal turnover is not represented in all sections (e.g., La Ceiba section) due to the occurrence of unconformities of varying duration.

Upper Maastrichtian benthic foraminiferal assemblages contain high percentages (30 to 62%) of agglutinated taxa such as *Clavulinoides trilatera*, *Gaudryina pyramidata* and *Spiroplectammina* (Fig. 10). The assemblages are diverse and heterogeneous, and contain both infaunal (e.g., *C. trilatera*, *E. subsculptura*, *Gyroidinoides beisseli*, laevidentalinids) and epifaunal taxa (e.g., *Cibicidoides proprius*, *Osangularia* spp., *S. beccariiformis*). The percentage of buliminids is low in the deepest sections (below 10% at La Ceiba and Coxquihui), slightly higher (~30%) at La Lajilla and El Mulato (Fig. 7). Relative abundances of infaunal species (e.g., *C. trilatera*, *E. subsculptura*, *G. beisseli*) increase to up to 70–90% towards the uppermost Maastrichtian (Fig. 8).

Benthic foraminifers are rare in the clastic unit, and consist of a mixture of poorly preserved, shallow neritic taxa such as *Lenticulina navarroensis*, *L. spissocostata* and *Planulina* sp., and bathyal species such as *Cibicidoides velascoensis*, *C. trilatera*, *G. pyramidata*, *G. globosus* (Alegret et al., 2002b; Alegret, 2003). Neritic faunal elements such as orbitoids and bryozoa are present in the clastic unit at La Ceiba (Smit et al., 1996). In the clastic unit at La Lajilla, muddy pebbles contain taxa that are common in the upper to middle slope (e.g., *Anomalinoides midwayensis*, *Quinqueloculina* spp., *Praeglobobulimina quadrata*, *P. lunata*; Alegret et al., 2001b).

Only two species, *Bolivinoides draco* and *E. subsculptura*, have their uppermost occurrence at the base of the clastic unit. These two taxa range from 3% at Coxquihui to 10% at La Lajilla. *P. reussi* disappeared locally in the Mexican sections. Some species (e.g., *Cibicidoides dayi*, *N. florealis*) temporally disappeared in coincidence with the K/Pg boundary (Lazarus taxa). The most significant change in benthic foraminiferal assemblages at the K/Pg boundary consists of a drastic decrease in the percentage of infaunal morphogroups by 25–45% (Alegret et al., 2001a, 2002a,b; Arz et al., 2001a; Fig. 8). The relative abundance of buliminids, an important infaunal group, is lower in the lower Danian than in the Maastrichtian in the La Lajilla and El Mulato sections (Fig. 7). Diversity, heterogeneity and genus richness decreased at the K/Pg boundary, especially in the shallower sections La Lajilla and El Mulato (Figs. 4–6).

Benthic foraminiferal assemblages in the lowermost Paleogene (just above the clastic unit, *G. cretacea* biozone) are dominated by epifaunal species includying *S. beccariiformis*, *Anomalinoides acutus* and *Cibicidoides hyphalus* (Fig. 8). Assemblages remain dominated by epifaunal taxa such as *Globorotalites* sp. A. and *S. beccariiformis* through the first half of *Pv. eugubina* Biozone, although the relative abundance of some infaunal taxa (species of *Haplophragmoides*, *Dorothia*, *Marssonella*) increases slightly (Alegret et al., 2001a; Alegret, 2003). As a result, genus richness, diversity and heterogeneity increase (Figs. 4–6).

The relative abundance of infaunal taxa (e.g., *Euuvigerina elongata*, *Pleurostomella* spp. and laevidentalinids; Alegret et al., 2001a) as well as the diversity of the assemblages (Fig. 4) increases upwards towards the lower half of *Ps. pseudobulloides* Biozone, although the abundance of epifaunal species (including *N. truempyi*, which makes up 21–37% of the assemblages) remains high (60–65% at El Mulato and Coxquihui, 45% at La Lajilla; Fig. 8).

Assemblages increase slightly in genus richness and heterogeneity in the upper part of the *Ps. pseudobulloides* Biozone and the lower part of *Gl.*

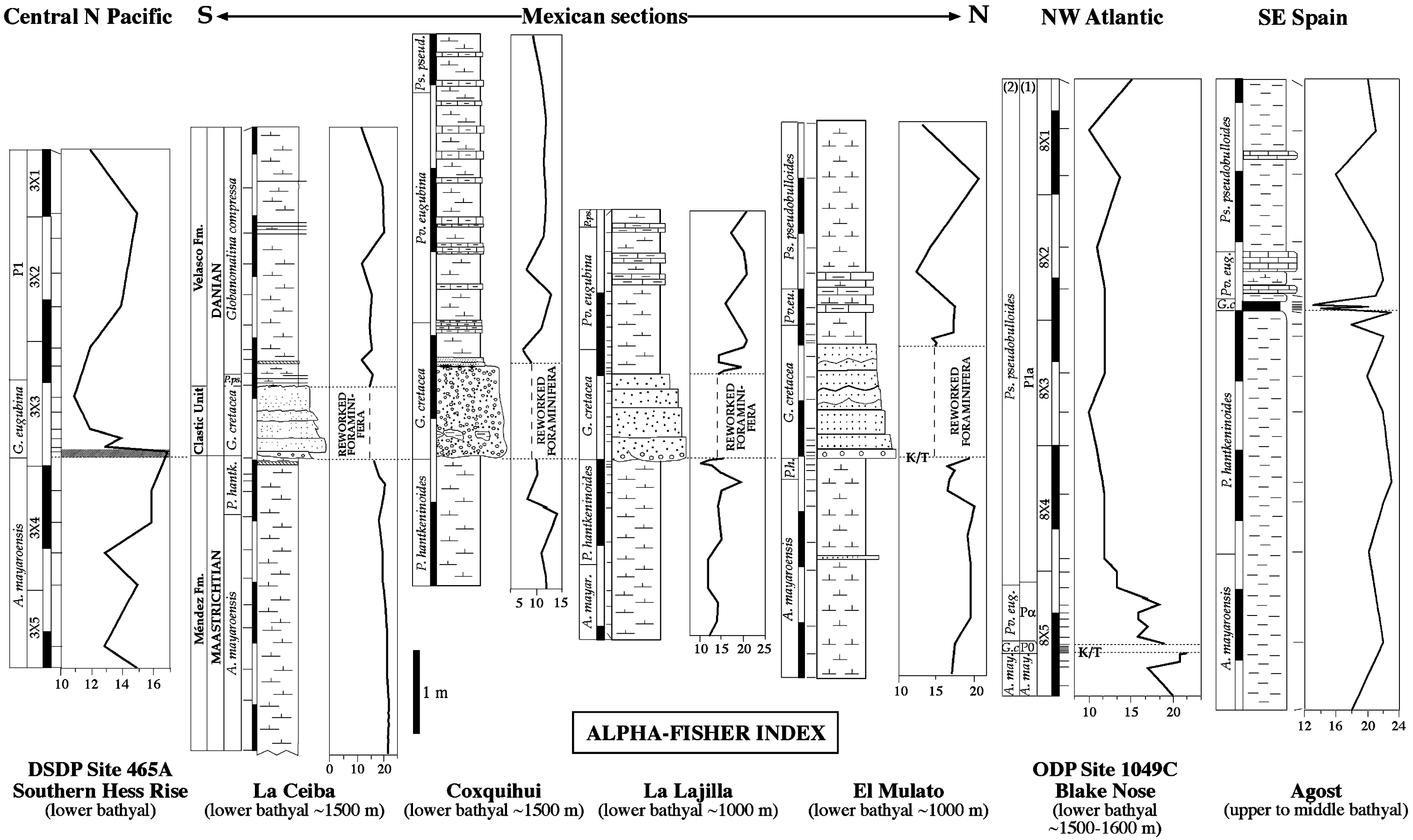

Fig. 4. Fisher-α diversity index in Upper Maastrichtian and lower Danian benthic foraminiferal assemblages from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1) Biostratigraphy by Norris et al. (1999) and Huber et al. (2002); (2) comparison to the biozonation proposed by Molina et al. (1996a).

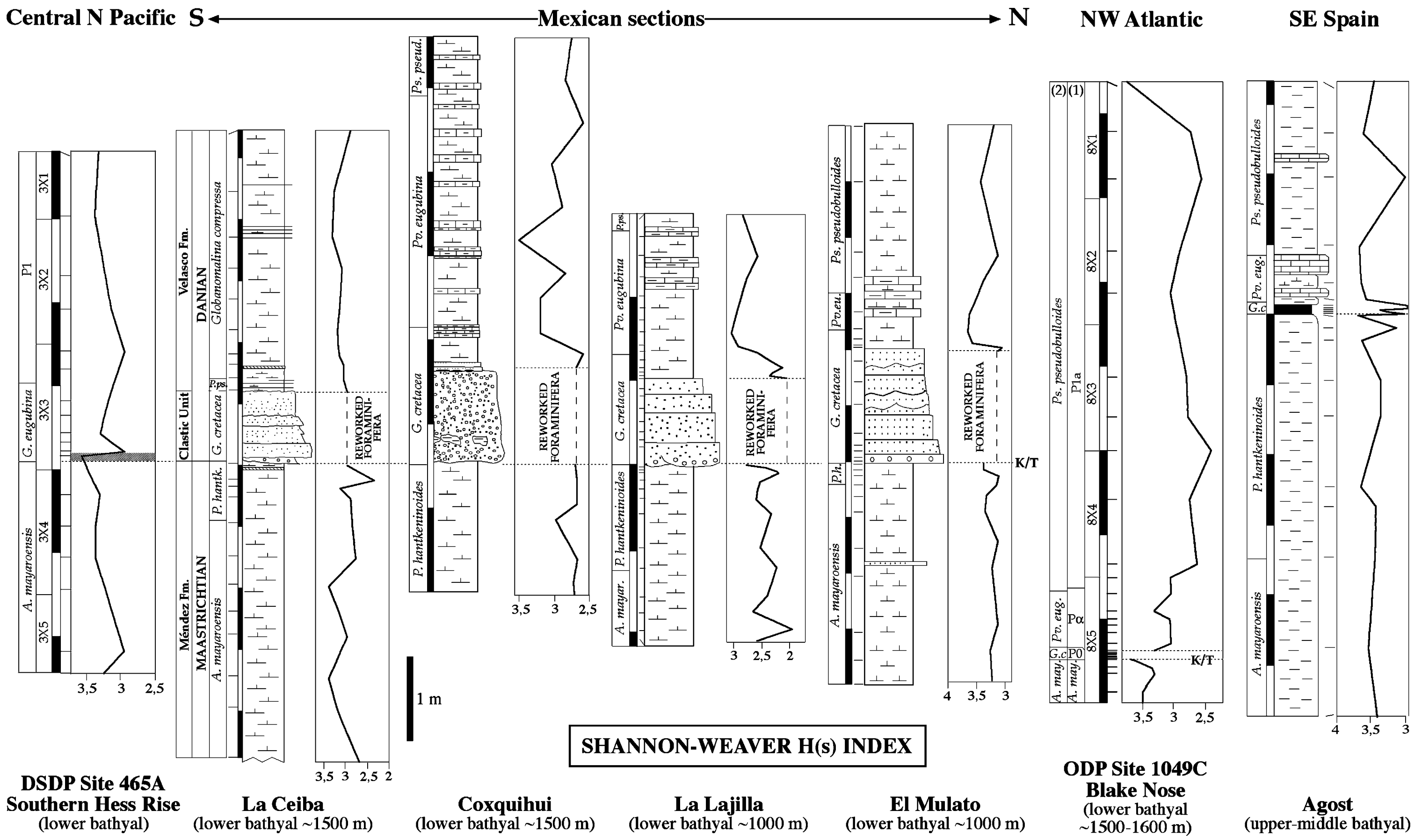

Fig. 5. Shannon–Weaver heterogeneity index $H(S)$ in Upper Maastrichtian and lower Danian benthic foraminiferal assemblages from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

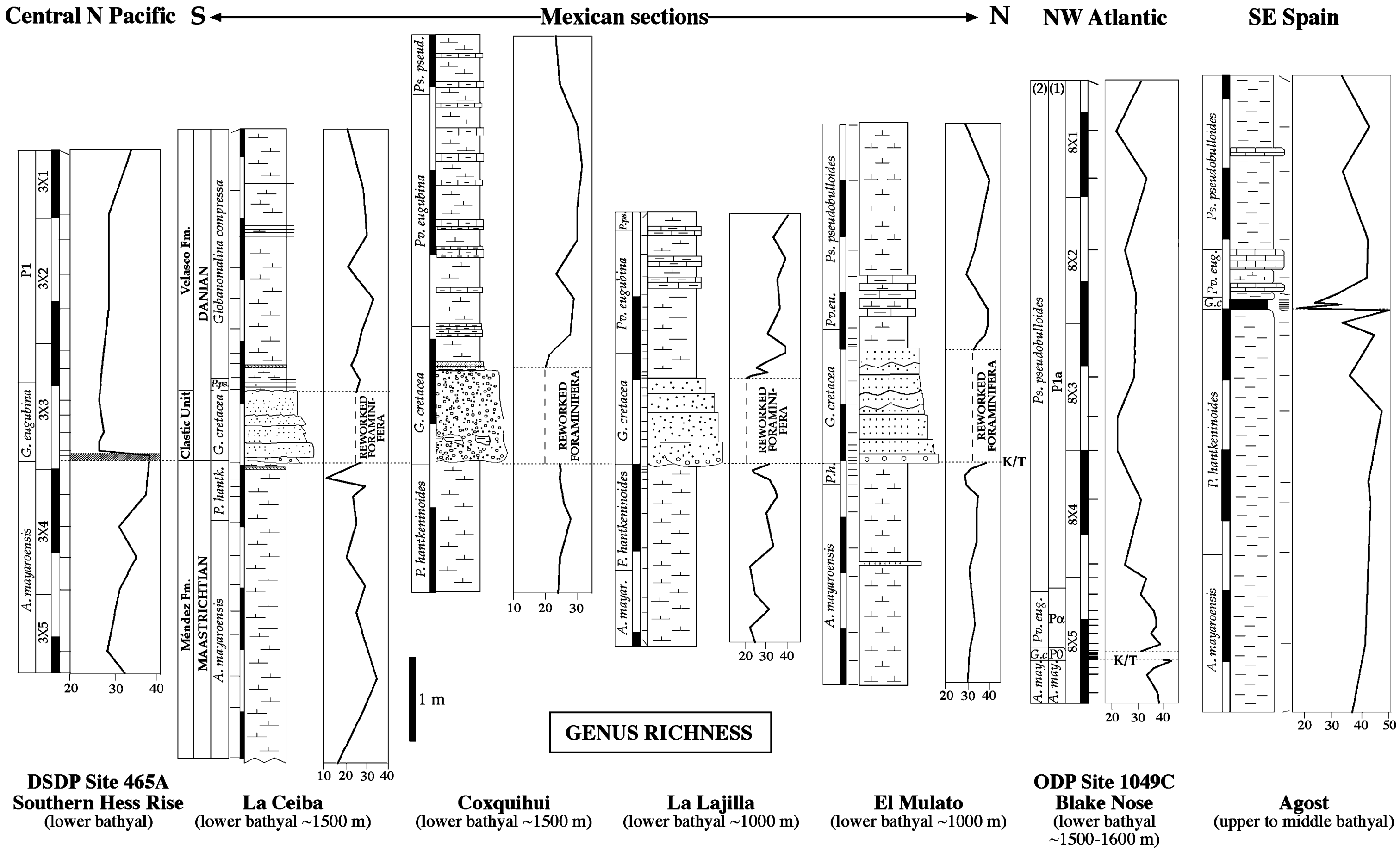

Fig. 6. Genus richness of Upper Maastrichtian and Lower Danian benthic foraminiferal assemblages from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

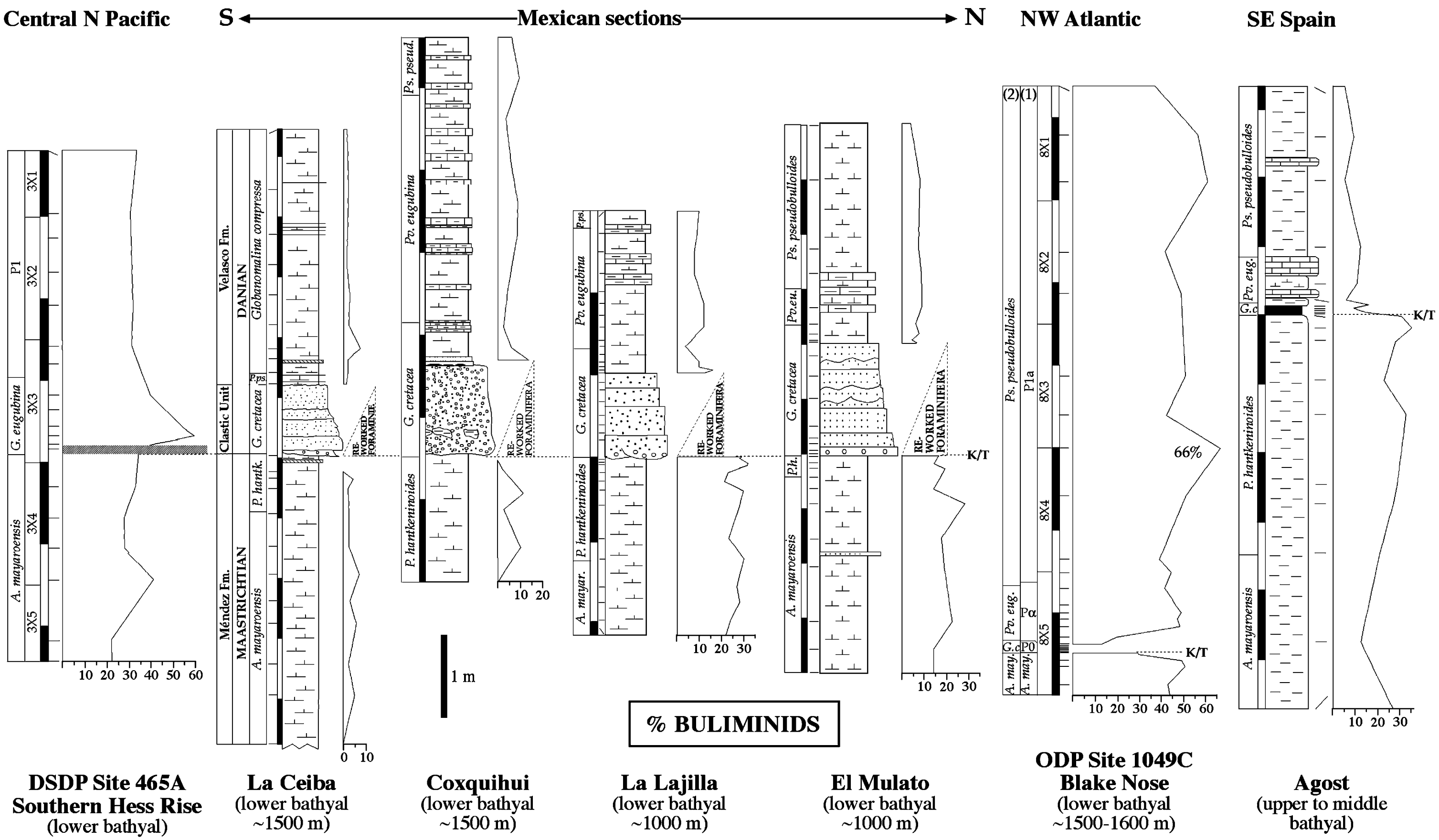

Fig. 7. Relative abundance of buliminids in upper Maastrichtian and lower Danian sediments from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

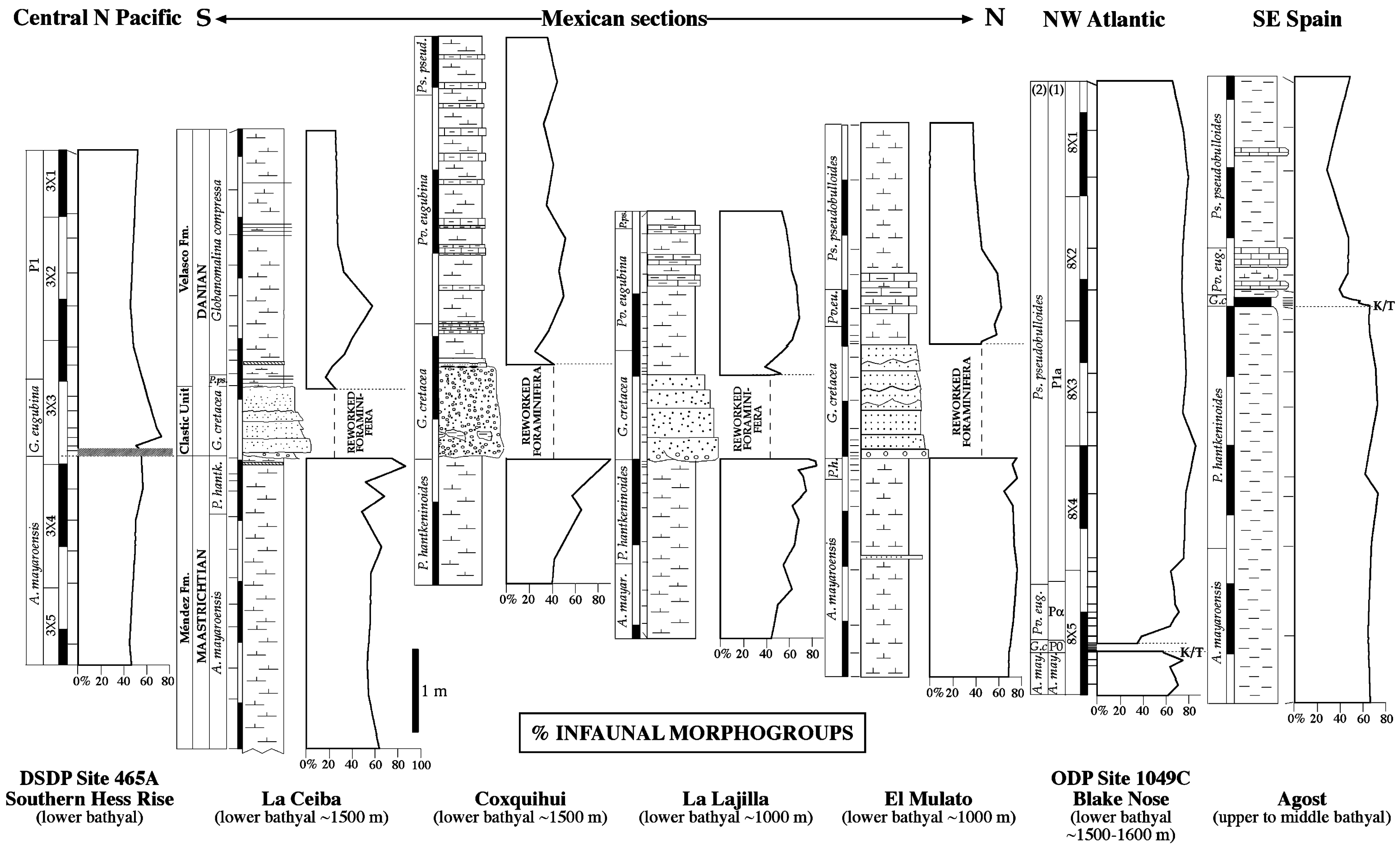

Fig. 8. Relative abundance of infaunal morphogroups in upper Maastrichtian and lower Danian sediments from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

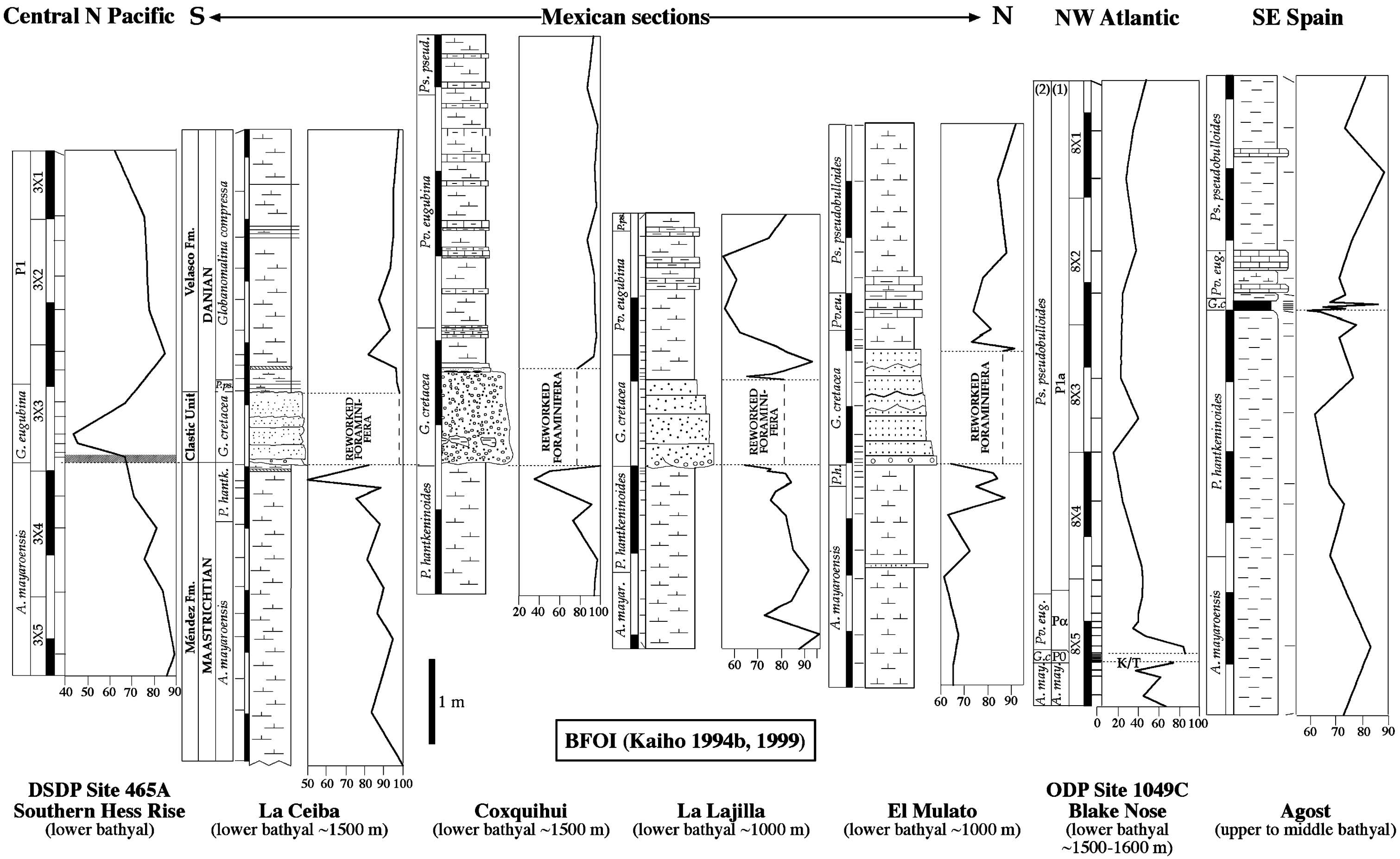

Fig. 9. Benthic foraminiferal oxygenation index (BFOI; Kaiho, 1994b), calculated in upper Maastrichtian and lower Danian sediments from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

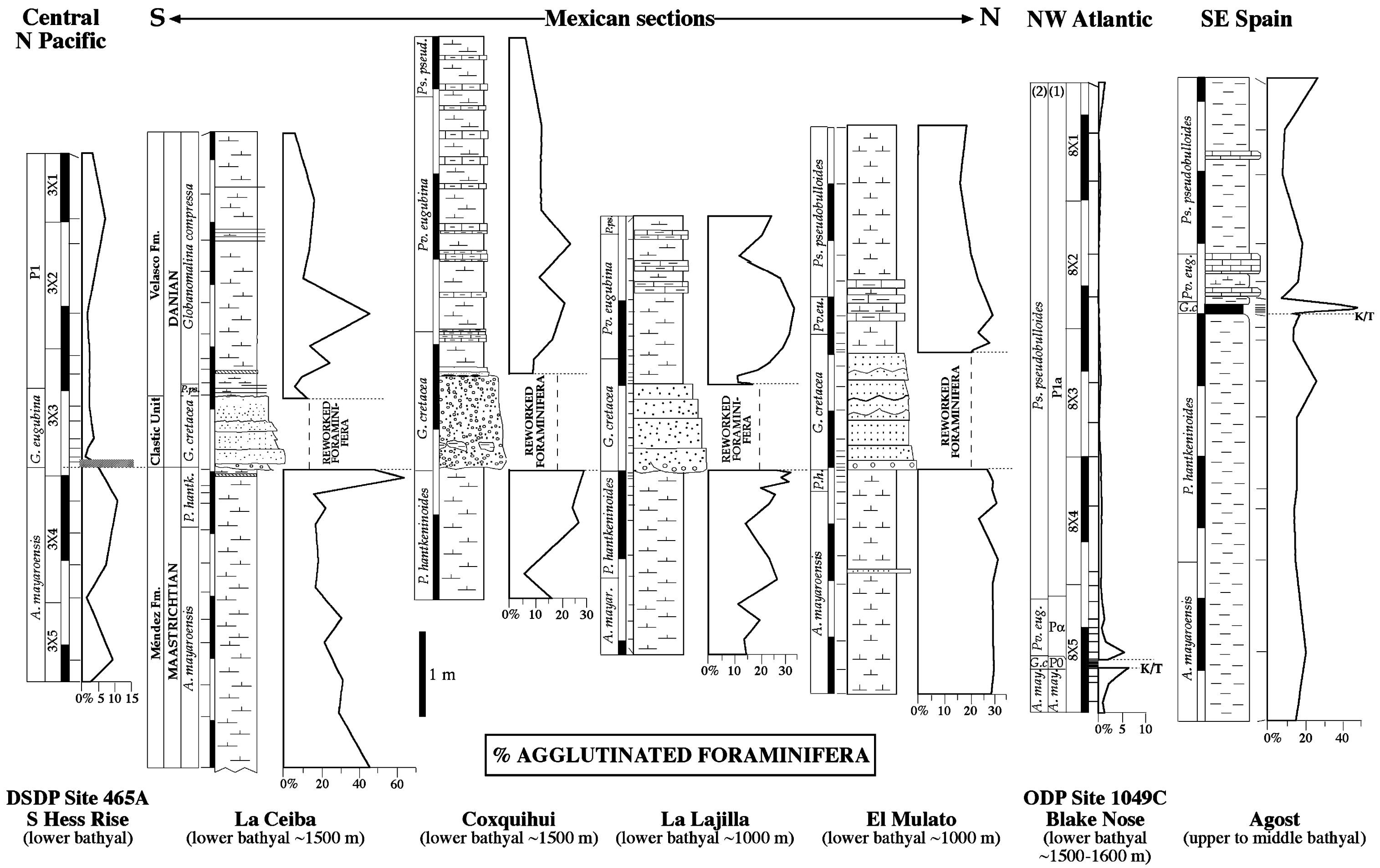

Fig. 10. Relative abundance of agglutinated foraminifers in upper Maastrichtian and lower Danian sediments from DSDP Hole 465A (Southern Hess Rise), from the Mexican sections, ODP Hole 1049C (Blake Nose) and from Agost (SE Spain). (1), (2), see note in caption for Fig. 4.

*compressa* Biozone (Figs. 5 and 6), while the relative abundance of infaunal morphogroups (30–40%) remains below Maastrichtian values (Fig. 8), and *Haplophragmoides* are abundant (7–25%) in the sections at greastest paleodepth (Alegret, 2003).

### 3.3. Benthic foraminiferal assemblages from Hole 1049C (Blake Nose, Northwestern Atlantic)

Benthic foraminiferal assemblages in Hole 1049C are dominated by calcareous forms (~94% of the assemblages; Fig. 10) in all samples (Alegret and Thomas, 2004). Upper Maastrichtian assemblages contain high percentages (58–74%) of infaunal taxa such as *Bulimina kugleri*, *B. beaumonti*, *P. reussi* (Fig. 8); among epifaunal morphogroups, *Globorotalites* sp. A, *N. truempyi*, *Gyroidinoides depressus* and *Anomalinoides* spp. are most abundant. Buliminids make up to 50% of the assemblages in the latest Maastrichtian (Fig. 7).

Benthic foraminifers are rare to absent in the green spherule-bed (base of the Danian), and the scarce foraminifers in this layer vary strongly in their preservation. The presence of both neritic (*Cibicidoides* aff. *welleri*, *Lenticulina rotulata*, *Oridorsalis plummerae*) and bathyal species (*Aragonia velascoensis*, *C. trilatera*, *G. pyramidata*, *G. globosus*, *N. truempyi*, *N. florealis*, *Osangularia velascoensis* and *S. beccariiformis*) corroborates that this layer is allochthonous (Alegret and Thomas, 2004).

Only 7% of the benthic foraminiferal species (*Reussella szajnochae* and *B. velascoensis*) last appear at the K/Pg boundary. The relative abundance of infaunal morphogroups decreases from 60% in the Maastrichtian to 35% in the lowermost Danian (Alegret and Thomas, 2004; Fig. 8). Genus richness, heterogeneity and diversity of the assemblages also decrease at the K/Pg boundary (Figs. 4–6). Just above the spherule-bed, samples from the lower part of *Pv. eugubina* Biozone are dominated by epifaunal taxa (64% of the assemblages), and contain abundant *Globorotalites* sp. A (up to 31% of the assemblages) and *Paralabamina* spp. (14% of the assemblages). Infaunal morphogroups, especially buliminid species such as *B. kugleri* and *F. tegulata*, increase and become dominant towards the middle part of *Pv. eugubina* Biozone (Alegret and Thomas, 2004; Figs. 7 and 8).

Infaunal taxa, especially *Nonionella robusta* and buliminids such as *B. kugleri* and *F. tegulata*, dominate in the *Ps. pseudobulloides* Biozone, making up to 84% of the assemblages, whereas diversity, heterogeneity and species richness reach the lowest values of the studied interval (Figs. 4–6). Higher in the core, towards Section 8X-1, all the diversity indices increase, whereas the relative abundances of *B. kugleri* and *F. tegulata* decrease and return to values similar to those in the Maastrichtian (Alegret and Thomas, 2004).

### 3.4. Benthic foraminiferal assemblages from Agost (Southeastern Spain)

Alegret et al. (2003) described the benthic assemblages at Agost. We include data on diversity, genus richness and the relative abundance of buliminids across the K/Pg boundary. Benthic foraminiferal assemblages contain ~80% of calcareous taxa throughout the section, except for the lowermost 10 cm of the Danian, where the agglutinated foraminifers make up ~70% of the assemblages (Fig. 10). Genus richness, diversity and heterogeneity of the assemblages are very high in the Maastrichtian (Figs. 4–6). *Loxostomum eleyi*, *E. subsculptura*, *Globorotalites* spp., laevidentalinids and *Sitella cushmani* are abundant in the first half part of the *P. hantkeninoides* Biozone; *P. reussi* becomes dominant in the second half of the *P. hantkeninoides* Biozone, where the percentage of buliminids is slightly higher than in the lowermost part of the section (Fig. 7).

The percentage of buliminids decreases at the K/Pg boundary, and it remains low throughout the rest of the section (Fig. 7). Genus richness, diversity and heterogeneity of the assemblages (Figs. 4–6) also decrease at the K/Pg boundary, as does the percentage of infaunal species (to 30%; Fig. 8). Only 5% of the species (e.g., *B. draco*, *E. subsculptura*) disappeared at the K/Pg boundary at Agost (Alegret et al., 2003).

In the lowermost Danian black clays *S. beccariiformis* increases in relative abundance, and there are several peaks in the relative abundance of opportunistic taxa such as *Ammodiscus*, *Glomospirella grzybowski*, *Pyramidina rudita*, *Repmanina charoides*, *Stilostomella* and especially *Haplophragmoides* (Alegret et al., 2003).

In the *Pv. eugubina* Biozone, *Globorotalites* and *Pleurostomella* become dominant; diversity and heterogeneity of the assemblages increase and reach the pre-K/Pg boundary values (Figs. 4 and 5). The genus richness increases but its values are lower than in the Upper Maastrichtian (Fig. 6). *S. beccariiformis* becomes very abundant in the *Ps. pseudobulloides* Biozone, where species such as *Cibicidoides ekblomi*, *C. hyphalus*, *G. beisseli*, laevidentalinids and *N. truempyi*, among others, are also common (Alegret et al., 2003).

## 4. Discussion

### 4.1. Paleoenvironmental reconstruction across the K/Pg boundary at DSDP Hole 465A (Hess Rise, central North Pacific)

Benthic foraminiferal assemblages from the uppermost Maastrichtian *A. mayaroensis* Biozone are diverse, contain abundant buliminids and consist of both infaunal and epifaunal morphogroups (Fig. 3). According to, e.g., Jorissen et al. (1995) and Gooday (2003), assemblages composed of mixed infaunal and epifaunal morphogroups may well have lived under mesotrophic conditions, with enough organic matter not only at the sediment surface but also in the deeper layers of the sediment. We thus interpret mesotrophic conditions during the *A. mayaroensis* Biochron, with a food flux to the sea floor high enough to sustain both infaunal and epifaunal morphogroups. BFAR values are fairly low to medium as compared to recent values (e.g., Gooday, 2003), also suggesting mesotrophic conditions. We are uncertain about interpretation of BFAR values, however, because no values have been published for other Cretaceous sections.

The uppermost Maastrichtian nannofossil and foraminiferal ooze is overlain by a thin “mixed zone” of drilling-disturbed Danian and Maastrichtian sediments. Kyte et al. (1980) interpret reducing conditions during the deposition of at least part of the mixed layer, represented by the dark clay fragments. Neither Widmark and Malmgren (1992) nor we found evidence for hypoxia; if such conditions existed they must have persisted for a much shorter time period than the duration of the *Pv. eugubina* Biochron, and we could not resolve them in the disturbed sediments.

The local extinction rates at the K/Pg boundary are low (up to 8.3% of the species), but there were dramatic changes in the assemblages at the K/Pg boundary as seen in the temporary disappearance of Lazarus taxa (Fig. 2), the drastic decrease in diversity, heterogeneity and genus richness, and the peak in BFAR (Fig. 3). BFAR data are generally used to infer productivity and delivery of food to the sea floor (see e.g., review by Gooday, 2003), and these data thus indicate a high supply of food to the sea floor during the period of lowest diversity and highest relative abundance of buliminids. The small size of the benthic foraminifers in the samples with high BFAR values might indicate high productivity of opportunistic species during a period of high food supply.

It is rather puzzling that BFAR values already are about 10 times as high as in the Maastrichtian during the lowermost Danian sample, in which peak relative abundances of epifaunal taxa appear to indicate lower food flux than in the Maastrichtian. We suggest that both this peak and the BFAR values are under-estimates because of the mixing of Cretaceous and Paleogene sediment. The rapid increase in the relative abundance of the epifaunal *P. lunata* in one sample just above the K/Pg boundary event might represent a very short period of slightly reduced food flux to the sea floor followed by a rapid recovery to a much higher food flux than in the Maastrichtian, as indicated by both high percentages of buliminids and high BFAR numbers.

A high abundance of buliminids and the occurrence of small specimens may indicate a high food supply or a reduced oxygen concentration (e.g., Bernhard and Reimers, 1991; Sen Gupta and Machain-Castillo, 1993; Bernhard et al., 1997), but the former is considered more likely (e.g., Fontanier et al., 2002), and the co-occurrence of high BFAR values definitely points to a high food flux. We thus suggest that, even if low oxygen conditions occurred just after the K/Pg boundary, they did not prevail through the *Pv. eugubina* Biozone, where the relative abundance of buliminids indicates high food supply to the sea floor.

The high percentage of *S. beccariiformis* and the rarity of *N. truempyi* corroborate the hypothesis that the food flux was high during the first half of Zone P1. However, the low diversity and heterogeneity of the assemblages, as well as the high dominance (assemblages mainly dominated by buliminids and by *S. beccariiformis*) suggest some environmental stress during this interval. We suggest that this stress was not in the amount of food supplied, but in the nature of the food. The *Thoracosphaera* bloom, for instance, indicates that plankton species different from those present before the extinction bloomed opportunistically, supplying a large amount of food that may have fluctuated in abundance and composition. We thus argue, in agreement with D'Hondt et al. (1998), that phytoplankton became highly productive again shortly after the K/Pg boundary. These authors also argued that little of this organic material may have reached the seafloor because the collapse the pelagic ecosystem might have decreased pellet production, thus delivery of food to the sea floor. Even in the near absence of pellet-producers, however, coagulation of phytoplankton may have delivered food to the benthos (Jackson, 2001). It probably took much longer to recover diversity than it took to recover biomass, however, and the high productivity was maintained by opportunistically blooming taxa (e.g, *Thoracosphaera*). Similar blooms have also been observed in the zooplankton at many locations (Keller and Pardo, 2004).

A recovery to pre-K/Pg boundary environmental conditions, including increased heterogeneity, genus richness, low dominance and decreased percentages of buliminids, occurred from the second half of P1 Zone towards the top of the studied interval (Fig. 3), throughout which interval BFAR values remained far above Maastrichtian values.

### *4.2. Comparison of paleoenvironmental turnover across the K/Pg boundary in the central North Pacific, the Northwestern Atlantic, the Gulf of Mexico and the Tethys*

Upper Maastrichtian benthic foraminiferal assemblages from all the studied sections are diverse, with values of the Fisher-α diversity index between 15 and 20 at most sites (Fig. 4). Shannon–Weaver index values are around 3.2–3.5 at Sites 465, 1049, and at Agost, and somewhat lower (2.4–3.4) in the Mexican sections (Fig. 5; Table 1). Genus richness is highest at Agost and Site 1049 (35–40), with values increasing from about 30 to 40 in the uppermost Maastrichtian at Site 465, and between 20 and 30 in the Mexican sections (Fig. 6). The Mexican sections differ from all others by their high relative abundances of agglutinated taxa (>20%), which according to Alegret et al. (2001a) could be related to the presence of larger amounts of terrigenous material in these sections (Fig. 10; Table 1).

In the upper Maastrichtian part of the sections the highest percentages of buliminids occur at Site 1049 (~40%), with values of 25–30% at Agost, Site 465, La Lajilla and El Mulato, even lower values (<10%) in the two deepest Mexican sections, La Ceiba and Coxquihui (Fig. 7). The high percentages of buliminids and other infaunal morphogroups and the low percentage of species typical for a low food supply (e.g., *C. hyphalus*, *N. truempyi* and *G. globosus*) suggest that Site 1049 was located in an upwelling area with high productivity and seasonally fluctuating high food supply to the sea floor (e.g., Widmark and Speijer, 1997; Alegret and Thomas, 2004).

Buliminids are common constituents of the infaunal group, but the trends in these two parameters are not fully parallel (Figs. 7 and 8; Table 1). Infaunal percentages in the upper Maastrichtian were highest at Site 1049, La Lajilla, El Mulato and Agost (60–80%; Table 1), with lower values at the other 2 Mexican sections (40–80%) and Site 465 (40–50%). The relative abundance of infaunal morphogroups increased towards the uppermost Maastrichtian in the Mexican sections, suggesting an increased flux of organic matter to the sea floor at the very end of the Cretaceous (Alegret et al., 2001a). The lowermost bathyal sections contain the lowest percentages of buliminids, suggesting that the organic flux decreased with depth as expected (Berger and Wefer, 1992).

BFOI values (Fig. 9) are in our opinion not true indicators of oxygenation at the observed values, and thus reflect food flux rather than oxygenation, in agreement with e.g., Gooday (2003) and many works reviewed by that author.

In the Mexican sections and at Site 1049 the benthic foraminiferal record is not complete across the K/Pg boundary (Figs. 4–10), because of the occurrence of layers with allochthonous assemblages.

The clastic unit in the Mexican sections mainly consists of food-poor, terrigenous sediments. According to Alegret et al. (2001a), these organic-poor sediments may have contributed to starving deep-sea benthic foraminifers after the K/Pg boundary in these sections. More complete records of the benthic faunas across the K/Pg boundary are provided at Agost and at Site 465. Benthic foraminiferal extinction rates are lower than 10% in all studied sections. Rather than significant extinction, benthic foraminifers show a reorganization of their community structure, including the temporal disappearance of some taxa and a decrease in diversity, heterogeneity and genus richness.

At Agost, geochemical and sedimentological evidence (Martínez-Ruiz et al., 1992, 1999) suggest a strong decrease in oxygenation (anoxia/hypoxia) during deposition of the black clays of the lowermost Danian. In this interval benthic foraminifers are rare, diversity and heterogeneity are low (Figs. 4 and 5), and several species show short peaks in relative abundance (Alegret et al., 2003). These authors speculate that these species may have been opportunistic taxa, with the blooms reflecting environmental instability possibly related to the presence of blooms of primary producers such as dinoflagellates.

We see no evidence for low oxygen conditions in the benthic foraminifers at DSDP Site 465, in agreement with Widmark and Malmgren (1992). There may have been a very short (much shorter than the duration of the *Pv. eugubina* Biozone) interval of low oxygen conditions reflected in the thin dark layer present only in drilling-disturbed fragments. At the Mexican sections and Site 1049 we cannot argue for or against the occurrence of hypoxia, because the record is interrupted by downslope transport. If there was such an episode of hypoxia, however, it must have had a duration considerably shorter than the duration of the *G. cretacea* Biozone: sediments of the upper *G. cretacea* Biozone are present above the allochthonous layers (Figs. 4–10) and their faunas show no indications for hypoxia.

Various authors, including Kajiwara and Kaiho (1992) and Kyte et al. (1980), suggested that the ocean might have been anoxic globally after the K/Pg boundary, but using our data as well as published data, we argue that local or regional anoxia only is supported by the evidence, e.g., from the Fish Clay in Denmark (Coccioni and Galeotti, 1998), and in some parts of the Tethys such as sections Agost and Caravaca (Coccioni et al., 1993; Coccioni and Galeotti, 1994, 1998; Kaiho et al., 1999; Alegret et al., 2003). We think that the preponderance of evidence indicates that dysoxic or anoxic conditions were not widespread in Tethys. For instance, it has been argued that low oxygen conditions occurred after the K/Pg boundary in Tunisian sections (e.g., Keller, 1988; Speijer and Van der Zwaan, 1994, 1996; Kouwenhoven, 2000), but geochemical evidence and the benthic foraminiferal faunas do not support this (e.g., Tribovillard et al., 2000; Peryt et al., 2002). The argument for low oxygen conditions in the above papers is mainly based on the occurrence of low diversity benthic faunas just above the K/Pg boundary. These low-diversity benthic faunas, however, were dominated by large, heavily calcified epifaunal species, suggesting that adverse conditions other than low oxygen conditions were involved (see below).

We do not have evidence for detailed paleoenvironmental reconstructions at all our sections because of the presence of the allochthonous material in the Mexican sections and at Site 1049, but we can compare lower Danian and upper Maastrichtian faunas. At Agost, diversity and heterogeneity were low in the black clays (*G. cretacea* Biozone), but returned to values similar to those in the Maastrichtian in the *Pv. eugubina* Biozone. At Site 1049 diversity and heterogeneity decreased somewhat at the K/Pg boundary, but more so at the end of the *Pv. eugubina* Biozone, remaining low throughout the studied section (*Ps. pseudobulloides* Biozone). In the Mexican sections, diversity and heterogeneity fluctuated through the *Pv. eugubina* and *Ps. pseudobulloides* Zones.

The decrease in diversity, heterogeneity and genus richness is slight at the deepest Mexican sections La Ceiba and Coxquihui (Figs. 4–6). Smaller changes in the deepest sections may be due to (1) the less dramatic faunal turnover in lowermost bathyal environments, where benthic foraminiferal assemblages were used to living under more oligotrophic conditions; or (2) the incompleteness of these sections and the presence of unconformities in the uppermost Maastrichtian and/or lowermost Danian. At Site 465 diversity and heterogeneity decreased at the K/Pg boundary, were low in the *Pv. eugubina* Biozone, and recovered somewhat but not completely in Zone P1. There is thus a tendency to decreasing diversity and heterogeneity, but to different degrees in different sections.

The percentage of infaunal morphogroups and buliminids decreased at the K/Pg boundary in the Mexican sections and at Agost, and at these sections did not recover to Maastrichtian values in the studied interval (*Ps. pseudobulloides* Biozone; *Gl. compressa* Biozone at La Ceiba; Alegret et al., 2001a, 2003). Such a decrease was also observed at Site 1049, but recovery occurred within the *Pv. eugubina* Biozone (Alegret and Thomas, 2004). At Site 465 only one sample shows a higher relative abundance of epifaunal morphogroups, and even that sample has a high BFAR (Fig. 3). Unfortunately, we do not have BFAR values for the other locations.

A decrease in infaunal taxa and in the percentage of buliminids suggests a decrease in the food supply to the sea floor, probably related to the catastrophic mass extinction of calcareous plankton at the K/Pg boundary and the subsequent collapse of primary productivity (e.g., Zachos et al., 1986; D'Hondt et al., 1998; Alegret et al., 2001a). During this period of oligotrophic conditions, epifaunal species that lived close to the sediment surface were able to feed on the scarce food available, whereas infaunal taxa decreased in abundance (e.g., Jorissen et al., 1995). Our data thus suggest that a decrease in food supply was long-lived at Agost and the Mexican sections (lasting through at least part of the *Ps. pseudobulloides* Biozone), much shorter lived at the more eutrophic Site 1049 (less than the *Pv. eugubina* Biozone), and may have been even shorter or absent at Site 465 in the Pacific Ocean, distal from the impact site.

At Site 465 the food supply in the Danian was much higher than in the Maastrichtian, as suggested by the BFAR values as well as high percentages of buliminids, while diversity and evenness were low in the samples with high BFAR values (Fig. 3). We speculate that the overall biomass produced by the phytoplankton over this site increased strongly after the K/Pg boundary extinction of primary producers. The food supplied to the benthos, however, differed in nature from that produced before the mass extinction of phytoplankton, in agreement with D'Hondt et al. (1998). In agreement with Peryt et al. (2002; Aïn Settara section, Tunisia), Alegret et al. (2003; Agost section, Spain), Alegret and Thomas (2004; Site 1049, NW Atlantic) and Alegret et al. (2004; Bidart section, SW France), we argue that the phytoplankton composition changed as a result of the mass extinction, with the dominant role being taken over by such organisms as dinoflagellates or *incertae sedis* organisms (e.g., *Thoracosphaera*). In the present oceans few organisms consume dinoflagellates, and the unusually low diversity faunas may have lived in a stressful environment because of this change in the composition of food supply.

At NW Atlantic ODP Hole 1049C and central North Pacific DSDP Hole 465A, the food supply recovered quickly, and at Site 465 was probably higher than in the Maastrichtian, but the environmental conditions did not stabilize until, at least, the upper half of the *Ps. pseudobulloides* Biozone (~300 ky after the K/Pg boundary impact event), as indicated by the low diversity, low heterogeneity and high dominance of the assemblages, as well as the low genus richness (Figs. 4–6).

The question remains what could have caused local or regional hypoxia or anoxia after the K/Pg boundary? In general, low oxygen conditions are caused by the use of oxygen in decomposition of organic matter, abundant at high productivity. Alegret et al. (2003) wondered whether the geographically and temporally limited phytoplankton blooms just after the K/Pg boundary could have supplied sufficient organic matter to the sea floor for conditions at Agost to become hypoxic to anoxic for 10–15 ky (Martínez-Ruiz et al., 1992, 1999). Kyte et al. (1980), Coccioni et al. (1993), and Coccioni and Galeotti (1998) suggested that low oxygen conditions resulted from rotting organisms that died in the mass extinction. Kuhnt and Kaminski (1996) and Alegret et al. (2003), however, argued that this hypothesis is improbable because oceanic biomass in the present world is only a very small fraction of the world's total biomass, and oxidation of even the complete oceanic biomass would not use up enough oxygen to keep the oceans anoxic/hypoxic for thousands of years. A large influx of terrigenous biomass into the oceans does not appear likely, because much of the terrestrial biomass may have been destroyed in huge fireballs (e.g., Max et al., 1999), although this is a matter of debate. For instance, Arinobu et al. (1999) argue that only up to ~25% burned. Alegret et al. (2003) speculated that the oxidation of methane released by destabilization of gas hydrates (e.g., Norris and Berger, 2003) along the continental margins triggered by the K/Pg impact may have been at least in part the cause of low-oxygen conditions.

We do not yet have enough evidence to evaluate the severity, geographic and depth extent of hypoxia following the K/Pg boundary, or its cause. Such hypoxia cannot have been severe globally, however, because global hypoxia would have caused a major extinction of deep-sea benthic foraminifers, which did not occur (e.g., Culver, 2003).

## 5. Conclusions

Benthic foraminiferal assemblages in lower bathyal sections from DSDP Hole 465A (Hess Rise, central North Pacific), ODP Hole 1049C (Blake Nose, Northwestern Atlantic), central-East and Northeastern Mexico, and from the upper to middle bathyal Agost section (Tethys area, Southeastern Spain) indicate mesotrophic conditions during the uppermost Maastrichtian, with conditions some more eutrophic at ODP Hole 1049C. Benthic assemblages indicate that the food supply to the sea floor decreased in all these sections in coincidence with the K/Pg boundary (with the possible exception of Site 465), suggesting that a major event suddenly destabilized the oceanic food web. These data, together with the sedimentological, mineralogical and geochemical evidence, are compatible with an asteroid impact at the K/Pg boundary. Although the impact caused a widespread severe drop in primary productivity, it did not lead to major extinction of benthic foraminifers but only to temporary faunal restructuring, possibly because deep-sea benthic foraminifers tolerate oligotrophy, or because productivity resumed rapidly at some locations (such as Site 465).

The recovery of benthic foraminiferal assemblages through the lower Danian indicates that the recovery of the amount of food supplied to the sea floor (as distinguished from a recovery of taxonomic diversity) was geographically variable in timing. This flux recovered earlier (within the *Pv. eugubina* Biozone) at DSDP Hole 465A and ODP Hole 1049C, although a longer period of environmental stress (extending through the *Ps. pseudobulloides* Biozone) may have been related to a dominance of the food supply by opportunistic bloom species. The food delivery to the sea floor in the Mexican and in the Spanish sections did not recover until, at least, the *Ps. pseudobulloides* Biozone, i.e., 300,000 years after the K/Pg boundary.

No evidence for global hypoxia, but only for local, regional low oxygen conditions at the sea floor has been inferred from benthic foraminiferal assemblages, although short episodes of hypoxia could not be recognized in the Mexican sections and Site 1049 because of downslope transport of allochthonous material at the K/Pg boundary and resulting incompleteness of the sections. The causes for such local low oxygen conditions are not clear, but the accumulation of dead oceanic biomass is quantitatively improbable. K/Pg impact-triggered dissociation of methane hydrates (caused by mass wasting) is a possible hypothesis to explain the local, oxygen-depleted conditions at the sea floor.

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## Appendix A. Counts of benthic foraminifers from DSDP Hole 465A (Southern Hess Rise)

| Section | 3X5 | 3X5 | 3X4 | 3X4 | 3X4 | 3X4 | 3X3 | 3X3 | 3X3 | 3X3 | 3X3 | 3X3 | 3X2 | 3X1 | 3X1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sample (cm) | −93–95 | −65–68 | −143–146 | −104–107 | −66–69 | −29–32 | −132–135 | −126–129 | −115–118 | −105–108 | −64–67 | −6–9 | −106–109 | −144–147 | −64–67 |
| mbsf | 64.94 | 64.66 | 63.94 | 63.55 | 63.17 | 62.8 | 62.33 | 62.27 | 62.16 | 62.06 | 61.65 | 61.07 | 60.57 | 59.45 | 58.65 |
| *Species* | | | | | | | | | | | | | | | |
| *Clavulinoides amorpha* | 0.00 | 0.37 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Clavulinoides trilatera* | 0.00 | 0.74 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Clavulinoides* spp. | 0.00 | 1.12 | 0.00 | 0.46 | 0.49 | 0.62 | 0.32 | 0.00 | 0.00 | 2.83 | 1.39 | 0.71 | 0.00 | 0.85 | 0.67 |
| *Dorothia pupa* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.64 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Dorothia* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.71 | 0.00 | 0.42 | 0.00 |
| *Gaudryina pyramidata* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.00 |
| *Gaudryina* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | 0.32 | 0.51 | 0.49 | 0.00 | 0.00 | 0.36 | 0.46 | 0.00 | 0.00 |
| *Marssonella oxycona* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Marssonella* spp. | 0.35 | 0.00 | 0.00 | 0.00 | 1.46 | 0.62 | 1.29 | 0.00 | 0.49 | 0.81 | 0.00 | 0.00 | 0.46 | 0.00 | 0.34 |
| *Spiroplectammina excolata* | 0.00 | 0.37 | 0.00 | 0.23 | 0.49 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Spiroplectammina* spp. | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Spiroplectammina spectabilis* | 1.42 | 5.20 | 0.35 | 3.93 | 2.43 | 4.64 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.36 | 0.00 | 5.51 | 2.35 |
| *Vulvulina* sp. | 0.71 | 1.86 | 0.35 | 2.31 | 3.88 | 4.33 | 1.29 | 0.51 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Alabamina wilcoxensis* | 0.00 | 0.37 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Anomalinoides acutus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.34 |
| *Anomalinoides affinis* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 0.00 | 1.05 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Anomalinoides ammonoides* | 0.71 | 0.00 | 0.35 | 0.00 | 0.00 | 0.31 | 3.54 | 2.03 | 1.46 | 0.81 | 8.36 | 3.93 | 2.30 | 0.85 | 3.36 |
| *Anomalinoides* spp. | 0.35 | 0.00 | 1.05 | 0.23 | 0.97 | 0.62 | 0.96 | 2.03 | 1.46 | 0.40 | 1.39 | 5.36 | 4.61 | 2.12 | 0.00 |
| *Aragonia* sp. | 1.06 | 0.00 | 3.16 | 0.00 | 0.49 | 0.00 | 0.00 | 4.57 | 7.28 | 7.69 | 1.05 | 0.36 | 0.00 | 2.12 | 0.00 |
| *Aragonia velascoensis* | 2.13 | 1.86 | 1.05 | 2.54 | 1.46 | 1.86 | 5.14 | 0.00 | 0.97 | 3.24 | 0.70 | 1.43 | 0.00 | 2.12 | 0.34 |
| *Bolivinoides decoratus* | 0.00 | 0.00 | 0.00 | 0.69 | 0.00 | 0.00 | 0.64 | 4.06 | 6.31 | 3.64 | 6.62 | 2.50 | 2.30 | 1.27 | 3.36 |
| *Bolivinoides delicatulus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.36 | 0.00 | 0.85 | 2.01 |
| *Bulimina* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.05 | 3.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Bulimina midwayensis* | 0.35 | 0.37 | 0.00 | 1.15 | 0.97 | 0.31 | 1.29 | 3.05 | 1.46 | 4.86 | 5.92 | 2.86 | 1.84 | 3.81 | 2.01 |
| *Bulimina ovula* | 0.35 | 0.00 | 5.26 | 0.00 | 0.49 | 0.00 | 1.93 | 12.18 | 11.65 | 10.12 | 3.83 | 3.57 | 8.29 | 6.36 | 8.05 |
| *Bulimina trinitatensis* | 0.00 | 0.00 | 0.00 | 0.46 | 0.97 | 0.93 | 5.79 | 3.05 | 12.14 | 6.88 | 6.62 | 8.21 | 4.15 | 0.85 | 0.00 |
| *Bulimina velascoensis* | 4.96 | 5.95 | 3.51 | 3.46 | 3.88 | 3.41 | 3.22 | 2.54 | 8.74 | 6.48 | 5.23 | 5.00 | 7.37 | 5.08 | 3.02 |
| *Buliminella beaumonti* | 3.55 | 6.32 | 10.88 | 6.93 | 2.91 | 5.57 | 1.61 | 2.03 | 3.40 | 3.24 | 2.09 | 1.43 | 0.46 | 3.39 | 3.02 |
| *Buliminella* spp. | 0.71 | 0.00 | 1.75 | 0.46 | 0.97 | 0.31 | 0.00 | 2.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.00 |
| *Cibicidoides hyphalus* | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.64 | 1.02 | 0.97 | 0.00 | 2.09 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Cibicidoides velascoensis* | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.31 | 0.64 | 0.00 | 0.00 | 0.40 | 0.00 | 0.00 | 0.46 | 0.42 | 0.34 |
| *Cibicidoides howelli* | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.96 | 0.00 | 0.00 | 0.00 | 0.00 | 1.07 | 0.92 | 1.27 | 0.00 |
| *Cibicidoides* spp. | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.21 | 0.00 | 1.07 | 0.46 | 0.00 | 0.00 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Coryphostoma* sp. | 0.00 | 0.00 | 0.70 | 0.46 | 0.00 | 0.31 | 0.64 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Ellipsodimorphina* spp. | 0.71 | 1.86 | 0.35 | 1.15 | 0.49 | 0.93 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Eouvigerina subsculptura* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Eouvigerina* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.34 |
| *Euuvigerina elongata* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.02 | 0.97 | 1.21 | 1.74 | 1.79 | 0.92 | 0.00 | 0.34 |
| *Fissurina* spp. | 0.35 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.70 | 0.00 | 0.92 | 0.85 | 0.34 |
| *Frondicularia* sp. | 0.35 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Fursenkoina tegulata* | 2.48 | 1.12 | 1.05 | 3.23 | 4.37 | 5.57 | 4.82 | 0.51 | 0.97 | 4.05 | 3.14 | 1.43 | 1.84 | 1.27 | 5.70 |
| *Glandulina* spp. | 1.06 | 0.37 | 0.00 | 1.15 | 0.00 | 1.24 | 0.00 | 0.00 | 0.00 | 0.40 | 0.00 | 0.36 | 1.38 | 0.00 | 0.00 |
| *Globulina prisca* | 0.00 | 0.37 | 0.00 | 0.00 | 0.00 | 0.93 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Globulina* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.32 | 1.02 | 0.49 | 0.00 | 0.35 | 0.00 | 0.00 | 0.00 | 0.67 |
| *Guttulina* sp. | 0.35 | 0.00 | 0.00 | 0.23 | 0.00 | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Globorotalites* sp. | 5.67 | 2.60 | 7.02 | 3.70 | 4.85 | 2.48 | 4.82 | 1.02 | 0.49 | 0.40 | 0.00 | 0.00 | 0.00 | 9.32 | 7.05 |
| *Gyroidinoides beisseli* | 5.67 | 1.86 | 0.00 | 0.92 | 2.43 | 1.55 | 0.32 | 0.00 | 0.00 | 0.40 | 0.35 | 0.71 | 0.00 | 0.85 | 3.36 |
| *Gyroidinoides depressus* | 0.35 | 0.74 | 1.40 | 0.69 | 0.00 | 0.00 | 1.61 | 2.03 | 0.00 | 0.81 | 1.74 | 1.79 | 2.76 | 0.85 | 3.69 |
| *Gyroidinoides globosus* | 0.00 | 0.74 | 0.70 | 0.00 | 0.00 | 0.62 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Gyroidinoides gyrardanus* | 0.00 | 0.00 | 0.35 | 0.00 | 0.00 | 0.31 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.71 | 0.00 | 0.42 | 0.00 |
| *Gyroidinoides* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.35 | 0.00 | 0.46 | 0.00 | 0.00 |
| *Heronallenia lingulata* | 0.35 | 0.00 | 0.00 | 0.23 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.34 |
| Laevidentalinids | 6.03 | 2.60 | 1.40 | 5.77 | 3.40 | 2.17 | 3.86 | 1.02 | 2.91 | 2.02 | 4.53 | 5.36 | 4.61 | 3.81 | 6.04 |
| *Lagena* spp. | 1.06 | 1.49 | 0.35 | 0.69 | 1.94 | 1.86 | 0.32 | 0.00 | 0.49 | 0.40 | 0.70 | 0.00 | 0.92 | 0.42 | 0.34 |
| *Lenticulina* spp. | 0.35 | 0.00 | 0.35 | 0.69 | 0.49 | 0.62 | 0.64 | 0.51 | 0.00 | 0.00 | 0.00 | 0.71 | 0.00 | 0.42 | 0.67 |
| *Marginulina* sp. | 0.35 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Neoflabellina* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Nuttallides* spp. | 2.13 | 0.00 | 2.81 | 0.00 | 3.88 | 0.62 | 0.32 | 0.00 | 0.49 | 0.40 | 0.00 | 0.00 | 0.00 | 1.69 | 0.00 |
| *Nuttallides truempyi* | 1.42 | 13.01 | 0.00 | 4.85 | 2.91 | 2.17 | 2.89 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.92 | 1.69 | 4.03 |
| *Nuttallinella florealis* | 7.45 | 1.49 | 1.40 | 2.08 | 1.46 | 1.24 | 0.32 | 1.02 | 0.97 | 0.00 | 0.00 | 0.00 | 1.38 | 2.12 | 0.00 |
| *Nuttallinella* spp. | 1.06 | 1.86 | 6.67 | 4.16 | 1.46 | 0.00 | 1.29 | 6.60 | 0.97 | 2.43 | 2.44 | 0.00 | 3.23 | 3.39 | 2.35 |
| *Oridorsalis plummerae* | 0.00 | 0.00 | 0.35 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Oridorsalis umbonatus* | 1.06 | 1.86 | 2.11 | 1.85 | 0.97 | 1.55 | 2.25 | 1.02 | 1.46 | 3.24 | 1.05 | 1.43 | 4.61 | 4.24 | 2.01 |
| *Oridorsalis* spp. | 1.42 | 2.60 | 1.05 | 2.08 | 1.94 | 3.72 | 0.96 | 0.51 | 0.49 | 0.81 | 0.00 | 0.00 | 1.38 | 1.69 | 0.00 |
| *Osangularia cordieriana* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Osangularia velascoensis* | 2.84 | 0.37 | 2.46 | 3.93 | 0.97 | 4.33 | 1.93 | 0.51 | 0.49 | 2.02 | 1.74 | 0.71 | 0.46 | 1.69 | 1.34 |
| *Osangularia* spp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.51 | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Paliolatella* sp. | 0.00 | 0.00 | 0.70 | 0.23 | 0.00 | 0.62 | 0.96 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.34 |
| *Paralabamina hillebrandti* | 0.71 | 0.74 | 0.00 | 0.23 | 0.49 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.00 | 0.36 | 0.00 | 1.69 | 0.00 |
| *Paralabamina lunata* | 1.77 | 1.12 | 9.12 | 5.77 | 5.34 | 5.26 | 8.36 | 25.38 | 8.74 | 9.72 | 5.23 | 9.64 | 18.89 | 11.86 | 15.44 |
| *Paralabamina* sp. thick | 3.55 | 0.74 | 1.05 | 4.85 | 3.88 | 1.24 | 0.00 | 0.00 | 0.00 | 0.81 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Pleurostomella* spp. | 0.00 | 0.00 | 0.35 | 1.15 | 0.97 | 1.24 | 2.57 | 1.52 | 1.94 | 1.21 | 1.74 | 0.36 | 1.38 | 0.85 | 0.00 |
| *Praebulimina reussi* | 4.61 | 4.46 | 8.07 | 6.24 | 6.31 | 10.22 | 3.22 | 1.52 | 2.43 | 1.21 | 1.05 | 0.00 | 0.92 | 0.00 | 0.00 |
| *Praebulimina* spp. | 1.77 | 0.74 | 3.86 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.21 | 0.35 | 1.07 | 0.00 | 0.00 | 0.34 |

*(continued on next page)*

**Appendix A** (*continued*)

| Section | 3X5 | 3X5 | 3X4 | 3X4 | 3X4 | 3X4 | 3X3 | 3X3 | 3X3 | 3X3 | 3X3 | 3X3 | 3X2 | 3X1 | 3X1 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sample (cm) | −93–95 | −65–68 | −143–146 | −104–107 | −66–69 | −29–32 | −132–135 | −126–129 | −115–118 | −105–108 | −64–67 | −6–9 | −106–109 | −144–147 | −64–67 |
| mbsf | 64.94 | 64.66 | 63.94 | 63.55 | 63.17 | 62.8 | 62.33 | 62.27 | 62.16 | 62.06 | 61.65 | 61.07 | 60.57 | 59.45 | 58.65 |
| *Pseudopolimorphina cuyleri* | 0.00 | 0.37 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Pseudopolimorphina* sp. | 0.71 | 0.00 | 0.00 | 0.23 | 0.00 | 0.31 | 0.64 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.34 |
| *Pullenia jarvisi* | 0.35 | 0.37 | 0.00 | 0.46 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.71 | 0.92 | 0.00 | 0.00 |
| *Pyramidina rudita* | 0.35 | 1.12 | 0.70 | 0.00 | 0.97 | 0.00 | 1.61 | 3.55 | 0.97 | 1.62 | 1.74 | 1.79 | 3.23 | 2.12 | 5.37 |
| *Pyramidina* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.93 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Pyrulinoides* sp. | 0.00 | 0.00 | 0.00 | 0.46 | 0.97 | 0.31 | 0.00 | 0.00 | 0.97 | 0.00 | 0.70 | 0.00 | 0.00 | 0.42 | 0.00 |
| *Quadratobuliminella pyramidalis* | 0.00 | 0.00 | 0.00 | 0.00 | 0.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Quadrimorphina allomorphinoides* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Quadrimorphina* sp. flat | 0.00 | 0.00 | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 | 1.02 | 0.00 | 0.40 | 0.35 | 0.00 | 0.00 | 0.42 | 2.01 |
| *Quinqueloculina* sp. | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.34 |
| *Reusella szajnochae* | 0.00 | 0.37 | 0.35 | 2.08 | 3.40 | 3.72 | 2.57 | 0.00 | 0.00 | 0.00 | 0.00 | 0.71 | 0.00 | 0.85 | 0.00 |
| *Scheibnerova* sp. | 9.22 | 10.78 | 8.07 | 7.16 | 9.71 | 3.72 | 1.29 | 0.51 | 0.97 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Stillostomella subspinosa* | 2.84 | 2.23 | 0.35 | 1.39 | 1.46 | 1.55 | 5.47 | 1.52 | 3.40 | 4.45 | 8.71 | 5.00 | 1.84 | 4.24 | 2.01 |
| *Stensioeina beccariiformis* | 14.89 | 17.47 | 5.26 | 8.55 | 11.65 | 13.93 | 10.29 | 5.08 | 7.28 | 8.10 | 14.29 | 25.36 | 10.60 | 5.51 | 3.69 |
| *Valvalabamina lenticula* | 0.00 | 0.00 | 0.35 | 0.00 | 0.00 | 0.31 | 1.29 | 0.00 | 0.00 | 0.00 | 0.00 | 0.71 | 0.46 | 0.00 | 1.34 |

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