Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, S.E. Spain

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ABSTRACT

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Planktonic foraminiferal extinctions at Caravaca and Agost occurred over an extended time period similar to El Kef and Brazos River. Some species disappeared well below the boundary. About 39–45% of the species, but less than 15% of the individuals in the population, became extinct at or near the K/T boundary. A second phase of extinction occurred at the top of the boundary clay (P0/P1a) and the remaining Cretaceous species (except *G. cretacea*) disappeared in Subzone P1a. Species extinctions were selective eliminating geographically restricted large, complex and deeper dwelling forms first and favoring survival of cosmopolitan small, simple surface dwellers. Only surface dwellers survived the K/T boundary event, whereas all deeper dwelling species, as well as some surface dwellers, disappeared at the boundary.

We interprete the selective abundance decline during the latest Cretaceous as a result of the seal level regression that reached a maximum just prior to the K/T boundary. The highly selective nature of the two-phased species extinctions at and above the boundary, we believe to be related to the major reduction in surface productivity and the breakdown in the water mass stratification that was associated with the rapid sea level transgression across the K/T boundary. A bolide impact however, may have hastened the demise of an already declining Cretaceous fauna.

Introduction

Planktonic foraminifera suffered the most dramatic species extinctions among marine organisms across the Cretaceous-Tertiary (K/ T) transition as a result of global environmental changes that have been variously interpreted as caused by a large meteorite impact (Alvarez et al., 1980), volumetrically and geographically widespread volcanism (McLean, 1985; Officer and Drake, 1985; Loper and McCartney, 1986, 1988; Rampino and Stothers, 1988; Courtillot and Besse, 1987) and climate and seal level changes (Donovan et al., 1988; Hallam, 1989; Stott and Kennett, 1989; Barrera and Huber, 1990; Pirrie and Marshall, 1990). The source and mechanism(s) of these global changes, however, are poorly understood. Because planktonic foraminifera are sensitive indicators of environmental changes such as shifts in temperature, salinity, oxygen, nutrients and water depth, their pattern of species extinctions and changes in the relative abundance of individual species populations can yield clues to the nature of this global change.

Well before the current round of the K/T boundary controversy, paleontologists recognized that most large Cretaceous planktonic foraminifera suddenly disappeared at the end of the Cretaceous and a number of small species survived into the Paleocene (Olsson, 1960; Berggren, 1962; Luterbacher and Premoli Silva, 1964; Smit, 1977; Hofker, 1978). Later studies, however, frequently ignored the presence of Cretaceous species in Tertiary deposits or interpreted them as reworked, thus claiming the sudden extinction of all but one Cretaceous species due to a meteorite impact (Smit. 1982, 1990; Smit and Romein, 1985) Examination of a large number of K/T sequences, however, reveals that species extinction patterns are variable between deep sea and continental shelf environments. In the deep sea, all but one Cretaceous species (Guembelitria cretacea) suddenly disappeared at the K/T boundary (Smit and Romein, 1985; D'Hondt and Keller, 1991) whereas in upper slope and shelf sequences, such as El Kef, Agost, Caravaca, Zumaya and Brazos River, species extinctions occurred over an extended time period (Keller, 1988, 1989a,b; Lamolda, 1990).

So, what caused this differential pattern of species extinctions between deep-sea and shelf environments? A recent chronostratigraphic analysis of 29 K/T boundary sequences has revealed that virtually all deep sea sections have a hiatus at the K/T boundary that variously spans between 70,000 and 400,000 years of earliest Tertiary sediments (MacLeod and Keller, in press). In contrast, sediment deposition continued during this time in upper slope to mid-shelf environments, although at a considerably reduced rate, and short hiatuses occurred above the boundary clay near the Zone P0/P1a boundary and in the upper part of Zone P1a. This differential hiatus pattern appears to be related to the rapid sea level rise in the earliest Tertiary following the end of the Cretaceous maximum regression (Brinkhuis and Zachariasse, 1988; Donovan et al., 1988). The effect of such a rapid sea level transgression would have been to trap terrigenous sediment and organic carbon high on the already extensive continental shelves, thus temporarily depriving deep ocean basins of an inorganic sediment source and enhancing carbonate dissolution (Berger, 1970; Berger and Winterer, 1974; Loutit and Kennett, 1981; Hag et al., 1987). Thus, the differential extinction patterns between deep sea and continental shelf environments are apparently the result of differential sedimentation patterns where the sudden extinction of all but one Cretaceous species in the deep sea is an artifact of an incomplete sedimentary record.

The most complete K/T boundary transition records of biological and environmental changes are thus found in upper slope to continental shelf sequences and among these El Kef, Agost, Caravaca and Brazos River sections contain the most continuous sedimentation record known to date (MacLeod and Keller, in press). In these sequences, Keller (1988, 1989a,b) and others (this study) have shown that there is no trace of a mass extinction among planktonic foraminifera encompassing all but a single Cretaceous species as has been claimed by Smit (1982, 1990). Instead, species extinctions occurred over an extended time period with up to one third of the species disappearing below the K/T boundary in the shallow neritic sections of El Kef and Brazos River and up to one third surviving into the early Tertiary in all sections (Keller, 1988, 1989a,b; this study). This differential extinction pattern preceeding the K/T boundary appears to be related to the Late Maastrichtian sea level regression and exclusion of deeper dwelling species in a shallowing sea. These studies show that the K/T transition in the marine realm is not likely caused by a single instantaneous event, but rather by a set of complex and interrelated factors including changes in climate, sea level and associated variations in ocean geochemistry. The patterns of species extinctions and evolution in marine microplankton must be viewed within this context.

The purpose of this study is to document the pattern of planktonic foraminiferal species extinctions, evolution and abundance changes in dominant species populations at Agost and Caravaca in order to assess the magnitude of the K/T boundary mass extinction, the selective nature of species extinctions and, if possible, isolate the effects of long-term environmental changes from short-term effects. Some taxonomic problems of the early Paleocene fauna are discussed in the Appendix. In addition, we will address the fundamental discrepancies between this report and the published reports of Caravaca and Agost by Smit (1982, 1990).

Lithology and geographic setting

Both Agost and Caravaca sections are located in the Betic Cordilleras of southeastern Spain. The K/T transition of the Caravaca section lies within the Jorquera Formation which outcrops in a ravine about 4 km southwest from the town of Caravaca (Barranco del Gredero, Fig. 1). Sediments consist of inercalated marls, marly limestones and occasional turbidites deposited within a low energy marine environment. Benthic foraminifera indicate a shallowing upper bathyal depositional environment during the latest Maastrichtian followed by a transgression during the early Tertiary (Keller, in press). The K/T boundary is marked by a sharp contact between grey Maastrichtian marls and a thin (7 cm) black clay layer with a 2-3 mm thin rust-red basal layer. The red color originates from relatively high amounts of goethite and haematite. Laterally, the black clay layer shows major changes in thickness due to intrasequence slump struc-



Fig. 1. Geographic location of Caravaca and Agost K/T boundary localities in southeastern Spain.

tures and occasional folding. Grey clayey marls overlie the black clay. No turbidite deposits are present in the boundary transition spanning from 1 m below to about 2 m above K/Tboundary.

The town of Agost is located about 100 km west of Caravaca and the section is located about 1 km northeast of the town (Fig. 1). Surface exposures of the K/T boundary transition can be found in a roadcutting near the 13 km marker post, in a nearby gully, and closer to the town opposite the cementary where a good Maastrichtian sequence is exposed (Groot et al., 1989). Sediments consist of intercalated grey marls and marly limestone beds. As at Caravaca the K/T boundary is marked by a sharp contact between Maastrichtian grey marls and a thin (6.5 cm) black clay layer with a basal 2-3 mm thin rust-red layer. No slump structures have been observed in this black clay layer. Grey early Tertiary marls overlie the black clay. Benthic foraminifera indicate deposition occurred in an upper bathyal to outer neritic environment and at somewhat shallower depth than at Caravaca (Keller, in press).

Materials and methods

The outcrops at Agost and Caravaca were trenched to remove surface contamination and obtain fresh unweathered bedrock. Samples were collected at cm-intervals across the K/T boundary and the black clay layer and at 2 to 5 cm continuous intervals from 1 m below to 1.35 m above the boundary. A total of 90 samples were analyzed for this study (46 in Agost, 44 in Caravaca).

Samples were disaggregated in water and dilute H_2O_2 and washed through a 32 micron screen. This procedure was repeated until a clean foraminiferal residue was recovered. Preservation of planktonic foraminifera is good

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CRETACEOUS/TERTIARY BOUNDARY EXTINCTION PATTERN

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G. dupeublei Caron et al., 1985		3		-				!		5				4	-	-	-	r	<	~ ~
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Spiroplecta americana Ehrenberg, 1844	7		-		6		1				1 2				4	S			4	_
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Guembeluria cretacea Cushman, 1933	24	21	9	27 7	0 7	1 3.	5 39	35	4	16	39	10	19	S	6	10	=	910	53 12	8 6	5	16
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TOTAL NUMBER COUNTED	293 5	57 4	77 3	13 67	3 80	3 67(5 623	643	429	504	832	522	526	376	573	516 4	56 4	9 69	14 58	12 69	9	69
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although original calcite shells are recrystallized. Dissolution effects are most notable 1-2 cm above and below the red layer and to a lesser degree in the boundary clay.

Population counts were based on representative splits (using an Otto microsplitter) of 300 or more specimens in the size fraction > 63 μ m. All specimens were picked and mounted on microslides for a permanent record and identified. The remaining sample was scanned for rare species. Faunal counts for the picked fraction are listed in Tables 1–4. The smaller size fraction (32–63 μ m) was also examined, but was found to be impractical for quantitative studies because of the larger number of juveniles present which could not be identified at the species level.

Biostratigraphy

The Caravaca and Agost sections are very similar in lithology, stratigraphy and faunal turnover and, moreover, they are similar to the El Kef section of Tunisia and sections in the Negev, Israel. Therefore, the biozonation of Keller (1988, 1989a,b) has been largely followed in this study. The zonations of Bolli (1966), Herm et al. (1981) and the recently revised zonation of Berggren and Miller (1988) are not applicable for the Spanish sec-

CHS	Datums events							BIOZONATION	S						
EPO	in the sections studied	This report		Keller, 1988	Sm	Smit, 1982 it & Romein,	, 1985	Bolli, 1966	Herm <i>et</i>	aL, 1981		Berggro Miller,	en & 1988	1	3tow, 1979
	G. planocompressa P. eugubina G. pseudoinconstans	udobulloides	P1c	Subbotina pseudobulloides		eudobulloides	a taurica	rotalia ulloides	pseudobulloides	rina edita		P 1b	Subbotina triloculinoides	Pla	urborotalia) lloides- urborotalia) apressa
0	S. triloculinoides	S. pse	P1b	Eoglobigerina taurica	P1b	gerina pse	globigerin	Globo pseudob	borotalia	Globige	P1		na Iloides		orotalia(1 pseudobu orotalia(1 rcheocom
aleocene	P. longiaperiura E. edita G. pentagona S. pseudobulloides & F. travialis	~		rina		Globi	Eo_8		Glol			P 1a	Subboti pseudobu		Glob
Early P	C. daubjergensis P. eugubina-G. taurica trans. C. dafi, pianocompressa E. minutula, G. irregularis & S. aff. piseudobulloides P. eugubina C. midwayensis E. cf. fringa E. cf. fringa D. foreimerture	P. longiaperturo	P1a	Parvularugoglobige. eugubina	P1a	IV/V III	Globigerina eugubina	Globigerina eugubina	Globigerina	eugubina	P∝	Dariulariandahian	I arvaia ugogiovigerina eugubina	P∝	Globorotalia (Turborotalia) longiapertura
	& C. danica E. cf. edita	retacea	POb	Globoconusa conusa		II I			Globiş frir	gerina 1ga				M 18	obigerina amerata
	W. claytonensis	C. C	P0a	Guembelitria cretacea	PO	Guembe cretac	litria cea								Rugogl hexac
Late Cretaceous	r. aejornus & ¥ A. mayaroensis	A. mayaroensis	Pseudotextularia	deformis deformis Abathomphalus mayaroensis	М 3	Abathomphalus	mayaroensis	Abathomphalus mayaroensis	Abathomphalus	mayaroensis				M 17	Abathomphalus mayaroensis

Fig. 2. Comparison of late Maastrichtian and early Paleocene planktonic foraminiferal biozonations with biozonation of this report.



Fig. 3. Species ranges of planktonic foraminifera at Caravaca, Spain. Blank intervals mark absence of species in those samples. Sample depths in cm above and below K/T boundary.

tions. Figure 2 illustrates the biozonation and sequence of planktonic foraminiferal datum events at Caravaca and Agost in comparison with other published biozonations. A brief discussion of the major zonal characteristics is given below.

Abathomphalus mayaroensis Biozone

This biozone is defined by the total range of *A. mayaroensis* and characterized the late Maastrichtian in tropical deep sea sequences including the Spanish sections. *A. mayaroensis*, however, is frequently absent in shallow continental shelf sections (Jones et al., 1987; Keller, 1988, 1989a) and in high latitudes disappears prior to the K/T boundary (Blow, 1979). Therefore, the *A. mayaroensis* Biozone is geographically and ecologically restricted and

an alternative biozone, *Pseudotextularia deformis* was proposed for shallow water sequences (Keller, 1988).

K/T Boundary

The El Kef section in Tunisia was recently chosen as stratotype for the K/T boundary by the working group on the Cretaceous-Paleogene boundary (International Commission of Stratigraphy). This working group characterized the K/T boundary by the major planktonic foraminiferal extinction event and/or the first appearance datum (FAD) of Tertiary species, and a major lithologic change, including the presence of a thin red layer at the base of the boundary clay, marked by various geochemical anomalies (including Ir, CaCO₃, δ^{13} C, TOC). At Caravaca and Agost the first Tertiary species (*Woodringina claytonensis*)



Fig. 4. Species ranges of planktonic foraminifera at Agost, Spain. Blank intervals mark absence of species in these samples. Sample depths in cm above and below the K/T boundary.

appears in the basal 0–1 cm and 1–2 cm of the black boundary clay respectively whereas the major Cretaceous species extinctions occur in the sample just below the black clay and basal red layer (Figs. 3,4, Tables 1–4). Moreover, the red layer in both sections shows a drop in CaCO₃ to less than 1%, a negative shift in δ^{13} C and enrichment of iridium, (Smit and ten Kate, 1982; Smit, 1990). Thus, the defining criteria for the K/T boundary are all present at Caravaca and Agost placing tight constraints on this boundary interval.

Guembelitria cretacea (P0) Biozone

This biozone spans the interval between the K/T boundary and the FAD *Parvularugoglobigerina longiapertura (P. eugubina* of Keller, 1988). Lithologically, this biozone generally

encompasses the black boundary clay. Keller (1988) proposed a subdivision of P0 based on the FAD of *Globoconusa conusa* (*G. minutula* of Smit, 1982) which characterizes the top of Smit's P0 Biozone (Fig. 2). Subdivision of P0 is only practical, however, where a thick boundary clay is present as at El Kef. Blow's (1979) Rugoglobigerina hexacamerata Zone is tentatively considered equivalent to P0 based on the similar faunal characteristics described by Blow and observed also in the Spanish sections (Fig. 2).

The presence of a boundary clay and Biozone P0 in both Caravaca and Agost sections indicates that a continuous, albeit condensed (5-7 cm) K/T boundary transition is present as previously noted by Smit (1977, 1982, 1990). But, graphic correlation of the Spanish sections with other K/T sequences could indicate a short hiatus or non-deposition in the upper part of Biozone P0 as discussed below.

Parvularugoglobigerina longiapertura (P1a) Biozone

This biozone is defined by the range of P. longiapertura which is generally included in the P. eugubina group of other authors (Fig. 2). We propose this change in the nominate taxon because P. eugubina is morphologically highly variable and first and last occurrences can be easily misidentified. In contrast, P. longiapertura has a very distinct and stable morphology with its compressed test and high slit-like aperture and is therefore a more suitable index taxon. In most sections examined, the FAD's of P. eugubina and P. longiapertura are very similar, but the last occurrence (LAD) of P. eugubina is difficult to identify due to its morphologic evolution towards Globigerina taurica. This problem is further discussed in the Appendix. In the Spanish sections the P1a Biozone is dominated by P. longiapertura, P. eugubina, G. conusa and in the upper part by increasing abundance of Woodringina.

Subbotina pseudobulloides (P1b-P1c) Biozone

This biozone defines the interval between the *P. longiapertura* LAD and *Morozovella trinidadensis* FAD and hence differs from the more traditional definition which uses the *S. pseudobulloides* FAD to mark the base of this biozone (Fig. 2). *S. pseudobulloides*, however, has been shown to be diachronous by as much as 250,000 years in a recent graphic correlation of 15 K/T boundary sections (MacLeod and Keller, in press) and is therefore a poor index taxon. In the Spanish sections the P1b–P1c biozone is characterized by abundant biserial (*Woodringina*) and triserial species (*Guembelitria Chiloguembelitria*).

Extinction pattern

In his study of Caravaca and Agost, Smit (1982, 1990) observed that all Cretaceous species except Guembelitria went extinct at the K/T boundary and this pattern is illustrated for Agost in Fig. 5 (from Smit, 1990). We cannot confirm this extinction pattern as Figs. 3 and 4 illustrate. At both the Agost and Caravaca sections some species disappear well below the K/T boundary and 39% and 45% respectively disappear at or near the boundary (Fig. 6). A second extinction phase coincides with the P0/P1a zonal boundary at Agost where 26% (12 species) disappear. But at Caravaca this extinction interval extends into the basal P1a Biozone (Figs. 3.4.6). The difference between the two sections is probably due to the more condensed section at Agost and a short hiatus which is particularly evident by the abrupt faunal abundance changes at this interval as discussed below. About eight Cretaceous species are present well into P1a Biozone and among these only Guembelitria survives into P1c Biozone.

This extended pattern of species extinction (illustrated for Caravaca in Fig. 6), including the two phases of accelerated extinctions at the K/T boundary and near the P0/P1a boundary, is similar to that observed at El Kef and Brazos River (Keller, 1989b). Moreover, as in these sections species extinctions in the Spanish sections are selective affecting large, ornamented, complex and tropical morphologies first and favoring survival of smaller, less ornamented and cosmopolitan species. The differences between these sections are likely due to paleodepth and local geographic effects.

The pattern of species extinctions at Caravaca is summarized in Fig. 6. It is evident from our data set that Cretaceous species diversity is high and relatively stable to just below the K/T boundary, drops at the boundary and gradually declines thereafter. This pattern is echoed in the percent species extinct and the percent of Cretaceous individuals disappear-



Fig. 5. Relative percent-abundances of planktonic foraminiferal species at Agost, Spain by Smit (1990). Note the abrupt disappearance of all Cretaceous taxa at the K/T boundary and compare with Figs. 7 and 8 of this report which show abundant Cretaceous taxa in the boundary clay.

ing from the total foraminiferal population. The latter parameter illustrates the unusually high presence of Cretaceous individuals in the boundary clay possibly as a result of dissolution (see increase in benthics) and some reworking as well as the abrupt decline of this group at the top of the boundary clay as a result of a short hiatus or non-deposition as discussed below. Tertiary species evolve gradually and their diversity remains low throughout the Danian.

With the large number of Cretaceous species present in basal Tertiary sediments in the Agost and Caravaca sections, we fail to understand Smit's conclusion that all but one Cretaceous species went extinct at the boundary and that he fails to mention their abundant presence in the boundary clay as illustrated in Figs. 7 and 8. Nevertheless, he noted that "A few reworked larger Cretaceous planktonic foraminifers occur, but small species like *Guembelitria cretacea, Hedbergella monmouthensis* and *Globigerinelloides messinae* are somewhat

more abundant relatively" (Smit, 1990, p. 192). Since Cretaceous species comprise over 90% of the faunal assemblages in Biozone P0 (Tables 1–4, Figs. 7,8), it is puzzling to us why Smit (1990, Fig. 5) chose to ignore this fauna in his illustration except for one species, Guembélitria cretacea. We must therefore assume that he elected to omit these species in the conviction that all are reworked as implied by his statement that "The 6.5 cm boundary clay represents the almost empty oceans directly after the mass-extinctions" and that the boundary clay "contains reworked and relict elements of the upper Maastrichtian planktonic fauna" (Smit, 1990, pp. 200,201). Unfortunately, this omission of data seriously biases Smit's data set.

There are several other problems with Smit's (1990) data (Fig. 5) that render direct comparison with our results impossible. For instance, no data table is provided of faunal counts and there is no information of the sample spacing used, or even what size fraction was



Fig. 6. Species diversity, percent Cretaceous species disappearance, percent Cretaceous and Tertiary individuals in population and planktic/benthic ratio of foraminifera. Note the gradual decline of Cretaceous species in the early Paleocene and the abundant presence of Cretaceous specimens in the boundary clay.

analyzed. This type of data is critical to any faunal study, particularly across the K/T boundary interval. Smit illustrated the faunal changes at Agost at a meter-scale with an apparent sample resolution of about 30 cm to 50 cm intervals (Fig. 5). Even if he had used 10 cm sample spacing across the K/T boundary (instead of 2 cm intervals as shown in our study), the critical information on species extinctions, survivors and amount of reworking could have been lost because the boundary clay layer is only 6–7 cm thick. Of course, such large sample spacing may have missed the boundary clay altogether which could explain the apparent catastrophic extinction shown by Smit (1990, Fig. 5). Our study shows that few Cretaceous taxa are present above the clay layer.

Another very serious problem in Smit's



Fig. 7. Relative population abundances of common species in the size fraction $> 63\mu$ m in the Caravaca section. Note the common to abundant occurrence of Cretaceous species in the boundary clay and ranging into Zone P1a. Sample depths in cm above and below the K/T boundary.

faunal analysis is his apparent use of a larger size fraction, probably greater than $125 \,\mu$ m, instead of the greater than 63 μ m fraction used in our study. We infer this from the abundant presence of large taxa (globotruncanids, pseudoguembelinids) and low abundance of small taxa in his data (Fig. 5) as compared to our analysis (Figs. 7,8, Tables 1–4) and his statement that the boundary clay represents an almost empty ocean (Smit, 1990, pp. 200,201). It is well known that because of the large number of very small taxa across the K/T boundary and especially in the boundary clay, a representative illustration of the faunal changes can only be obtained from analysis of the small $(>63 \ \mu m)$ size fraction. Smit's "empty ocean" is therefore most likely the result of using a large sieve size through which the small earliest Tertiary species were lost. The omission of these small taxa in Smit's data set, together with the apparent large sample spacing, renders Smit's analysis of Agost as non-representative of the K/T boundary transition.

Cretaceous survivors

Cretaceous species present in Tertiary deposits are poorly documented largely because they are generally assumed to be reworked.



Fig. 8. Relative population abundances of common species in the size fraction $> 63\mu$ in the Agost section. Note the common to abundant occurrence of Cretaceous species in the boundary clay and ranging into Zone Pla. Sample depths in cm above and below the K/T boundary.

This is invariably the case for some species, particularly globotruncanids, which can also be found in some intervals at Agost and Caravaca (Tables 1-4) and which are generally more poorly preserved than the Tertiary fauna in which they are found. However, many other Cretaceous species, including heterohelicids, hedbergellids, globigerinellids, guembelitrids and pseudotextularids, are continuously present in lower Paleocene sediments in Spanish sections as well as at El Kef and Brazos River (Keller, 1988; 1989a,b). Such continued presence in geographically widely separated regions implies survivorship. Moreover, specimens in Tertiary deposits are generally dwarfed relative to their Cretaceous ancestors indicating early sexual maturation (MacLeod and Keller, 1991). However, if reworking were the cause for their presence, one would also expect to find other species of the Cretaceous fauna. Finally, δ^{13} C measurements of two Cretaceous species, *Heterohelix globulosa* and *Guembelitria cretacea*, indicate 2‰ depletion in specimens from Tertiary sediments relative to their Cretaceous ancestors (Keller and Barrera, 1990; Barrera and Keller, 1990). This characteristic Tertiary carbon-13 isotopic signal conclusively shows that these species lived in the post-K/T environment.

The possible survivorship of Cretaceous species at Agost and Caravaca can be investigated from the quantitative faunal data. Figures 7 and 8 illustrate that in the Spanish sections all species that were dominant during the late Cretaceous range into the early Tertiary. But the high abundance of some of these species (P. costulata, P. kempensis, Globigerinelloides species) in the P0 Biozone is unusual and has not been observed before. This high abundance may in part be due to reworking and dissolution as indicated by the presence of common solution resistant globotruncanids (Figs. 7.8) and the increase in benthic species (Fig. 6). Moreover, all Cretaceous species decline sharply to < 3% above the boundary clay. Since no burrowing or mixing of sediments was observed in the boundary clay and major mixing of sediment must also be excluded in P1a Biozone because of the normal evolutionary sequence of Tertiary species, we believe that any significant redeposition of Cretaceous species is restricted to Biozone PO.

Tertiary evolution

The evolution of Tertiary species is very similar at Caravaca and Agost and varies little from El Kef and Brazos River sections. Differences between the sequential order of first appearance datums (FAD's) illustrated in Fig. 2 and that of El Kef (Keller, 1988) and Brazos (Keller, 1989a,b) are primarily due to diachronous first appearances of species and secondarily due to still poorly understood systematics of some species. In the Spanish sections Woodringina claytonensis (W. hornerstownensis of Keller, 1988, 1989a,b) is the first Tertiary species to appear immediately after the K/T boundary followed by G. conusa and E. fringa. At the top of the boundary clay Ch. danica, E. cf. edita and P. longiapertura appear and are immediately followed by Ch. midwayensis. E. minutula and P. eugubina. Other characteristics species which evolve in Biozone P1a include G. daubjergensis and S. pseudobulloides, G. pentagona and M. inconstans. This rapid evolutionary sequence through P1a Biozone marks an unstable period of high faunal turnover and short-lived species. A more stable fauna evolves in the succeeding P1b-P1c Biozone. All species evolving within Biozones P0 and P1a are small, unornamented, cosmopolitan and relatively short-lived, whereas larger and longer-lived forms evolved in P1b-P1c.

Faunal turnover

The faunal turnover across the K/T transition at Caravaca and Agost is illustrated in Figs. 7 and 8. Both sections indicate a relatively stable latest Maastrichtian marine environment dominated largely by a group of geographically widespread biserial species (heterohelicids, spiroplectids, pseudoguembelinids) and globigerinellids. No major environmental changes are indicated in the abundance fluctuations of these species up to the K/T boundary. At Caravaca, just below the lithologic change that marks this boundary, decreased abundance of S. navarroensis and anomalous peak abundance in Globotruncana spp. may mark both an environmental change and carbonate dissolution. In the P0 (G. cretacea) Biozone biserial species are still unusually common in both Spanish sections whereas at El Kef they decline at the base of this zone and disappear in Pla Biozone (Keller, 1988). At Agost and Caravaca anomalous abundance increases are found in Globigerinelloides, Hedbergella, P. kempensis and restricted to Agost in Rugoglobigerina and Globotruncana. These abundance increases are probably due to dissolution within the boundary clay as indicated by the increased abundance of benthic species (Fig. 6). In addition to dissolution, some reworking of Cretaceous sediments in the boundary clay is indicated by the presence of common Rugoglobigerina and Globotruncana which are not common in uppermost Cretaceous sediments and have not been observed in Tertiary deposits in other sections. Above the boundary clay (P0) all dominant Cretaceous species decline and gradually disappear during the (P1a) Biozone.

The Cretaceous survivor species Guembelitria cretacea is relatively rare in the uppermost Maastrichtian of Agost and Caravaca and increases to about 10-15% in the boundary clay (P0, G. cretacea, Biozone) and to 30% at the top of the boundary clay (P0/P1a) at Agost (Figs. 7,8). This low abundance of G. cretacea in the boundary clay is contrary to observations by Smit who noted that this species is almost exclusively present (90% at Agost, Smit, 1990, p. 190; Fig. 5). Our data indicates that such high G. cretacea abundance can only be obtained at Caravaca and Agost if all other Cretaceous species present in the samples are excluded from the faunal counts (Tables 1-4, Figs. 7,8).

The boundary clay in the Spanish sections has only a sparse evolving Tertiary fauna which is characteristic of the initial 50,000 years after the K/T boundary event in all boundary sections (Herm et al., 1981; Smit, 1982; Brinkhuis and Zachariasse, 1988; Keller, 1988, 1989a,b; Keller et al., 1990). At Caravaca and Agost a dramatic faunal change occurs at the top of the boundary clay (Figs. 7,8). At this interval the disappearance of some Cretaceous species and abundance decline of others is accompanied by abrupt increases in G. cretacea, G. conusa and P. longiapertura. This abrupt faunal change could implie a short hiatus or condensed interval in the upper part of P0 (G. cretacea) Biozone which is estimated to span 20,000 to 30,000 years (MacLeod and Keller, in press).

The P1a (*P. longiapertura*) Biozone is characterized by floods of short-lived species including *G. conusa*, *P. longiapertura*, *E. edita* and *P. eugubina* (Figs. 7,8). An abrupt terminal decline in the dominant *P. longiapertura* and concurrent rise in *Woodringina* could mark another short hiatus in the upper part of P1a Biozone. Based on chronostratigraphic analysis and graphic correlation of the 15 most complete K/T boundary sequences from Tunisia, Spain, Texas, Israel and DSDP Sites 577 and 528 we estimate that about 70,000 years could be missing at this interval (MacLeod and Keller, in press).

Discussion

Planktonic foraminifers show the highest rate of extinction at the K/T boundary among all marine fossil groups. We demonstrate, however, that this mass extinction is not geologically instantaneous, but occurred over an extended time period. Moreover, this mass extinction pattern is not likely caused by a single event, but rather implies a complex interaction of long-term environmental changes with superimposed short-term perturbations. If we are to understand the response of the foraminiferal population to the K/T boundary disturbance and in the wider sense what drives mass extinctions and the subsequent evolutionary recovery, we must isolate long-term from short-term causal factors. Such information can be obtained from foraminiferal ecology and in particular the depth habitat of species becoming extinct, those surviving and evolving as discussed below.

A striking pattern emerges from the faunal abundance and diversity data across the K/T boundary at Caravaca and Agost as well as El Kef and Brazos River. All sections show a relatively stable dominant fauna during the latest Cretaceous composed of geographically widespread, simple small and weakly ornamented species (heterohelicids, spiraplectids, pseudoguembelinids; hedbergellids, globigerinelloidids). All of these species have light δ^{18} O and heavy δ^{13} C values which indicates they lived in surface waters within the photic zone (Boersma and Shackleton, 1981; Thierstein, Keller and Barrera, unpubl. data). Only species of this group survived into the Tertiary.

The geographically more restricted large, complex and highly ornamented species such as Globotruncana, Globotruncanita, Contusotruncana, Racemiguembelina and Planoglobu*lina* which are characteristic of late Cretaceous deposits are generally rare in latest Cretaceous sediments (see also Keller, 1989b). All of these rare and complex large species became extinct at the K/T boundary. At Caravaca and Agost up to 45% of the species disappeared at the boundary (including rugoglobigerinids), but these species represent only about 10-15% of the individuals in the foraminiferal population. Thus, the simple number of species which became extinct overestimates the effect on the foraminiferal population by a factor of 3. It is also interesting that all the large and complex species which disappeared at or before the K/ T boundary are deep and intermediate water dwellers as indicated by isotopic ranking of Cretaceous species. The K/T boundary event thus predominantly affected dwellers below the photic zone, although some surface dwellers (rugoglobigerinids) also died out.

Figure 9 illustrates the pattern of extinction based on isotopic ranking of species into surface, intermediate and deep dwellers for both the percentage of species in each group and for the percentage of individuals in each group at Caravaca and El Kef along with the δ^{18} O and δ^{13} C records for fine fraction carbonate (Keller and Lindinger, 1989). Note that among these two faunal parameters the percentage of species involved consistently overestimates the effect on the total foraminiferal population by a factor of 2 to 3.

The following trends are apparent from Fig. 9. Deep and intermediate dwelling species are more common at Caravaca ($\sim 35\%$) than at El Kef ($\sim 25\%$) and at both sites they decline below and disappear at the K/T boundary. Although a lower percentage of the individuals in the population is affected (less than 15% at both sites), an upward declining trend is also indicated. This trend is also notable in the intermediate group (globotruncanids) which is

reduced to less than 2% at Caravaca about 60 cm below the K/T boundary and rare at El Kef. Surface dwellers are a dominant and increasing faunal component during the latest Cretaceous and large numbers (although few species) survive into the Tertiary. New species evolving in the Tertiary are also surface dwellers. The isotope record indicates a stable latest Cretaceous surface ocean followed by a drop in δ^{13} C at the K/T boundary and warm unstably fluctuating conditions thereafter. The immediate rise in both δ^{18} O and δ^{13} C at the top of the boundary clay in Caravaca, however, probably indicates a diagenetic effect. Return to stable high surface productivity does not occur until P1c Biozone (Keller and Lindinger, 1989).

Figure 9 thus illustrates a long-term effect by the decreasing abundance in deep and intermediate dwellers and a short-term effect by their sudden disappearance at the K/T boundary. We interprete the long-term effect as a result of the late Maastrichtian sea level regression which culminated just below the K/T boundary (Hag et al., 1987; Donovan et al., 1988). A shallowing sea and the associated change in the watermass structure could have affected deeper dwelling species more than surface dwellers. Moreover, the shallower outer neritic environment at El Kef (as opposed to the upper bathyal environment at Caravaca) could account for the lower abundance of deep and intermediate dwellers at El Kef. The sudden extinction of all deep and intermediate dwellers at the K/T boundary, however, implies a short-term cause probably related to the drop in δ^{13} C values. This δ^{13} C shift implies dramatically reduced surface water productivity (Zachos and Arthur, 1986; Keller and Lindinger, 1989; Barrera and Keller, 1990) which would have favored survival of surface dwellers. Nevertheless, this faunal and isotopic shift also implies a complete change in watermass structure from a well stratified Cretaceous ocean to a non-stratified Tertiary ocean (pres-



Fig. 9. Planktonic foraminiferal species of Caravaca and El Kef grouped into surface, intermediate and deep water dwellers based on oxygen and carbon isotope ranking of species. These groupings are illustrated in terms of percent abundance of individuals in each group and percent abundance of species in each group. Note, the decline and extinction of deep and abundance of species in each group. Note, the decline and extinction of deep and intermediate water dwellers at the K/T boundary and survival of surface dwellers into the Tertiary.

ence of only surface dwellers). This shift is associated with a rapid sea level transgression (P0-P1a) at El Kef (Brinkhuis and Zachariasse, 1988) as also observed globally by Haq et al. (1987) and Donovan et al. (1988). We believe that the selective nature of species extinctions and faunal abundance changes across the K/T boundary observed in Spain, Tunisia and Texas are consistent with the effects of a latest Cretaceous sea level regression followed by a rapid transgression across the K/T boundary; the latter was associated with a breakdown in the watermass stratification and a reduction in surface productivity. Our data strongly implies that the planktonic foraminiferal record across the K/T boundary transition can be explained by earth derived environmental changes and that if an extraterrestrial bolide impact occurred, its effect on marine plankton was not of the catastrophic nature that is commonly assumed. A bolide impact, however, may have hastened the demise of the Cretaceous fauna already on the decline.

Conclusions

Planktonic foraminiferal extinctions at Agost and Caravaca occurred over an extended time period with some species disappearing well below the K/T boundary, a major group (39%-45% of the species but less than 15% of the individuals in the population) disappeared at or near the boundary, and the remaining species (except *G. cretacea*) disappeared near the P0/ P1a boundary and in Biozone P1a. Species extinctions are selective, eliminating geographically restricted large, complex and highly ornamented forms first and favoring survival of geographically widespread simple, small morphologies. This pattern of species extinctions and survival has also been observed at El Kef and Brazos River.

Stable isotope ranking of species reveals that all deep and intermediate dwelling species (large complex) declined in abundance during the latest Cretaceous and went extinct at the K/T boundary; only surface dwellers survived. We interprete this long-term abundance decline as a result of the late Cretaceous sea level regression that reached a maximum prior to the K/T boundary. The species extinctions at the K/T boundary and thereafter we attribute to the major reduction in surface productivity and breakdown in watermass stratification that was associated with the rapid sea level transgression. However, a bolide impact may have hastened the demise of the Cretaceous planktonic foraminifera.

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Appendix-taxonomic notes

Early Paleocene planktonic foraminiferal systematics is currently under revision. As a result genera designations are in a state of flux reflecting the current state of uncertainty. In this paper we have generally followed the latest published revisions, but are aware that further major revisions are necessary as phylogenies of Danian species are better understood. We discuss here preliminary observations on some genera that are important to this study.

Eoglobigerina Morozova 1959 emended Blow 1979

Morozova (1959) originally defined the genus *Eoglobigerina* based on smooth or microcellular wall structure. In this report we follow Blow's (1979) emended definition which emphasizes the importance of an intraumbilical aperture in addition to a wall texture with pore-pits and inter-pore ridges (cancellate wall). Recently, Berggren re-examined the holotype *E. eobulloides* and in apparent agreement with Blow (1979) observed that the "wall surface appears to be finely perforate with pseudoreticulate surface caused by depression of pores below the surface of the test wall" (W.A. Berggren, written commun. 1989).

Based on this emended description we tentatively place the following three species, which are currently in the genus *Globigerina*, in the genus *Eoglobigerina*: *E. edita* Subbotina 1953 sensu Blow 1979, *E. fringa* Subbotina 1950 sensu Stainforth et al. 1975, *E. trivialis* Subbotina, 1953.

Globanomalina Haque, 1956 emended Banner, 1989

We agree with Banner's (1989) emended description for this genus which includes a trochospiral test, apertural position interiomarginal, umbilical-extraumbilical with a porticus-like lip, a microperforate wall structure without spines and a non-carinate periphery. We tentatively place the globorotalid species *G. planocompressa* Shustkaya 1965 and *G. pentagona* Morozova 1961 in this genus.

Globastica Blow, 1979

The phylogenies of *Globigerina fodina* and *Globocon*usa conusa Khalilov 1956 sensu Keller 1988 are not well understood. We tentatively place these two species in the genus *Globastica* because of their finely perforate wall structure which suggests that they are primitive ancestors of *Globastica*.

Subbotina Brotzen and Pozaryska 1961, emended Blow 1979

Subbotina is characterized by a reticulate wall texture (spinose) and an intra-umbilical or umbilical-extraumbilical aperture with a porticus.

S. minutula Luterbacher and Premoli Silva 1964 sensu Krasheninnikov and Hoskins 1973 is a problematic species. Blow (1979) considered it an immature regressive form referable to Rugoglobigerina. Smit (1982) described a G. minutula with a very thin wall and smooth surface, umbilical aperture and three chambers in the last whorl (=Globastica conusa and G. fodina of this report). Luterbacher and Premoli Silva, however, considered G. minutula the precursor of S. triloculinoides (spinose with reticulate wall). These widely different taxonomic concepts are due to the poor original illustrations and the subsequent loss of this taxon, G. minutula should perhaps be considered, a nomen dubium non conservandum. In this paper we follow Luterbacher and Premoli Silva (1964), Krasheninnikov and Hoskins (1973) and retained this taxon for the first representatives of Subbotina and precursor of S. triloculinoides. We consider E. appressa of Blow a junior synonym of S. minutula S. pseudobulloides Plummer 1926 and S. varianta Subbotina 1953 sensu Blow 1979 are also retained in this genus.

Parvularugoglobigerina Hofker 1978 emended Brinkhuis and Zachariasse 1988

Hofker (1978) defined Parvularugoglobigerina as thin walled with small pustules, often in rows; he considered this genus "the atavistic end of the Hedbergella-Rugoglobigerina lineage" and designated P. eugubina as type species. However, the concept of this species is not firmly established in the literature largely because the original illustrations are very poor, the holotype is recrystallized and poorly preserved and the aperture is obscured. Luterbacher and Premoli Silva (1964) noted the aperture in umbilical position and a somewhat rugose test. Blow (1979) and Hofker (1978) therefore concluded generic affinities to the Cretaceous genus Hedbergella or Rugoglobigerina. Premoli Silva and Bolli (1973) and Boersma (1977) figured specimens of the G. eugubina group with a reticulate (? spinose) wall. Stainforth et al. (1975) described G. eugubina as possessing a smooth surface and a low arched umbilical to umbilical-extraumbilical aperture. But Premoli Silva (1977) noted that the aperture ranges from a comma-shaped arch to a lower arch. Smit (1982) included a smooth walled form with elongate aperture (=P. longia pertura) in G. eugubina. It is obvious from these variable descriptions that the concept of P. eugubina as currently used includes several distinct morphotypes which obscures the stratigraphic and phylogenetic utility of this group. We therefore propose to separate and retain both species, P. eugubina and P. longiapertura.

P. longiapertura

This morphotype is distinguished by its smooth wall, and narrow elongate aperture which is variable in its shape and height and generally positioned extraumbilical or umbilical-extraumbilical. In the lower part of the range chambers are generally more compressed (7-8 chambers) than in the upper part of the range. Because of the distinctive form and short range of this species we have designated it the nominate taxon for the P1a Biozone replacing *P. eugubina*, (*P. eugubina* sensu Stain?orth et al. 1975, Fig. 47, Nr. 2,3,5). This morphotype is restricted to the holotype of *P. eugubina* which has a low-arched aperture in umbilical to umbilical-extraumbilical position, rounded globular chambers without lateral compression and microperforate wall. In the Spanish sections *P. eugubina* appears shortly after the first appearance of *P. longiapertura*.

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