

The Cretaceous/Palaeogene (K/P) boundary at Aïn Settara, Tunisia: restructuring of benthic foraminiferal assemblages

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ABSTRACT

Benthic foraminiferal assemblages, in contrast to planktic foraminifera, generally did not suffer mass extinctions at the Cretaceous/Palaeogene (K/P) boundary; extinctions were fewer in deeper water. However, the outer shelf, upper bathyal section at Aïn Settara, Tunisia, records a dramatic change in the structure of benthic foraminiferal assemblages across the K/P boundary. At the level of extinction of planktic assemblages and enrichment in Ir and other geochemical anomalies, highly diversified, low-dominance Upper Maastrichtian assemblages with infaunal and epifaunal morphogroups were suddenly

replaced by taxonomically impoverished assemblages, strongly dominated by epifaunal morphogroups. This extinction or temporary emigration of most infaunal morphogroups is interpreted to be the result of a sudden breakdown in food supply. This, in turn, is the consequence of a sudden collapse in primary productivity, probably resulting from the impact of the K/P asteroid.

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Introduction

The Cretaceous/Palaeogene (K/P)¹ boundary marks one of the largest mass extinctions of the Phanerozoic but survival rates of different groups of marine organisms varied with habitat (e.g. Hansen *et al.*, 1987). Planktic foraminifera suffered a catastrophic mass extinction (e.g. Arenillas *et al.*, 2000), whereas the extinction rate within benthic foraminiferal assemblages decreased with increasing basin depth (e.g. Thomas, 1990). Benthic assemblages, however, exhibit various degrees of temporary faunal restructuring even in the absence of major extinction (e.g. Coccioni *et al.*, 1993; Alegret *et al.*, 2001). There is no agreement on the causes of extinction and restructuring of benthic foraminiferal assemblages across the K/P boundary. According to several authors, K/P benthic foraminiferal turnovers were directly (e.g. Emiliani *et al.*, 1981) or indirectly caused by the impact of an asteroid (e.g. Zachos *et al.*, 1989; Thomas, 1990; Widmark and Malmgren, 1992; Coccioni *et al.*, 1993; Kuhnt and Kaminski, 1993;

Coccioni and Galeotti, 1994; Speijer and van der Zwaan, 1994; Peryt *et al.*, 1997; Alegret *et al.*, 1999, 2001). Keller (1988), in contrast, proposed that a drop in sea level caused the benthic foraminiferal turnover across the K/P boundary.

The K/P boundary stratotype section at El Kef (Tunisia) (Fig. 1) is one of the best-documented K/P sections, but environmental conditions at the time of the impact have not been fully explained. Studies on benthic foraminiferal assemblages from El Kef document major palaeoenvironmental

changes following the biotic crisis at the K/P boundary (Keller, 1988; Speijer and van der Zwaan, 1994, 1996; Widmark and Speijer, 1997; Coccioni and Galeotti, 1998; Kouwenhoven, 2000). Benthic foraminifera indicate an uppermost slope to outer neritic palaeoceanographic setting (e.g. Speijer and van der Zwaan, 1994, 1996; Widmark and Speijer, 1997; Kouwenhoven, 2000) and mesotrophic conditions (Widmark and Speijer, 1997; Coccioni and Galeotti, 1998) during the latest Maastrichtian. Keller (1988) suggested that El Kef sedi-

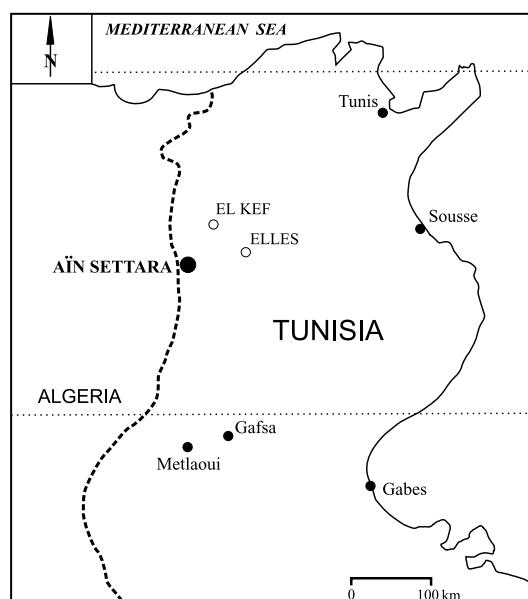


Fig. 1 Geographical location of the Aïn Settara section in Tunisia.

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¹The term Cretaceous/Palaeogene (K/P) boundary is used following recent stratigraphical concepts (e.g. Gradstein and Ogg, 1996) that regard the Palaeogene as a period within the Cenozoic.

ments were deposited in a neritic–upper bathyal setting, and postulated that a major sea-level fall and thermohaline circulation changes resulting in dysoxic conditions caused the extinction of benthic foraminifera during the latest Maastrichtian. Speijer & van der Zwaan (1994, 1996) and Kouwenhoven (2000) described the environmental setting as upper bathyal (300–500 m), and agreed that dysoxic conditions occurred after the K/P boundary. They interpreted changes in the structure of benthic foraminiferal assemblages to have resulted from a sudden drop in primary productivity, combined with dysoxic conditions caused by changes in thermohaline circulation. Coccioni and Galeotti (1998) agreed that there was a reduced organic flux to the sea floor in the earliest Palaeocene, but did not think that dysoxic conditions occurred. The present contribution gives the results of a benthic foraminiferal study of the Aïn Settara K/P section, about 50 km south of the El Kef stratotype. Information on the environmental requirements of Recent benthic foraminifera came from an extensive literature (e.g. Bernard, 1986, 1992; Corliss and Chen, 1988; Kaminski *et al.*, 1988, 1995; Bar-mavidjaja *et al.*, 1992; Jorissen *et al.*, 1992); broad classifications of depth-related morphotype associations were used (Corliss, 1985; Jones and Charnock, 1986; Corliss and Chen, 1988).

Rounded trochospiral, plano-convex trochospiral, biconvex trochospiral/planispiral, milioline and tubular morphotypes mainly live epifaunally. Rounded planispiral, flattened ovoid, tapered and cylindrical, flattened tapered morphotypes live dominantly infaunally, although exceptions occur. The depth in the sediment to which organisms can live is determined by oxygen availability; in the presence of oxygen, the vertical distribution of organisms is controlled by food availability (Jorissen *et al.*, 1992). A high flux of organic matter to the seafloor causes low oxygen concentrations within the sediment pore waters because of extensive oxidation of the organic material. Infaunal species dominate in assemblages associated with relatively high organic-carbon fluxes (e.g. Corliss and Chen, 1988; Jorissen *et al.*, 1995), and epifaunal ones in more oligotrophic environ-

ments (Thomas, 1990; Gooday, 1994; Jorissen *et al.*, 1995). In highly oligotrophic regions, all food particles will be consumed or oxidized at the sediment surface and the underlying sediment will contain only small quantities of organic matter, which cannot sustain an abundant infaunal population.

The aim of this study was to trace changes in benthic foraminiferal assemblages in the uppermost Maastrichtian and lowermost Danian, assuming that morphotypes were similar in trophic requirements to those of present foraminifera, in order to estimate the response of this group to the K/P boundary event.

Materials and methods

The Aïn Settara section is exposed about 50 km south of the El Kef stratotype section. The K/P boundary is within the lower part of the marly El Haria Formation, and is identified by lithological characteristics (Robaszynski *et al.*, 2000), the major planktic foraminiferal extinction (Arenillas *et al.*, 2000) and the occurrence of geochemical markers of a bolide impact (Ir anomaly, Ni-rich spinels; Tribouillard *et al.*, 2000). The layer with geochemical anomalies is located 55 cm below the top of the boundary clay at Aïn Settara (Arenillas *et al.*, 2000). A total of 34 samples from 2.5 m below to 9.6 m above the K/P boundary were studied. This interval encompasses the upper 2.5-m-thick part of the *Plummerita hantkeninoides* Zone, the 0.6-m-thick *Guembelitra cretacea* Zone, the 4.5-m-thick *Parvuloglobigerina eugubina* Zone and the lower 4.5-m of the *Parasubbotina pseudobulloides* Zone (Fig. 2). The uppermost 0.4-m of the *Plummerita hantkeninoides* Zone and the entire *Guembelitra cretacea* Zone were sampled at 10-cm intervals in the lower and the upper part of this interval. In the 15 cm immediately below the K/P boundary the sampling distance was 3 cm, and in the 10 cm immediately above the boundary it was 1–2 cm (Fig. 2).

All samples were disaggregated in tap water with diluted H₂O₂, then washed through a 63-µm sieve and dried at 50 °C. A split of the ≥ 63 µm fraction, containing 300 or more specimens, was used for foraminiferal

counts. Benthic foraminifera are abundant and very well preserved in the studied material except for a 5-cm-thick layer of sediment directly overlying the layer with geochemical anomalies (the ‘impact layer’), where benthic foraminifera are scarce and poorly preserved. There are no benthic foraminifera in the ‘impact layer’.

Benthic foraminifera were identified at the generic level following Loeblich and Tappan (1988), and foraminiferal taxa were allocated to morphogroups according to Jones and Charnock (1985) and Corliss and Chen (1988). Relative abundances of the commonest genera of agglutinated and calcareous-hyaline forms, of infaunal and epifaunal morphogroups and relative abundance of infaunal and epifaunal forms within benthic foraminiferal assemblages were calculated (Figs 2 and 3).

Results and discussion

Using information on present morphotypes of benthic foraminifera, six assemblages (I–VI) were recognized that were related to changes in the relative abundance of epifaunal and infaunal species (Fig. 3).

Assemblage I (uppermost *Plummerita hantkeninoides* Zone)

Assemblage I is highly diverse (Figs 2, 3) and composed of epifaunal as well as infaunal morphogroups (Fig. 3). Within the epifaunal morphogroup, the genera *Cibicidoides*, *Lenticulina*, *Valvulabamina*, *Cibicides*, *Gyrogoninoides* and *Anomalinoidea* are common. The morphogroup with inferred infaunal mode of life is dominated by the genera *Sitella*, *Vaginulina*, *Laevidentulina*, *Bulimina*. Agglutinated genera form 6–26% of the assemblage, and are represented by the infaunal taxa *Heterostomella*, *Bolivinaopsis*, *Tritaxia* and *Gaudryina* and the epifaunal *Ammodiscus*.

Assemblage I is typical for outer shelf–upper bathyal marine environments with moderate primary productivity and a flux of organic detritus that is sufficient to sustain infaunal bottom-dwellers. Many genera have been recognized worldwide, and the assemblage is very similar to that at El Kef (Keller, 1988; Speijer and van der Zwaan, 1996; Kouwenhoven, 2000).

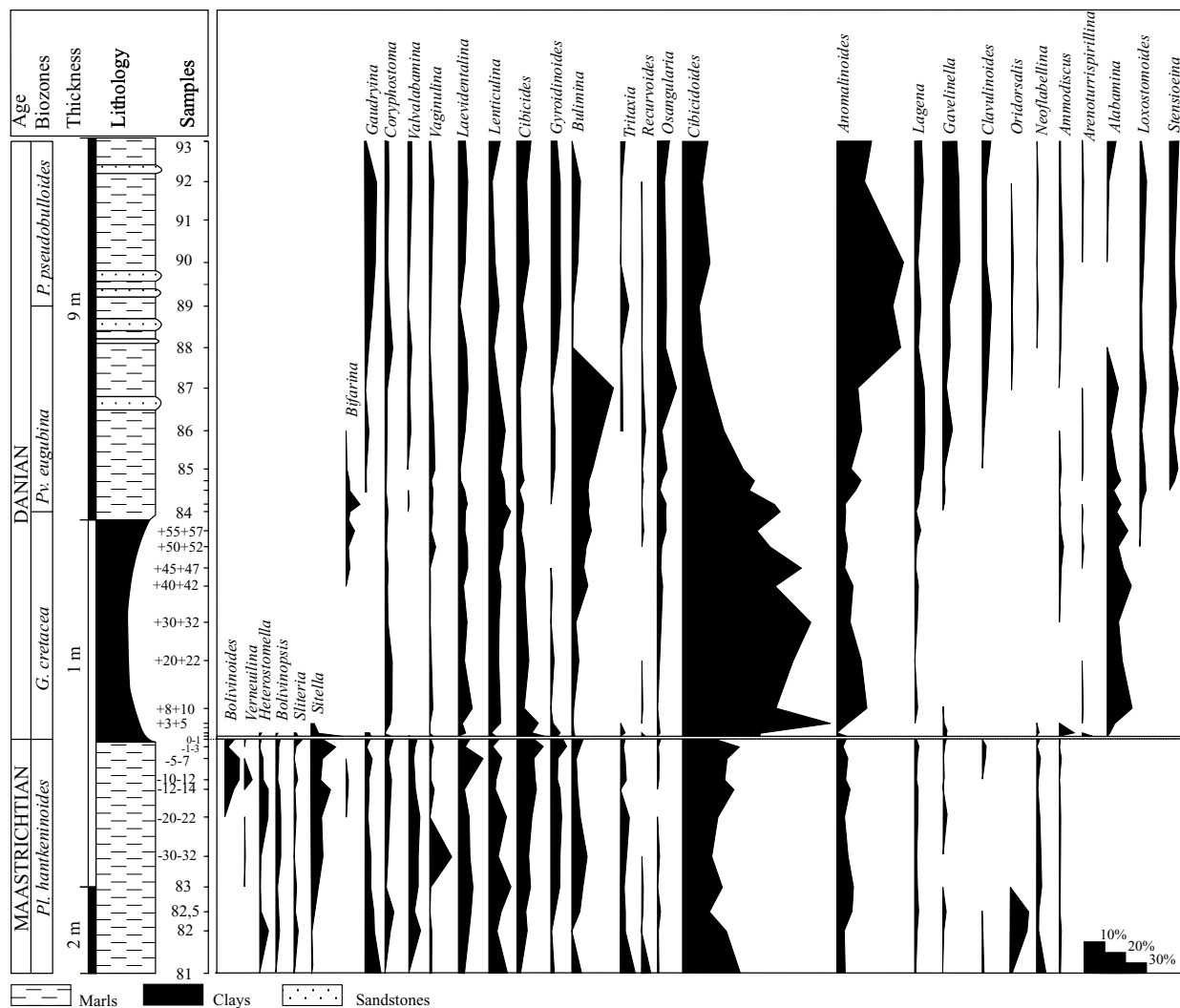


Fig. 2 Stratigraphy and relative abundances of dominant and common benthic foraminiferal genera across the Cretaceous/Palaeogene boundary at the Ain Settara section (biostratigraphy after Arenillas *et al.*, 2000).

Assemblage II (lowermost part of the *Guembelitra cretacea* Zone)

The dramatic change in the structure of benthic foraminiferal assemblages corresponds to the layer with geochemical anomalies, which itself does not contain benthic foraminifera, i.e. at the base of the *G. cretacea* Zone (Figs 2, 3). At this level several genera disappeared, e.g. *Bolivinoidea*, *Bolivina*, *Clavulinoides*, *Coryphostoma*, *Heterostomella*, *Eouvigerina*, *Gaudryina*, *Lagena*, *Neoflabellina*, *Tritaxia*, *Sitella*, *Sliteria*, *Valvulabamina* and *Verneuilina*. Some of these became extinct, such as *Bolivinoidea*, *Bolivina*, *Heterostomella*, *Sliteria*, and *Verneuilina*, whereas others reappeared

in the lower Danian as *Lazarus* taxa. This temporary disappearance of common Cretaceous benthic species was also pointed out by Speijer and van der Zwaan (1996) and Kouwenhoven (2000) at El Kef. Assemblage II contains very scarce benthic foraminifera (mainly *Cibicidoides* and *Ammodiscus*), and it is composed almost entirely of epifaunal species (82–90% of the assemblage). Agglutinated forms constitute up to 15% of the assemblage, and almost completely disappear at the top of this interval (Fig. 3).

Assemblage II reflects a drastic collapse in food supply to the seafloor, with assemblages dominated by epifaunal detritus and suspension feed-

ers. Genera that prefer a high nutrient supply such as *Heterostomella* and *Sitella* disappeared (Speijer and van der Zwaan, 1996).

The severe shortage of food resulted in complete oxidation or consumption of all organic matter before it could be buried in the sediment, so that no food remained for infaunal taxa. The common occurrence of *Ammodiscus*, however, suggests that some food particles were available at the sediment/water interface. However, it is unusual (as also noted by Speijer and van der Zwaan, 1996) to find such high-dominance, low-diversity faunas under oligotrophic conditions (see below).

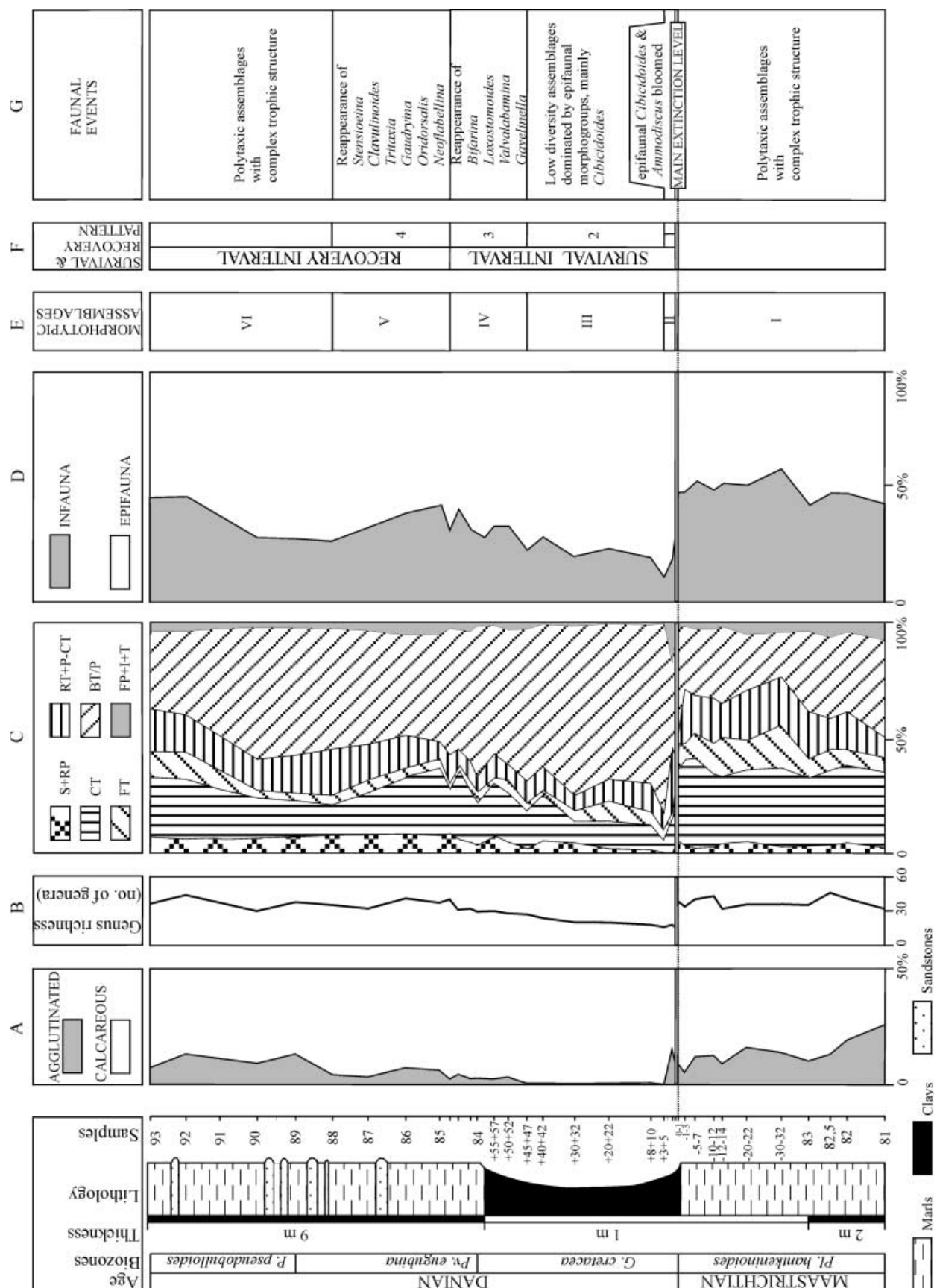


Fig. 3 Changes in benthic foraminiferal assemblage composition across the K/P boundary in the Aïn Settara section. Lithologies are explained in Fig. 2. (A) Relative abundances of calcareous and agglutinated benthic foraminifera within assemblages. (B) Foraminiferal genus richness (number of genera). (C) Proportion of benthic foraminiferal morphogroups within assemblages (infaunal morphotypes: s, spherical; rp, rounded planispiral; ct, cylindrical tapered; ft, flattened tapered; epifaunal morphotypes: rt, rounded trochospiral; p-ct, plano-convex trochospiral; bt/p, biconvex trochospiral/planispiral; fp, flattened planispiral; i, irregular; t, tubular). (D) Proportion of infaunal and epifaunal morphogroups within benthic foraminiferal assemblages. (E) Morphotypic assemblages. (F) Extinction, survival and recovery pattern across the K/P boundary in the Aïn Settara section. (G) Faunal events.

Assemblage III (lower-middle part of the *Guembelitra cretacea* Zone)

Assemblage III is characterized by low diversity: it is almost completely devoid of agglutinated foraminifera and dominated by epifaunal morphogroups (Figs 2, 3). The disappearance of common *Ammodiscus* suggests that food supply to the benthos decreased even more at the beginning of this interval. At about +40 cm, however, epifaunal forms (mainly *Cibicidoides* with minor percentages of *Anomalinoidea* and *Alabamina*) decreased gradually in relative abundance as the infaunal morphogroup (mainly *Laevidentalina*, *Coryphostoma* and *Bulimina*) increased gradually in abundance.

This assemblage indicates that very little food was available on the seafloor: an extreme oligotrophic environment. As for Assemblage II, such high-dominance, low-diversity faunas are not expected under oligotrophic, stress-free conditions (e.g. Kouwenhoven, 2000). Keller (1988), Speijer and van der Zwaan (1996) and Kouwenhoven (2000) explained such unusual dominance by assuming low oxygen conditions. They based this conclusion not on the morphology of the dominant benthic foraminiferal taxon, but instead on the occurrence of lamination in the sediments. It is difficult to understand how such low oxygen conditions could prevail at low productivity, and these authors assumed that the low-oxygen conditions were caused by changes in circulation. However, such lamination may have resulted from the lack of burrowing macrofauna as a result of the mass extinction at the end of the Cretaceous: there are no indications in the geochemical data that low-oxygen conditions occurred (Tribouillard *et al.*, 2000). The dominant *Cibicidoides* are large, thick-walled and multi-chambered, in contrast to the typical

low-oxygen, *r*-selected morphotypes, which generally have few chambers, small tests and thin walls.

It is therefore suggested that the low diversity of Assemblages II and III may have been caused by environmental stress of another kind, changes in the phytoplankton supplied to the benthic faunas. At the K/P boundary the dominant primary producers, calcareous nanoplankton, suffered a major extinction (Romein and Smit, 1981), whereas the organic-walled dinoflagellates did not (Brinkhuis *et al.*, 1998). In the present oceans many organisms do not consume dinoflagellates, and the especially low-diversity faunas may have been under stress because of this change in the composition of food directly supplied from the photic zone.

Assemblage IV (*Parvularugoglobigerina eugubina* Zone)

The trend of decreasing relative abundance of the epifaunal morphogroups (especially *Cibicidoides*) continued in Assemblage IV, where the first Lazarus taxa return. *Bifarina*, *Loxostomoides*, *Gavelinella*, *Valvulabamina* and agglutinated foraminifera gradually increased in relative abundance (Fig. 3).

These faunal changes indicate a gradual increase in the food supply, and possibly an increase in the diversity of the food supply away from dominance by dinoflagellate taxa.

Assemblage V (middle and upper part of the *Parvularugoglobigerina eugubina* Zone)

This assemblage is characterized by a high diversity and low dominance of benthic genera.

The relative abundance of epifaunal forms is similar to that in Assemblage IV, but *Cibicidoides* loses its dominance: its relative abundance drops to

values as low as 7%. *Anomalinoidea*, *Bulimina*, *Osangularia*, *Lenticulina* are common. *Gaudryina*, *Stensioeina*, *Tri-taxia*, *Oridorsalis*, *Clavulinoides* and *Neoflabellina* are long-term Lazarus taxa that reappear in this interval. The relative abundance of agglutinated forms increases to 8%.

This assemblage indicates return to the pre-K/P boundary mesotrophic conditions at outer shelf–upper bathyal depths.

Assemblage VI (uppermost part of the *Parvularugoglobigerina eugubina* Zone and *Parasubbotina pseudobulloides* Zone)

Assemblage VI is highly diverse (Figs 2, 3) and composed of mixed epifaunal and infaunal morphogroups (Fig. 3), where agglutinated foraminifera form 7–15% of the assemblages. Assemblage VI is typical for marine environments at outer shelf–upper bathyal depths, with a flux of organic detritus that is sufficient to sustain infaunal bottom-dwellers.

It is suggested that the benthic foraminiferal assemblages at Aïn Settara do not indicate sea-level changes across the K/P interval, in agreement with Speijer and van der Zwaan (1996), Coccioni and Galeotti (1998) and Kouwenhoven (2000). These authors disagreed with the drop in sea level at or shortly before the K/P boundary as proposed by Keller (1988). In agreement with Coccioni and Galeotti (1998), there probably were no low-oxygen conditions after the K/P extinction, and oxygenation thus did not cause faunal changes in benthic foraminifera. The morphotype analysis outlined herein suggests that the nature and abundance of the food supply to the seafloor conditioned the structure of the benthic foraminiferal assemblages and the faunal turnover.

Conclusions

In the studied section the level of extinction and faunal turnover of benthic foraminifera corresponds to the 'impact layer' at the base of the *Guembelitra cretacea* Zone. The *Guembelitra cretacea* Zone and the lowermost part of the *Parvularugoglobigerina eugubina* Zone represent a survival interval; the recovery interval encompasses the middle and upper part of the *Parvularugoglobigerina eugubina* Zone and the *Parasubbotina pseudobulloides* Zone (Fig. 3).

The survival interval is composed of (Fig. 3):

1 A very thin interval (≈ 1 kyr) at the base of the *Guembelitra cretacea* Zone with scarce, low-diversity, high-dominance assemblages dominated by epifaunal morphotypes. *Cibicidoides* and *Ammodiscus* were abundant, pointing to a sudden collapse in the food flux to the seafloor but continuing availability of food particles at the sediment/water interface. Evidence for a drastic decline in primary productivity is provided by a negative carbon isotope excursion across the K/P boundary (Zachos and Arthur, 1986; Keller and Lindinger, 1989). With very limited food flux to the seafloor, food particles were consumed at the sediment surface and therefore underlying sediment contained only small quantities of organic matter, and infaunal species were almost absent. The extreme dominance of just a few taxa (and thus stressed conditions) was probably not caused by low-oxygen conditions, but instead possibly by changes in the phytoplankton composition (from calcareous nannoplankton to dinoflagellates).

2 An interval with low-diversity, stressed assemblages dominated by opportunistic taxa, mainly epifaunal *Cibicidoides*: the lower and middle part of the *Guembelitra cretacea* Zone, corresponding to about 6 kyr; persistence of oligotrophic conditions unfavourable for infaunal morphotypes; and stress induced by phytoplankton composition.

3 An interval where short-term Lazarus taxa, such as *Bifarina*, *Loxostomoides*, *Valvalabamina* and *Gavelinella*, reappeared and epifaunal morphotypes decreased in relative abundance, during the upper part of the *Guembelitra cretacea* Zone and

the lowermost part of the *Parvularugoglobigerina eugubina* Zone (comprising about 10 kyr). This interval represents an increase in the nutrient level at the seafloor from oligotrophic to mesotrophic.

The recovery interval is characterized by high-diversity, low-dominance assemblages with a complex trophic structure. Long-term Lazarus taxa reappeared during the middle and upper part of the *Parvularugoglobigerina eugubina* Zone and *Parasubbotina pseudobulloides* Zone. This interval represents the return to the pre-K/P boundary conditions, with fully mesotrophic nutrient levels.

The simultaneous occurrence of geochemical anomalies (Tribouillard et al., 2000), the catastrophic extinction of planktic foraminifera (Arenillas et al., 2000) and the drastic reorganization of benthic foraminiferal assemblages at the K/P boundary at Ain Settara were probably the result of the impact of an asteroid on the Yucatan peninsula, which caused a global drop in primary productivity (D'Hondt et al., 1998), and thus triggered benthic foraminiferal turnover.

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