

Paleoenvironmental Recovery After the Cretaceous/Paleogene Boundary Crisis: Evidence From the Marine Bidart Section (SW France)

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*The study of Upper Cretaceous and Lower Paleogene benthic foraminifera from the Bidart section (SW France) provides detailed data on the paleobathymetry as well as paleoenvironmental conditions across the Cretaceous/Paleogene (K/Pg) boundary. A quantitative analysis of benthic foraminiferal assemblages from the Upper Maastrichtian *Abathomphalus mayaroensis* Biozone and the Danian *Guembelitria cretacea*, *Parvularugoglobigerina eugubina*, and *Parasubbotina pseudobulloides* Biozones was performed. Benthic foraminifera indicate that the upper Maastrichtian and lower Danian sediments at Bidart were deposited in the upper–middle part of the slope.*

Benthic foraminiferal assemblages indicate mesotrophic conditions during the late Maastrichtian and a strong decrease in the food supply to the sea floor coincident with the K/Pg boundary. This change in the trophic regime was related to the collapse of the food web triggered by the mass extinction of calcareous primary producers. Benthic assemblages in the lower Danian are strongly dominated by few species, and suggest that primary productivity was dominated by blooms of non-calcareous primary producers, creating a stressful environment for the benthic fauna. The faunal turnover, together with the geochemical evidence, is compatible with an asteroid impact scenario. Benthic foraminiferal assemblages suggest that primary productivity had not completely recovered more than 200 kyr after the K/Pg boundary event.

INTRODUCTION

The Cretaceous/Paleogene (K/Pg) boundary marks one of the major mass extinctions in Earth's history. Most authors now accept that a large meteorite impacted the Yucatan Peninsula in Mexico (Alvarez et al., 1980; Smit and Hertogen, 1980; Hildebrand et al., 1991) and triggered the catastrophic mass extinction of calcareous plankton (e.g., Luterbacher and Premoli-Silva, 1964; Smit, 1982, 1990; Molina et al., 1998), as well as an anomalous enrichment in Ir and other extraterrestrial impact evidence, such as microspherules (interpreted as altered microtektites) and shocked quartz grains in the boundary sediments globally

(Alvarez et al., 1980; Smit and Hertogen, 1980; Smit and ten Kate, 1982; Sharpton et al., 1992). Furthermore, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in bulk sediment and in tests of benthic and planktic foraminifera show abrupt changes just after the K/Pg extinction (Zachos and Arthur, 1986; Kaminski and Malmgren, 1989; Kaiho et al., 1999), and reflect important environmental changes that occurred immediately after the impact. Nevertheless, there are still some researchers who do not support a catastrophic mass extinction model (Keller, 1989 a, b; Keller et al., 1995; Abramovich and Keller, 2002), but an extended pattern of extinction generated by multiple causes that may be due to the Signor-Lipps effect and reworking processes affecting microfossils in the sediments immediately below and above the K/Pg boundary (Huber et al., 2002; Soria et al., 2001, Molina et al., 2002).

Whereas planktic foraminifera suffered a catastrophic mass extinction coincident with the K/Pg boundary (e.g., Molina et al., 1998), benthic foraminifera do not show significant extinctions, as reviewed by Culver (2003). Deep-sea benthic foraminifera show drastic, temporal changes in their community structure coincident with the K/Pg boundary, followed by a gradual, staggered pattern of recovery across the early Danian (see review by Culver, 2003). These temporary changes in benthic foraminiferal assemblages have been interpreted as resulting from the collapse of the pelagic food web and the subsequent drop in food supply to the benthos (e.g., Kuhnt and Kaminski, 1993; Thomas, 1990a, b; Alegret et al., 2001, 2003; Culver, 2003).

The Bidart section (southwestern France, Fig. 1) is considered as one of the most complete K/Pg boundary sections in southwestern Europe (Seyve, 1990; Haslett, 1994). Nevertheless, the paleoenvironmental turnover across the K/Pg boundary in this area remains unclear, and benthic foraminifera from Bidart have not been studied previously. Kuhnt and Kaminski (1993) analyzed the agglutinated benthic foraminiferal changes in the nearby Zumaya and Sopelana sections (Basque Basin, Northern Spain), and concluded that deep-water agglutinated foraminiferal turnover indicates a drastic decrease in surface productivity and a collapse of the food-web coincident with the K/Pg boundary. Apart from that study, no detailed analyses on benthic foraminifera have been performed in

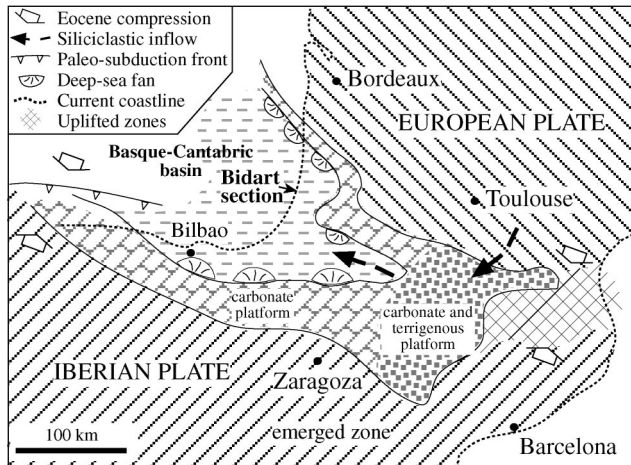


FIGURE 1—Paleogeographical reconstruction of the Pyrenean domain during the Paleocene (modified from Pujalte et al., 1994), and location of the Bidart section.

this area, so the results presented here provide important data to infer environmental changes across the K/Pg boundary.

In addition to its completeness and excellent exposure, the Bidart section is particularly important because of its paleogeographical location—between the Tethys and the North Atlantic—during the Late Cretaceous and Early Paleogene. According to Renard et al. (1982), the Maastrichtian of Bidart was deposited under Tethyan influences, whereas the Paleocene was influenced primarily by the North Atlantic. Consequently, the Bidart section has been the focus of various studies, such as stable isotope analysis (Romein and Smit, 1981; Renard et al., 1982; Nelson et al., 1991), iridium content (Smit and Ten Kate, 1982; Delacotte, 1982; Bonté et al., 1984), or biostratigraphy (Bonté et al., 1984; Delacotte et al., 1985), among others. Detailed biostratigraphical studies across the K–Pg interval have been based on calcareous nannofossils (Perch-Nielsen, 1979; Seyve, 1990) and planktic foraminifera (Haslett, 1994; Fondcave-Wallez et al., 1995; Apellaniz et al., 1997). Nevertheless, benthic foraminifera from Bidart have not been studied in detail, as pointed out by Haslett (1994).

The aim of this study is to perform a detailed, quantitative study of Upper Cretaceous and Lower Paleogene benthic foraminiferal assemblages from the Bidart section (SW France). Benthic foraminifera, which are closely related to the sea-bottom conditions, provide detailed data on the paleobathymetric setting of the uppermost Cretaceous and lowermost Paleogene sediments at Bidart, as well as on the paleoenvironmental changes across the K/Pg boundary.

MATERIAL AND METHODS

The Bidart section is situated between Hendaye and Biarritz (southwestern France), within the Basque-Cantabric Basin. The outcrop is located behind the beach of Bidart, towards the north of this village (for a more precise location of the outcrop, see Peybernès et al., 1996). The upper 4 m of the Maastrichtian and the lower 3.6 m of the Pa-

leogene were studied at Bidart. The Maastrichtian sediments correspond to the “Bidart marls” (Seunes, 1891), which consist of gray marls and calcareous marls containing abundant foraminifera and scarce macrofossils such as echinoids. The uppermost two centimeters of the Maastrichtian consist of gray clayey marls. The K/Pg boundary is marked by a sharp contact between the Maastrichtian marls and a 6-cm-thick layer of dark clays with a 2-mm-thick, red ferruginous level at its base (Fig. 2). The rest of this clay layer consists of brownish clays towards its lower part, and thinly laminated dark gray clays towards the top. Delacotte (1982) and Bonté et al. (1984) identified an iridium anomaly in the dark clay layer, coinciding exactly with a drop in the $\delta^{13}\text{C}$ curve and in the $\delta^{18}\text{O}$ values (Peybernès et al., 1996). Apellaniz et al. (1997) documented the presence of microspherules with Ni-rich crystals in the middle part of the clay layer. This layer is overlain by a ~25-cm-thick level of gray to brown clays, which become more grayish and calcareous towards the top, reflecting an increase in total bulk carbonate after a drastic reduction identified just above the K/Pg boundary (i.e., in the dark clay layer; Renard et al., 1982). Fish teeth were observed towards the upper part of this level, which is overlain by 1.30 m of massive gray limestones. Higher in the section, a 50-cm-thick, tabular breccia was identified (Fig. 2); the matrix has a mudstone texture, and the pebbles are calcareous, poorly sorted (the maximum length ranges from 1 mm to 10 cm), and subangular to rounded. This body is overlain by two tabular, 60-to-90-cm thick levels of massive gray limestones, each of which is strongly bioturbated towards the top.

The K/Pg boundary at Bidart, as well as in other K/Pg boundary sections from the Bay of Biscay, is included within a single depositional sequence (Maastrichtian–Danian Depositional Sequence; e.g., Apellaniz et al., 1997). According to these authors, the base of this sequence is located 10 m below the K/Pg boundary, whereas the top of the sequence is erosive.

Flysch deposition persisted from Albian to Eocene times in this area, which was situated in close proximity to a paleoslope to the northeast (Seyve, 1984). A distal deep-sea fan environment with a 40-mm/kyr sedimentation rate (Nelson et al., 1991) prevailed in this area during the Maastrichtian, whereas an increase in the activity on the slope is recorded in the Paleocene (Haslett, 1994), therefore, the Paleocene sediments are locally slumped (Seyve, 1990). According to Peybernès et al. (1996), the breccia identified at Bidart was deposited under conditions of low sea level, whereas the underlying limestones were deposited under high sea-level conditions. Alternatively, this breccia could be interpreted as a slump triggered by local tectonics during the early Danian. In spite of this geological context, the Paleocene foraminifera from Bidart are unlikely to have been affected by major reworking processes, although the microfossils found in the breccia have not been taken into account in the paleoenvironmental interpretations.

The studies by Hasslet (1994), Peybernès et al. (1996), and Apellaniz et al. (1997) have been followed for biostratigraphic control. These authors identified the upper Cretaceous *Abathomphalus mayaroensis* Biozone, as well as the Danian *Guembelitra cretacea*, *Parvularugoglobigerina eugubina* and *Parasubbotina pseudobulloides* Bio-

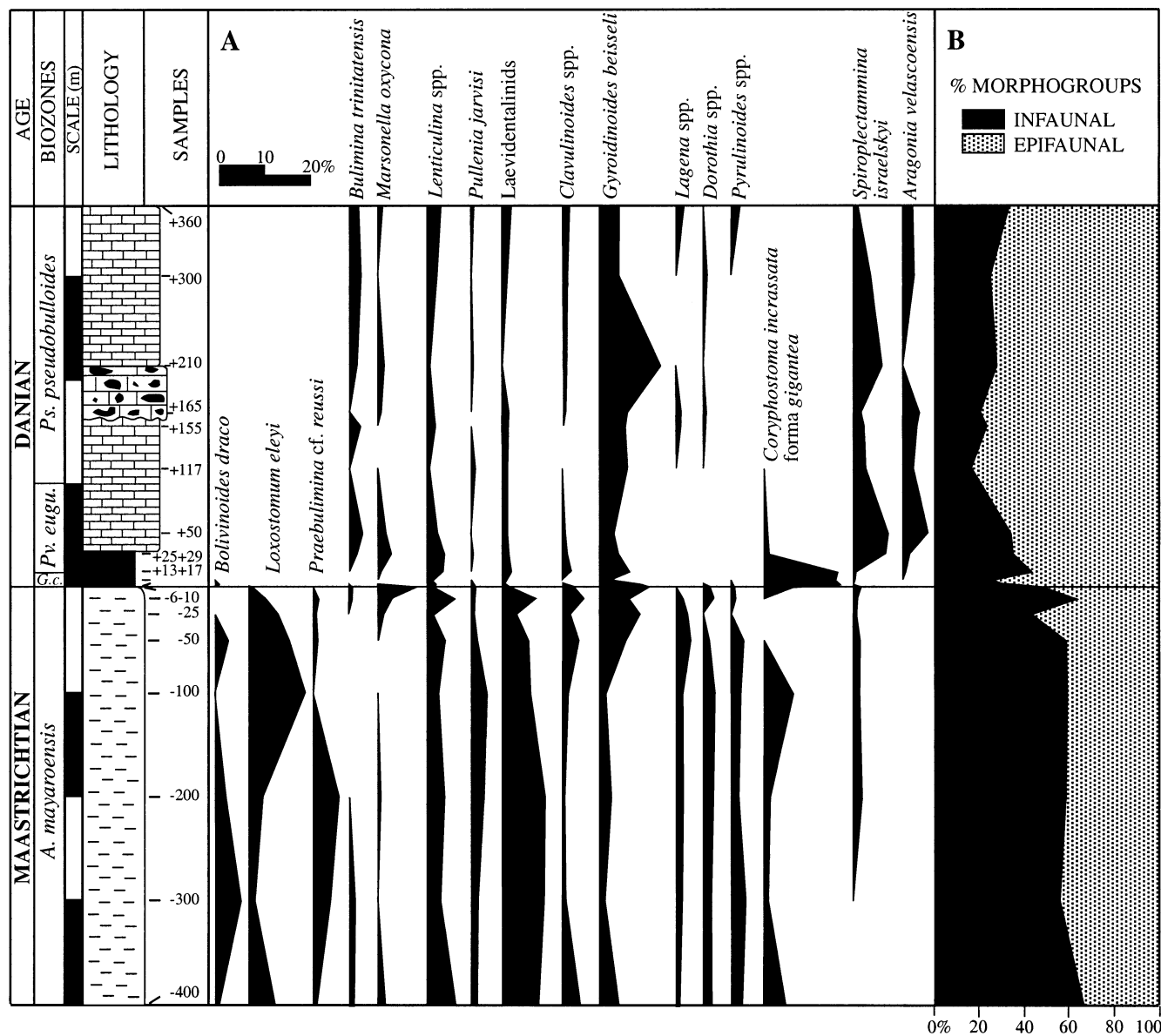


FIGURE 2—Occurrence and relative abundance of infaunal morphogroups across the K–Pg transition at Bidart. (A) Most-characteristic infaunal taxa. (B) Relative percentage of infaunal and epifaunal morphogroups. G. c. = *G. cretacea* Biozone; Pv. eugu. = *Pv. eugubina* Biozone. Biostratigraphy by Haslett (1994), Peybernès et al. (1996), and Apellaniz et al. (1997). See legend in Figure 4.

zones (Figs. 2–3). Foraminiferal assemblages from the lowermost 10 cm of the Danian are dominated by benthic foraminifera, and planktic foraminifera are almost absent. Haslett (1994) and Apellaniz et al. (1997) suggested that this level may correspond to the *Guembelitra cretacea* Biozone of Smit (1982); the first appearance of *Pv. eugubina* 10 cm above the K/Pg boundary marks the *Pv. eugubina* Biozone, and the base of the *Ps. pseudobulloides* Biozone is located ~1 m above the K/Pg boundary.

Twenty samples were studied in the upper 4 m of the Maastrichtian and the lower 3.5 m of the Danian. According to the biomagnetostratigraphic correlation and calibration recently proposed by Arenillas et al. (2004), the base of the *Ps. pseudobulloides* Biozone has an estimated age of 64.945 Ma (based on the calibration by Berggren et al., 1995, who placed the K/Pg boundary at 64.745 Ma) or

65.436 Ma (based on the astronomical calibration by Röhl et al., 2001, who placed the K/Pg boundary at 65.5 Ma). Arenillas et al. (2004) subdivided the *Ps. pseudobulloides* Biozone into the *Eoglobigerina trivialis* Interval Subzone, which has a duration of 171.5–201.1 kyr (based on the calibrations proposed by Berggren et al., 1995 and by Röhl et al., 2001, respectively) and the *Subbotina triloculinoidea* Interval Subzone. Although these subzones have not been identified by Haslett (1994), Peybernès et al. (1996), or Apellaniz et al. (1997) at Bidart, comparison of this section to the nearby Zumaya section, where the *E. trivialis* Subzone spans 2.75 m, suggests that at least this subzone is represented at Bidart. Further biostratigraphical studies are needed to test the presence of the *Subbotina triloculinoidea* Subzone at Bidart. However, in the lack of a better biostratigraphical analysis, it may be tentatively inferred

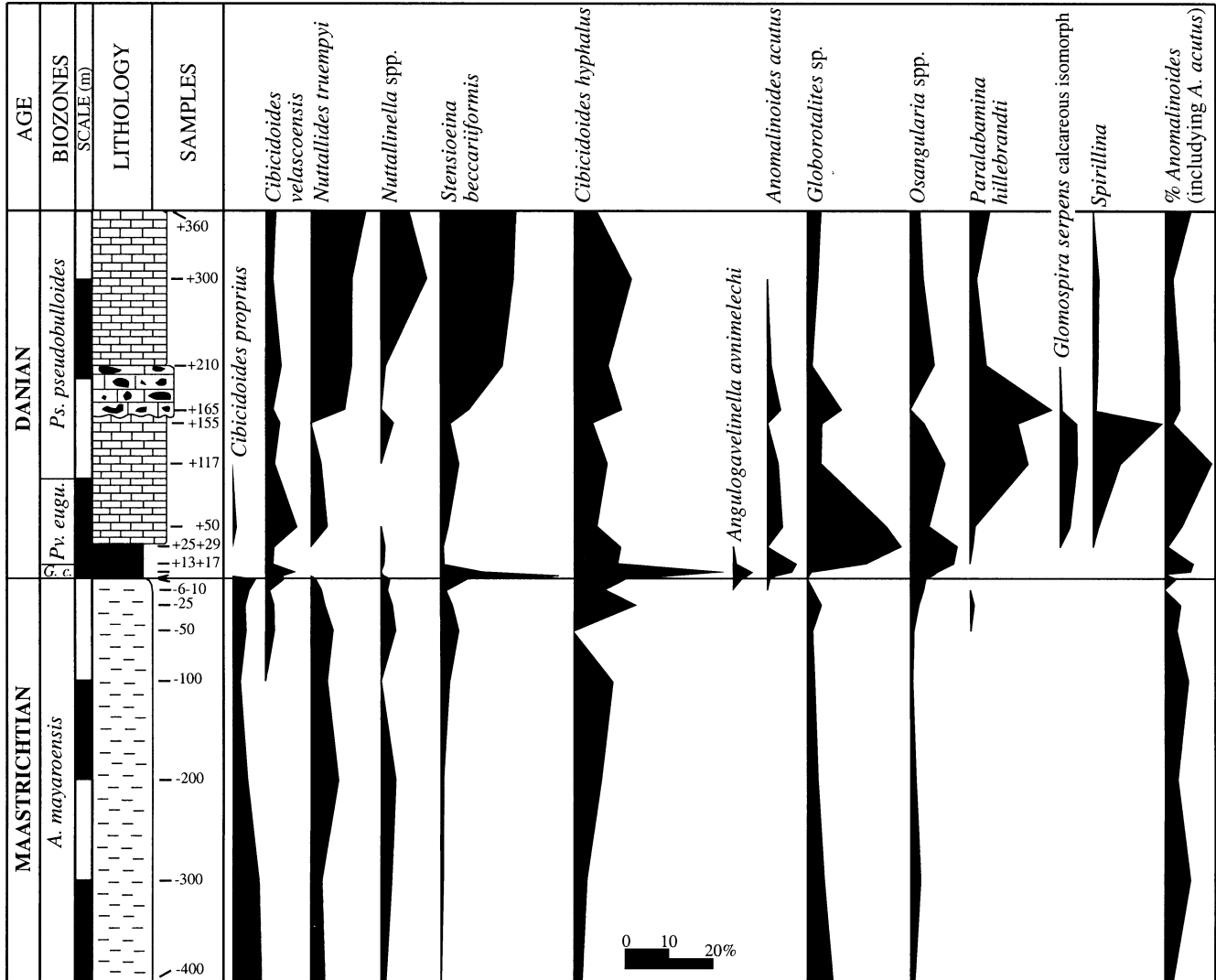


FIGURE 3—Occurrence and relative abundance of the most-characteristic epifaunal benthic foraminiferal taxa across the K–Pg transition at Bidart. *G. c.* = *G. cretacea* Biozone; *Pv. eugu.* = *Pv. eugubina* Biozone. Biostratigraphy by Haslett (1994), Peybernès et al. (1996), and Apellaniz et al. (1997). See legend in Figure 4.

that, at least, the whole *E. trivialis* Subzone is represented at Bidart. These data suggest that the top of the studied interval corresponds, approximately, to the top of the *E. trivialis* Subzone, 225.6–264.5 kyr after the K/Pg boundary (according to the calibrations proposed by Berggren et al., 1995 and by Röhl et al., 2001, respectively); if the *S. triloculinoidea* Subzone were partially represented at Bidart, the top of the studied section would be even younger.

Samples were collected at one-meter intervals at the lower part of the section and at decimeter intervals towards the top, with closer sampling in the uppermost Maastrichtian and the lowermost Danian (Appendix 1). Only one micropaleontological sample from the basal 5 cm of the breccia was analyzed, but the results were not considered for paleoenvironmental interpretations due to the possible reworking processes affecting the microfossils in this unit. Samples were disaggregated in water with diluted H_2O_2 , washed through a 63- μ m sieve, and dried at 50°C. Species richness calculations and quantitative studies were based on representative splits (using a modified

Otto micro-splitter) of approximately 300–400 specimens of benthic foraminifera larger than 63- μ m. All representative specimens were mounted on microslides for a permanent record and identification. Classification at the generic level follows Loeblich and Tappan (1988); when possible, benthic foraminifera were identified to the specific level largely following the taxonomy of Alegret and Thomas (2001), since the Mexican faunas studied by these authors contain around 80% of the benthic foraminiferal species identified at Bidart. Moreover, 90% of the species identified in this study were reported from the Upper Cretaceous and lower Paleogene at the Agost section (south-eastern Spain) by Alegret et al. (2003). Benthic foraminiferal counts are presented in Appendix 1.

The Fisher- α diversity index and the H(S) Shannon-Weaver information function, another index of diversity, were calculated in order to observe possible changes in diversity across the K–Pg interval. 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.

In order to infer probable microhabitat preferences and environmental parameters such as the nutrient supply to the sea floor and seawater oxygenation (e.g., Bernhard, 1986; Jorissen et al., 1995; Fontanier et al., 2002), all benthic foraminiferal taxa were allocated into morphogroups following Corliss (1985, 1991), Jones and Charnock (1985), and Corliss and Chen (1988). According to these authors, there is a general relationship between test morphology and the microhabitat preferences of benthic foraminifera. Thus, benthic foraminifera with plano-convex, biconvex, and rounded trochospiral tests, as well as tubular and coiled flattened tests, have an inferred epifaunal mode of life, living at the sediment surface. Infaunal foraminifera, living in deeper layers of the sediment, have cylindrical or flattened tapered, spherical, rounded planispiral, flattened ovoid, globular unilocular, or elongate multilocular tests. Major changes in percentages of these morphogroups (Fig. 2), as well as in the abundance of selected taxa (Figs. 2–3), and the comparison of fossil and recent communities of benthic foraminifera have been considered in this study to infer the paleoenvironmental turnover across the K/Pg boundary. Nonetheless, one should be careful with these interpretations due to the complex and not fully understood ecology of modern faunas, and their questionable comparison to Upper Cretaceous and lower Paleogene faunas (Alegret et al., 2003).

PALEOBATHYMETRY

Benthic foraminiferal assemblages are dominated by calcareous tests (~97%) through the whole section, except for the upper 10 cm of the Maastrichtian, where they make up 75% of the assemblages (Fig. 4). These values indicate deposition well above the calcite compensation depth. The planktic/benthic ratio is high (85–90%) in all samples except for those from the lowermost Danian, which are dominated by benthic foraminifera.

Paleobathymetric assignments were obtained mainly following the depth distributions and upper depth limits of benthic foraminiferal species, as reviewed by Alegret et al. (2003). Benthic foraminiferal assemblages contain abundant representatives of the bathyal and abyssal Velasco-type fauna (Berggren and Aubert, 1975), namely *Aragonia velascoensis*, *Cibicidoides velascoensis*, *Nuttallides truempyi*, or *Stensioeina beccariiiformis*, as well as other deep-water species such as *Bulimina trinitatensis*, *Cibicidoides hyphalus*, or *Marssonella oxycona*. The upper depth limit of some of the most abundant species at Bidart (e.g., *Bulimina trinitatensis*, *Nuttallides truempyi*, *Stensioeina beccariiiformis*) is located at 500–700 m depth (Alegret et al., 2003). These data suggest that the upper Maastrichtian and lower Danian sediments at Bidart were deposited in the upper-middle part of the slope.

An increase in the percentage of *Loxostomum eleyi* has been observed in the uppermost meter of the Maastrichtian (Fig. 2). The preservation of these specimens is very similar to that of other species in the same samples, and there is no apparent size sorting. These data indicate that the abundant specimens of *Loxostomum eleyi* identified in the uppermost Maastrichtian sediments are unlikely to have been reworked. Although *Loxostomum eleyi* is typical

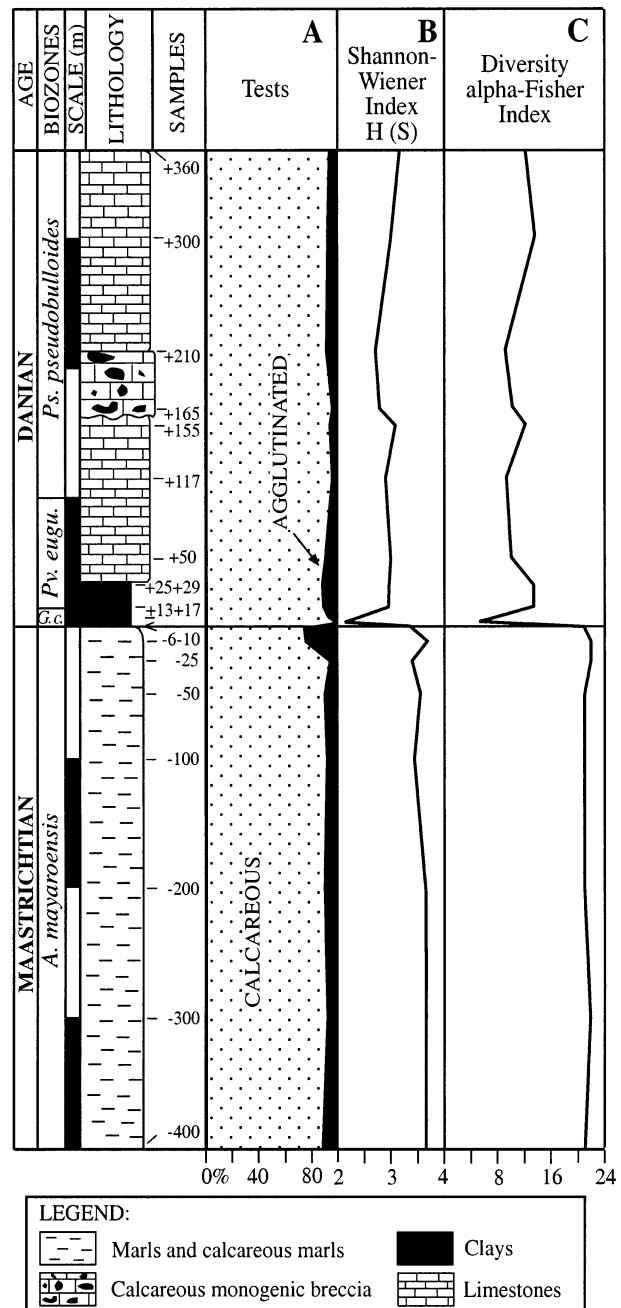


FIGURE 4—Characteristics of benthic foraminiferal assemblages across the K–Pg transition at Bidart. (A) Percentages of calcareous and agglutinated benthic foraminiferal tests. (B) Shannon-Weaver heterogeneity index. (C) Fisher- α diversity index. G. c. = *G. cretacea* Biozone; Pv. eugu. = *Pv. eugubina* Biozone. Biostratigraphy by Haslett (1994), Peybernès et al. (1996), and Apellaniz et al. (1997).

of outer-shelf environments (MacNeil and Caldwell, 1981; Nyong and Olsson, 1984), its depth occurrence may increase under a high food supply, as suggested by Alegret et al. (2003) at the Agost section. The high relative abundance of infaunal morphogroups in the Maastrichtian at Bidart (Fig. 2) indicates an abundant food supply to the sea-bottom floor, as in Agost. Under these conditions, the depth of occurrence of *L. eleyi* may have been somewhat greater than at other locations.

BENTHIC FORAMINIFERAL TURNOVER

Upper Maastrichtian assemblages are diverse and heterogeneous (Fisher- α index \sim 21, Shannon-Weaver index $H(S) \sim$ 3.5; Fig. 4B, C), and they consist of a mixture of infaunal (\sim 58%) and epifaunal morphogroups (Fig. 2B). Among the infaunal morphogroups, species with cylindrical-tapered (e.g., *Praebulimina* cf. *P. reussi*, laevidentalinids), flattened-tapered (e.g., *Loxostomum eleyi*, *Bolivinoidea draco*), and spherical tests dominate (Fig. 2), whereas taxa with trochospiral-planoconvex (e.g., *Cibicidoides hyphalus*, *Cibicidoides proprius*) and biconvex (*Nuttallides truempyi*) tests dominate among the epifaunal morphogroups (Fig. 3). These data suggest mesotrophic conditions during the uppermost Maastrichtian, and a nutrient supply to the sea-bottom floor enough to sustain both infaunal and epifaunal morphogroups.

Only three species (*Bolivinoidea draco draco*, *Loxostomum eleyi*, and *Praebulimina* cf. *P. reussi*) disappear at Bidart in coincidence with the K/Pg boundary (Fig. 2). Two specimens of *Bolivinoidea draco draco* were found two centimeters above the K/Pg boundary, but the different color of the sediment inside their shells as compared to the other foraminifera in the same sample suggests that they are reworked. Although benthic foraminiferal assemblages were not significantly affected by the K/Pg extinctions, the percentage of infaunal morphogroups (Fig. 2) and the diversity of the assemblages (Fig. 4) drastically decreased just after the K/Pg boundary. Lowermost Danian assemblages (dark clay layer) contain up to 74% of epifaunal morphogroups, which are dominated mainly by the trochospiral planoconvex *Stensioeina beccariiiformis* and *Cibicidoides hyphalus* (Fig. 3). Such a decrease in the abundance of infaunal taxa and the presence of peaks in the abundance of two epifaunal species suggest a drastic decrease in the food supply to the sea floor related to the catastrophic mass extinction of calcareous plankton at the K/Pg boundary (Zachos and Arthur, 1986; Thomas 1990a, b; Widmark and Malmgren, 1992; Kuhnt and Kaminski, 1993; d'Hondt et al., 1998; Widmark, 2000; Alegret et al., 2001, 2002a, b, 2003). Under oligotrophic conditions, the epifaunal *Stensioeina beccariiiformis* and *Cibicidoides hyphalus*, living at the sediment surface, bloomed together with the infaunal species *Coryphostoma incrassata* forma *gigantea*.

Benthic foraminifera from the lower *Pu. eugubina* Biozone are still dominated by epifaunal morphogroups (Fig. 2B), especially by trochospiral biconvex (*Osangularia* spp.) and planoconvex (*Globorotalites* spp.) tests (Fig. 3). It may be argued that this interval is dominated by epifaunal taxa not because of the paleoecological characteristics at that time, but only due to the fact that they correspond to the solution-resistant forms. Nevertheless, both infaunal and epifaunal species show evidence of dissolution, not only in these samples but also in the upper two centimeters of the Maastrichtian and through the whole Danian part of the section. Moreover, in spite of the fact that epifaunal species are more susceptible to dissolution in the modern oceans, a peak in the abundance of epifaunal morphogroups is observed in the lower Danian, thus suggesting that the percentage of epifaunal morphogroups may have been even greater and that dissolution was present but not overwhelming. In addition, a wide range of sizes

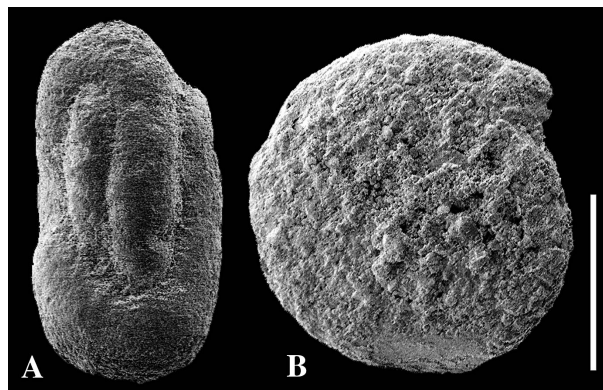


FIGURE 5—Scanning electron micrographs of two opportunistic benthic foraminiferal species. Scale bar = 50 μ m. (A) *Glomospira serpens* calcareous isomorph. (B) *Spirillina*.

may be observed in all the studied samples, which contain both thick-walled, solution-resistant forms, and thin-walled benthic foraminiferal tests. Two taxa, namely *Glomospira serpens* calcareous isomorph and *Spirillina* (Fig. 5), first appear during this interval. Both taxa morphologically are very similar to *Glomospira serpens* and *Ammodiscus*, respectively, which have been documented to be mobile epifaunal forms that feed on organic detritus (Ly and Kuhnt, 1994) and tolerate environmental instability, thus blooming whenever other taxa cannot compete (Kaminski et al., 1996). The *Glomospira serpens* calcareous isomorph and *Spirillina* were not the only taxa in the *Pu. eugubina* Biozone and in the lower part of the *Ps. pseudobulloides* Biozone, but their appearance and increase in abundance, together with the low diversity and low percentage of infaunal morphogroups, possibly indicate environmental instability at the sea floor (Figs. 2–3). An increase in the relative abundance of the infaunal *Spiroplectammia israelskyi* and *Aragonia velascoensis* also is recorded in the *Pu. eugubina* Biozone (Fig. 2). The percentages of *Spirillina* and *Paralabamina hillebrandti* significantly increase towards the lower part of the *Ps. pseudobulloides* Biozone, at which point, their abundance rapidly starts to decrease (Fig. 3).

Higher in the section, benthic foraminiferal assemblages from the rest of the *Ps. pseudobulloides* Biozone are dominated by the epifaunal *Stensioeina beccariiiformis*, *Cibicidoides hyphalus*, *Nuttallides truempyi*, and *Nuttallinella* spp. (Fig. 3). The percentage of infaunal morphogroups increases slightly, but remains low (Fig. 2), as do the diversity and heterogeneity indices (Fig. 4B, C). The abundance of typically bathyal, oligotrophic species, together with the dominance of epifaunal morphogroups towards the top of the studied interval, suggest that the food supply to the sea floor had not completely recovered at that time, at least more than 200 kyr after the K/Pg boundary.

DISCUSSION

The dominance of calcareous benthic foraminifera through the whole section (Fig. 4A) may indicate a small supply of terrigenous sediment at Bidart as compared to the coeval north Spanish Sopolana and Zumaya sections

(Kuhnt and Kaminski, 1993), where agglutinated foraminifera make up two-thirds of the benthic foraminiferal assemblages. Upper Cretaceous benthic foraminiferal assemblages are diverse at Bidart, and consist of a mixture of both infaunal and epifaunal morphogroups, suggesting mesotrophic conditions during the late Maastrichtian.

The drastic decrease in the relative abundance of infaunal taxa and in the diversity and heterogeneity of the assemblages coincident with the K/Pg boundary indicates oligotrophic conditions, which are related to the decrease in the organic flux from surface waters as the result of the mass extinction of primary producers (e.g., Kuhnt and Kaminski, 1993; d'Hondt et al., 1998; Alegret et al., 2001, 2003). Under conditions of very limited food supply to the sea floor, food particles were consumed at the sediment surface by epifaunal species, whereas the percentage of infaunal species decreased due to the lack of organic matter in the underlying sediment. The drastic reorganization of benthic foraminiferal assemblages, together with the geochemical evidence at Bidart (e.g., Delacotte, 1982; Bonté et al., 1984; Peybernès et al., 1996), are compatible with an asteroid impact at the K/Pg boundary.

Peybernès et al. (1996) documented the rapid increase in the abundance of the dinoflagellates *Thoracosphaera operculata*, *Cyclagelosphaera reinhardii*, and *Braadurosphaera bigelowii* in the dark clay layer (*G. cretacea* Biozone and lower part of the *Pv. eugubina* Biozone) at Bidart. Such blooms would have provided large amounts of food that reached the sea floor even in the absence of pellet-producing zooplankton, which suffered a mass extinction (e.g., Ittekkot, 1993; Verity et al., 1996). According to these data, the following questions arise: why do benthic foraminifera indicate oligotrophic conditions just after the K/Pg boundary, when phytoplankton blooms suggest an important food supply to the sea floor? Under these high-productivity conditions driven by non-calcareous phytoplankton blooms, why are lowermost Danian benthic foraminiferal assemblages apparently stressed, of low diversity, and dominated by few species? Speculatively, the observed peaks of the epifaunal species *Stensioeina beccariiiformis* and *Cibicidoides hyphalus*, and the increase in the percentage of the infaunal *Coryphostoma incrassata* forma *gigantea* just after the K/Pg boundary (Figs. 2–3), may be related to the drastic increase in the abundance of dinoflagellates documented in the lowermost Danian at Bidart. Although the species composition of the assemblages and the low percentage of infaunal morphogroups (Fig. 2), as well as the drop in the $\delta^{13}\text{C}$ curve and in total bulk carbonate (Renard et al., 1982; Bonté et al., 1984), indicate a drastic decrease in primary productivity just after the K/Pg boundary, some of the benthic foraminiferal species that bloomed just after the K/Pg boundary might have been able to feed on short-lived, local phytoplankton blooms that occurred even in the absence of carbonate-rich sediment contributed by nannoplankton, as described by Alegret et al. (2003) in the Agost section (southeastern Spain). In the Modern oceans, many organisms do not consume dinoflagellates, and the unusually low-diversity faunas live under a stressful environment because of this change in the composition of food directly supplied from the photic zone (Peryt et al., 2002). Therefore, most of the benthic foraminiferal species could not easily use the food nutrients supplied by the abundant dinoflagellates, thus

accounting for the low diversity and heterogeneity of the lowermost Danian benthic foraminiferal assemblages. It may be concluded that it was not only the drastic decrease in primary productivity, but also the changes in phytoplankton type (from calcareous to organic-walled phytoplankton) just after the K/Pg boundary that caused the low-diversity, high-dominance benthic foraminiferal assemblages from the lower part of the dark clay layer.

The appearance of the opportunistic taxa *Spirillina* and *Glomospira serpens* calcareous isomorph, together with the high percentages of epifaunal taxa such as *Globorotalites* or *Paralabamina hillebrandti* during the *Pv. eugubina* Biochron and the early *Ps. pseudobulloides* Biochron (Fig. 3), suggest that the food supply was still low, and probably dominated by non-calcareous phytoplankton.

The percentage of infaunal taxa increases slightly through the studied part of the *Ps. pseudobulloides* Biozone, although it does not reach the high values of the late Maastrichtian (Fig. 2). Benthic foraminiferal assemblages from this interval are dominated by the deep-water species *Nuttallides truempyi*, *Stensioeina beccariiiformis*, and *Cibicidoides hyphalus* (Fig. 3), which are common in bathyal settings with a scarce nutrient supply to the sea floor (Van Morkhoven et al., 1986; Widmark and Malmgren, 1992; Speijer and Van der Zwaan, 1996; Alegret et al., 2001). The species composition, together with the low diversity and heterogeneity of the assemblages (Fig. 4 B–C), suggests that primary productivity had not completely recovered by that time—more than 200 kyr after the K/Pg boundary.

Kuhnt and Kaminski (1993) reported a similar faunal turnover in the northern Spanish Zumaya and Sopelana sections, including *Gavelinella* and *Stensioeina*-dominated calcareous assemblages in the lower part of the boundary clay and a strong increase in the abundance of *Spiroplectammia israelskyi* at the top of this clay layer. They documented a drastic increase in the relative abundance of opportunistic species just after the K/Pg boundary during a period of reduced primary productivity, and a gradual reestablishment of a normal trophic structure that took place, at least several hundred thousand years after the K/Pg boundary. A similar pattern of recovery has been reported from the South Atlantic (Widmark and Malmgren, 1992), Mexico (Alegret and Thomas, 2001; Alegret et al., 2001, 2002a, b), Austria (Peryt et al., 1997), Tunisia (Speijer and Van der Zwaan, 1996; Peryt et al., 2002), and southeastern Spain (Alegret et al., 2003). The benthic foraminiferal turnover is compatible with the collapse and recovery of surface productivity as the result of the K/Pg-boundary mass extinction of calcareous primary producers (Zachos and Arthur, 1986; Kuhnt and Kaminski, 1993; d'Hondt et al., 1998; Alegret et al., 2001, 2003). The lack of significant extinction of benthic foraminifera at a time of mass extinction of planktic fauna suggests a weak benthopelagic coupling at that time (Thomas et al., 1999; Alegret et al., 2001). Nevertheless, the drastic reorganization of benthic foraminiferal assemblages coincident with the K/Pg boundary at Bidart, and at many other sections worldwide is compatible with a geologically instantaneous, widespread, and catastrophic event, such as the impact of a large asteroid at the K/Pg boundary.

CONCLUSIONS

Upper Maastrichtian and lower Danian benthic foraminiferal assemblages from the Bidart section (southwestern France) are dominated by calcareous taxa, and indicate upper-middle bathyal depths of deposition for the whole studied interval.

Upper Maastrichtian benthic foraminiferal assemblages are diverse and heterogeneous, and contain a mixture of infaunal and epifaunal morphogroups, thus indicating mesotrophic conditions during the latest Cretaceous. The strong decrease in diversity and heterogeneity of the assemblages, as well as the drastic drop in the percentage of infaunal morphogroups, indicate a dramatic decrease in the food supply to the sea-bottom floor coincident with the K/Pg boundary, which is related to the collapse of the food web triggered by the mass extinction of primary producers. The benthic foraminiferal turnover, together with the geochemical and mineralogical evidence, is compatible with an asteroid impact at the K/Pg boundary.

Primary productivity during the early Danian was dominated by blooms of non-calcareous primary producers; such a change in phytoplankton composition induced a stressful environment for the benthic fauna. The low diversity of the assemblages, as well as the low percentage of infaunal morphogroups through the *Pv. eugubina* and *Ps. pseudobulloides* Biozones, suggests that primary productivity had not completely recovered more than 200 kyr after the K/Pg boundary.

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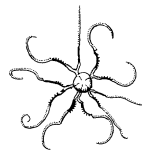
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12. Tax Status (For completion by nonprofit organizations authorized to mail at nonprofit rates) (Check one) The purpose, function, and nonprofit status of this organization and the exempt status for federal income tax purposes: <input checked="" type="checkbox"/> Has Not Changed During Preceding 12 Months <input type="checkbox"/> Has Changed During Preceding 12 Months (Publisher must submit explanation of change with this statement)					

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(See Instructions on Reverse)

13. Publication Title PALAIOS		14. Issue Date for Circulation Data Below August 2004	
15. Extent and Nature of Circulation		Average No. Copies Each Issue During Preceding 12 Months	No. Copies of Single Issue Published Nearest to Filing Date
a. Total Number of Copies (Net press run)		1700	1700
b. Paid and/or Requested Circulation			
(1) Paid (Requested Outside-County Mail Subscriptions Stated on Form 3541 (Include advertiser's proof and exchange copies))		849	879
(2) Paid In-County Subscriptions Stated on Form 3541 (Include advertiser's proof and exchange copies)		---	---
(3) Sales Through Dealers and Carriers, Street Vendors, Counter Sales, and Other Non-USPS Paid Distribution		---	---
(4) Other Classes Mailed Through the USPS		498	525
c. Total Paid and/or Requested Circulation (Sum of 15b. (1), (2), (3), and (4))		1347	1404
d. Free Distribution by Mail (Carriers, complimentary, etc., and other free)			
(1) Outside-County as Stated on Form 3541		6	6
(2) In-County as Stated on Form 3541		---	---
(3) Other Classes Mailed Through the USPS		69	6
e. Free Distribution Outside the Mail (Carriers or other means)		---	---
f. Total Free Distribution (Sum of 15d. and 15e.)		75	12
g. Total Distribution (Sum of 15c. and 15f.)		1422	1416
h. Copies not Distributed		278	284
i. Total (Sum of 15g. and h.)		1700	1700
j. Percent Paid and/or Requested Circulation (15c. divided by 15g. times 100)		95%	99%

16. Publication of Statement of Ownership:
 Publication required. Will be printed in the _____ issue of this publication. Publication not required.

17. Signature and Title of Editor, Publisher, Business Manager, or Owner
 Theresa Scott, Business Manager, SEPM
 Date: 9-1-04

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions (including fines and imprisonment) and/or civil sanctions (including civil penalties).

Instructions to Publishers

- Complete and file one copy of this form with your postmaster annually on or before October 1. Keep a copy of the completed form for your records.
- In cases where the stockholder or security holder is a trustee, include in items 10 and 11 the name of the person or corporation for whom the trustee is acting. Also include the names and addresses of individuals who are stockholders who own or hold 1 percent or more of the total amount of bonds, mortgages, or other securities of the publishing corporation. In item 11, if none, check the box. Use blank sheets if more space is required.
- Be sure to furnish all circulation information called for in item 15. Free circulation must be shown in items 15d, e, and f.
- Item 15h, "Copies not Distributed," must include (1) newsstand copies originally stated on Form 3541, and returned to the publisher, (2) estimated returns from news agents, and (3) copies for office use, leftovers, spoiled, and all other copies not distributed.
- If the publication had periodic authorization as a general or requestor publication, this Statement of Ownership, Management and Circulation must be published; it must be printed in any issue in October or, if the publication is not published during October, the first issue printed after October.
- In item 16, indicate the date of the issue in which this Statement of Ownership will be published.
- Item 17 must be signed.
Failure to file or publish a statement of ownership may lead to suspension of Periodicals authorization.

PS Form 3526, October 1999 (Reverse)

APPENDIX Continued.

	K-400	K-300	K-200	K-100	K-50	K-25	K-6-10	K-0-2	T+0+2	T+3+6	T+13+17	T+25+29	T+50	T+117	T+155	T+165	T+210	T+300	T+360	
<i>Oridorsalis plummerae</i>	5	4										2								
<i>Oridorsalis</i> sp.				1																
<i>Oridorsalis umbonatus</i>	3	3	1	2	1	2	2	2		12	6	6	1	2	2	2	2	2	3	3
<i>Osangularia</i> cf. <i>velascoensis</i>					2															
<i>Osangularia</i> cf. <i>cordieriana</i>	3	4	3	1	2	2	5	3	20	1		16	8							2
<i>Osangularia</i> cf. <i>plummerae</i>											39	35	18	21	11	22	22	6	8	8
<i>Osangularia</i> spp.	1	1	2	2	2	2	6	8	22	19	39	35	18	21	11	22	22	6	8	8
<i>Paliolotella orbignyana</i>					3															
<i>Paliolotella</i> sp.	2	2			3															2
<i>Paralabamina hillebrandi</i>						2							4	47	35	58	17	5	17	17
<i>Planulina</i> sp.									2											4
<i>Pleurostomella</i> sp.			2	2	2	2	1	1						1		1				4
<i>Praebulimina</i> cf. <i>reussi</i>	2	8	14	3	3	2	5													
<i>Praebulimina</i> sp.				8	1															
<i>Praeglobobulimina</i> spp.	2	2	1	1									3			1				
<i>Pseudouvirgerina plummerae</i>															2					
<i>Pseudouvirgerina</i> sp.																				1
<i>Pullenia cretacea</i>																				
<i>Pullenia jarvasi</i>	3	2	7	9	3	1	3	3						2		1				1
<i>Pyramidina rudita</i>							6													
<i>Pyramidina</i> sp.													6							6
<i>Pyruilinoidea</i> sp.	7	7	4	6	7	7	2	1												
<i>Quadrinorphina allomorphi-</i> <i>noides</i>																				2
<i>Quadrinorphina</i> sp.																				
<i>Quinqueloculina</i> sp.	2																			
<i>Ramulina</i> spp.	1																			
<i>Recurviroidea</i> sp.						1	2													
<i>Repmania charoides</i>			2	3	1	1	4													
<i>Reusella</i> sp.	3																			
<i>Rhizammina</i> sp.	1						1	1												
<i>Saccamina placenta</i>									3											
<i>Saccamina</i> spp.										3										
<i>Sarcenaria</i> sp.	1								1	4	1									1
<i>Scheibnerova</i> sp.																				2
<i>Sitella</i> sp.	1						3													
<i>Slitella varsoviensis</i>				1	1															
<i>Spiroplectammia</i> cf. <i>dentata</i>									5	11										
<i>Spiroplectammia</i> cf. <i>israeli</i>			4	3	3	1	3	6												3
<i>Spiroplectammia spectabilis</i>	2																			
<i>Spiroplectammia</i> spp.																				
<i>Spiroplectinella</i> sp.	1																			
<i>Spirillina</i> sp.																				
<i>Stensioeina beccariformis</i>		1	1	6	12	8	4	19	112	64	4	3	7	15	7	20	57	58	63	63
<i>Stensioeina excolata</i>	6	2	3	1	2	1	2	2												
<i>Stilostomella</i> sp.	4	2	1	1	1	1	1	1	2	2	3	2	2	1	3	1	1	1	1	1
<i>Tappanina selmensis</i>																				
<i>Thadnamammia</i> sp.																				
<i>Trochammia</i> sp.	3	1	1	1	3	1	4	6	7	3	3	1	3	1	1	1				1
<i>Vaginulina trilobata</i>	1																			
<i>Valdalabamina lenticula</i>																				
TOTAL	321	197	254	273	288	283	325	238	416	651	401	462	373	343	328	310	393	345	370	370