An independent test of planktic foraminiferal turnover across the Cretaceous/Paleogene (K/P) boundary at El Kef, Tunisia: Catastrophic mass extinction and possible survivorship

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ABSTRACT: Planktic foraminiferal biostratigraphy and assemblage turnover across the Cretaceous/Paleogene (K/P) boundary at El Kef revealed the largest and most abrupt extinction event in the history of planktic foraminifera. Cretaceous assemblages were very abundant and diverse and included 67 stable identified species within the terminal Maastrichtian. The mass extinction was characterized by the disappearance of 6 (8.9%) species in the last 12 meters of the upper Maastrichtian and the extinction of 46 (68.7%) species at the K/P boundary as well as 15 (22.4%) possible survivors ranging into the lowermost Danian. The range of planktic foraminifera only based on six samples (equivalent to the previous El Kef blind sample test) showed an even more catastrophic extinction pattern, with only 1 species disappearing before the K/P boundary.

The K/P debate is the result of several problems which include the "Signor-Lipps" effect, the possibility of reworking and the existence of hiatuses. However, irrespective of the different interpretations we conclude that there were no significant extinction nor quantitative changes before the K/P boundary and that most Cretaceous species suddenly became extinct at the K/P boundary. The El Kef section is one of the most continuous marine K/P boundary sections known and hiatuses have not been identified. Furthermore, possible Cretaceous survivors had a smaller size and lower absolute abundance in the lower Danian than in the upper Maastrichtian and the planktic foraminiferal evolutionary radiation began above the K/P boundary and not below. The same results have been found in other subtropical-temperate sections and may be sufficient proof for the existence of a catastrophic mass extinction at the K/P boundary. The planktic foraminiferal K/P extinction pattern is also very compatible with the catastrophic effects caused by the impact of a large extraterrestrial asteroid.

INTRODUCTION

The model of planktic foraminifera extinction at the Cretaceous/Paleogene (K/P) boundary is currently a controversial paleontological problem since it raises doubts about the greater part of micropaleontological methodology (Glen 1994). Initially many paleontologists assumed that almost all Cretaceous planktic foraminifera went extinct at the K/P boundary (Smit 1982, 1990) and this view is quite compatible with the asteroid impact hypothesis (Alvarez et al. 1980; Smit and Hertogen 1980). Most data supporting this conclusion come from the Gubbio section in northern Italy which is very condensed (Luterbacher and Premoli Silva 1964; Premoli Silva 1977; Alvarez et al. 1980; Arenillas 1998). However, several studies in more continuous and expanded sections have found contradictory evidence. Surviving cosmopolitan Cretaceous species were first noted by Maurrasse et al. (1979), Maurrasse (1980) and Keller (1988, 1989a,b) and have been more fully documented in several sections worldwide (Canudo et al. 1991; Keller et al. 1993; MacLeod and Keller 1994). Nonetheless, there is still no doubt that planktic foraminifera suffered the major extinction at the K/P boundary (Luterbacher and Premoli Silva 1964; Smit 1982, 1990; Molina 1994, 1995; Molina et al. 1996, 1998).

Part of the controversy stems from studies performed independently by Smit (1982, 1990) and Keller (1988, 1989a), who, although they analyzed the same sections (El Kef, Agost, Caravaca), proposed two different extinction models. Smit concludes that nearly all Cretaceous species suddenly became extinct at the K/P boundary, with the exception of *Guembelitria cretacea* and probably two to three other species. On the contrary, Keller concludes that species extinctions were gradual and selective, with approximately 25-50% of the species going extinct before the K/P boundary and 30-35% of the species surviving into the Paleocene. These findings have generated an intense debate between specialists who favor either a more sudden (Liu and Olsson 1992; Olsson and Liu 1993; Haslett 1994, D'Hondt et al. 1996; Molina et al. 1996, 1998; Apellaniz et al. 1997; Lamolda et al. 1997; Arenillas et al. 1998; Arz and Arenillas 1998; Kaiho and Lamolda 1999) or a more gradual mass extinction model (Keller 1989b; Canudo et al. 1991; Keller et al. 1995; MacLeod 1996; Keller 1996; Pardo et al. 1996; López-Oliva and Keller 1996; Abramovich et al. 1998). In essence, this problem has questioned the precision of planktic foraminiferal biostratigraphy and how it is applied to assess the magnitude and intensity of a biotic crisis.

To resolve the long-standing controversy between Keller and Smit, four "blind" specialists (Canudo 1997; Master 1997; Olsson 1997; and Orue-etxebarria 1997). examined unlabeled samples of the El Kef section; three from below the K/P boundary and three from above (Smit et al. 1997). The results were presented at the Snowbird III Conference and published in Ma-
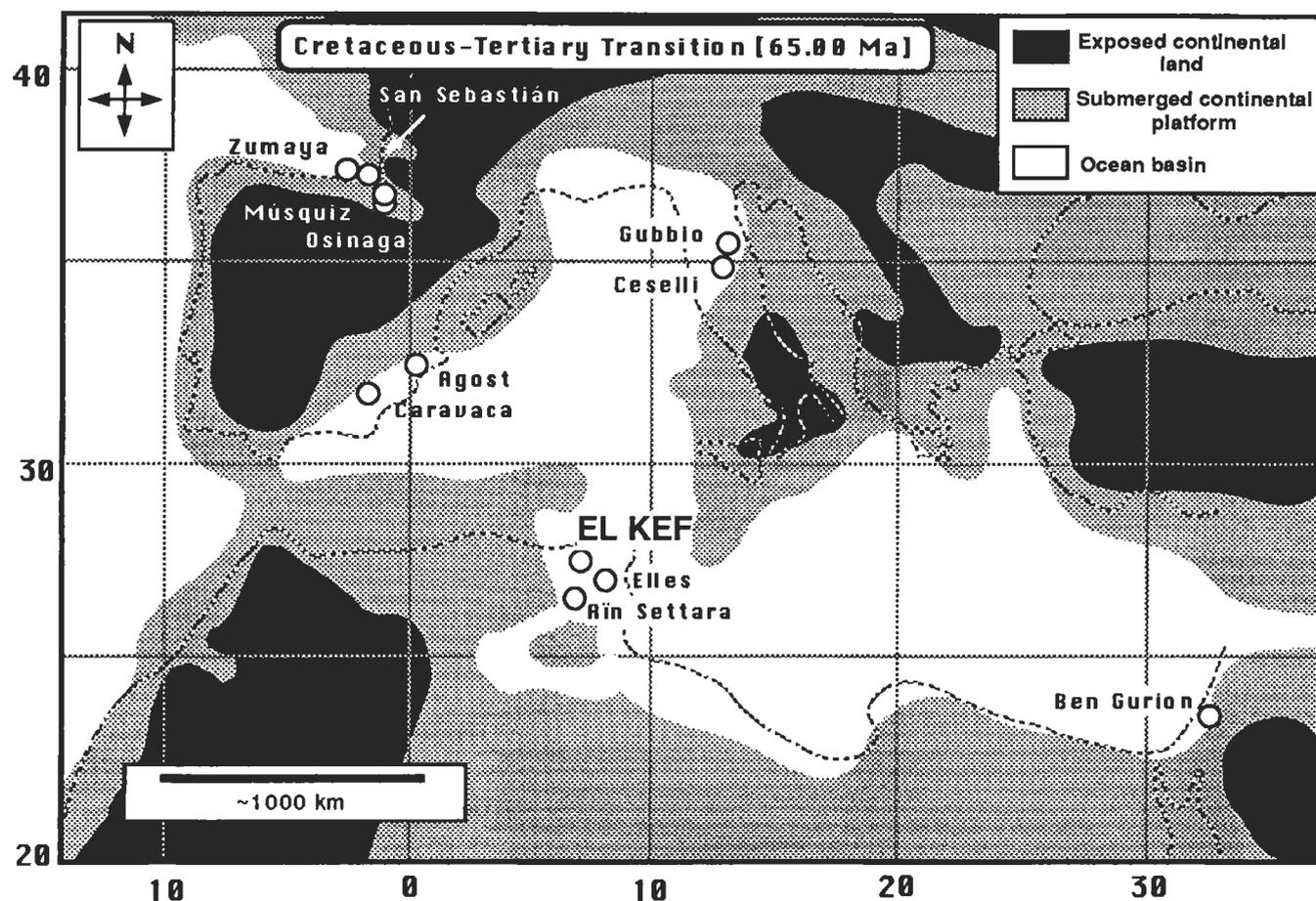
TEXT-FIGURE 1
Paleolatitudinal and paleogeographic location of the main sections studied (modified from Denham and Scotese 1987).

rine Micropaleontology (Lipps 1997; Ginsburg 1997a). Both Smit (1994) and Keller et al. (1995) claimed that the outcome supported their views (also see Smit and Nederbragt 1997; Keller 1997). Thus, the controversy continues.

What is the reason for these contradictory findings? It is probably the result of several extensively documented variables that affect data interpretation which include the "Signor-Lipps" effect, taxonomic assignments, the possibility of reworking and the existence of hiatuses (Signor and Lipps 1982; Keller et al. 1993; Molina 1994, 1995; MacLeod 1994; Glen 1994; Huber 1996; Smit and Nederbragt 1997; Keller 1997; Lipps 1997). These problems are used to justify one or another interpretation depending on the theory of preference (Pardo et al. 1997; Arz et al. 1998; Arz and Arenillas 1998). This state of affairs has lead to tautological explanations which should obviously be avoided (Arenillas et al. 1998).

In the search for a consensus, we examined the planktic foraminiferal biostratigraphy and assemblages turnover at the El Kef section. This section is one of the most complete K/P boundary sections known and our interpretations were easily comparable with previous studies (Molina et al. 1996, 1998; Arenillas et al. 1998; Arz and Arenillas 1998; Arz et al. 1999; Dupuis et al. in press). We also provide additional data to elucidate the extinction model, analyze the previous El Kef blind test and suggest an independent interpretation.

LOCATION, MATERIALS AND METHODS

The El Kef section is located about 5km southwest of the town of El Kef in northwestern Tunisia and was officially designated the K/P boundary global stratotype section and point (GSSP) in 1989 at the 28th International Geological Congress in Washington. The El Kef section was first studied by Salaj (1974) and was found to have good continuity and exposure. It was later analyzed by numerous specialists in micropaleontology and geochemistry, including planktic foraminifera, nannoplankton, benthic foraminifera, dinoflagellates, ostracods and palynoflora (Brinkhuis and Zachariasse 1988; Keller 1988, 1989a,b, 1993; Keller et al. 1995) and isotope geochemistry (Smit and Ten Kate 1982; Keller and Lidinger 1989; Robin et al. 1991).

The K/P boundary section is contained within the El Haria formation, which consists of hemipelagic brown-gray marls with sporadic limestone intercalations. The Maastrichtian sediments consist of relatively carbonate rich gray marl with about 40% $CaCO_3$. The K/P boundary is marked by a 50cm black clay layer with about 3-4% $CaCO_3$ and an overlying 50-60cm marly clay layer with about 10% $CaCO_3$. A 2-3mm thin rust-red layer at the base of this clay unit marks the boundary event. The Paleocene

EPOCHS	AGES	Datums events in the section studied	BIOZONATIONS						
			This paper	Keller 1989a, 1993 Pardo *et al.* 1996	Berggren *et al.* 1995	Canudo *et al.* 1991	Smit 1982	Blow, 1979	Bolli, 1966
PALEOGENE (DANIAN)		S. triloculinoides — Pr. inconstans — Pv. eugubina — Pb. pseudobulloides — Pv. longiapertura — Pr. taurica — Pv. eugubina — Pv. longiapertura / Gb. alticonusa —	Parasubbotina pseudobulloides	P1b	P1b S.triloculinoides G. compressa / P1a Pv. eugubina- Subbotina triloculinoides	Parasubbotina pseudobulloi- des	Globigerina pseudobulloides / Eoglobigerina taurica	P1a Globorotalia (Turborotalia) pseudobulloides Globorotalia (Turborotalia) archeocompressa	Globigerina pseudobulloi- des
			Parvularugoglob. eugubina	P1a / P1a(2) / P1a(1)	Pα Parvularugog. eugubina	Parvularugog. longiapertura	P1a G. eugubina	Pα Globorotalia (Turborotalia) longiapertura	Globigerina eugubina
			Guembelitria cretacea	P0	P0 G. cretacea	G. cretacea	P0 G. cretacea	M18 Rugoglob. hexacamerata	Unzoned
CRETACEOUS (MAASTRICHTIAN)		P. hantkeninoides ⌐ A. mayaroensis — P. hantkeninoides ⌐	Plummerita hantkeninoides	Plummerita hantkeninoides	Abathomphalus mayaroensis	Abathomphalus mayaroensis	Abathomphalus mayaroensis	M17 Abathomphalus mayaroensis	Abathomphalus mayaroensis
		A. mayaroensis ⌐	Abathomphalus mayaroensis	Abathomphalus mayaroensis					

TEXT-FIGURE 2

Comparison of uppermost Maastrichtian and lowermost Danian planktic foraminiferal biozonations with the biozonations used in this paper.

sediments consist of relatively carbonate rich (40%) gray marls with sporadic clayey marl intercalation with about 20-30% CaCO3. The thin rust-red layer shows a drop in CaCO3, a maximum of organic carbon and a negative excursion in $\delta^{13}C$ (Keller and Lidinger 1989). This red layer contains the Ir anomaly and other impact evidence such as the Ni-rich spinels, Os anomaly and spherules of sanidine and hematite (Smit 1982; Robin et al. 1991). These spherules are described by Smit (1982) as altered microtektites, although other authors suggest an authigenic origin (Keller and Lidinger 1989).

We took 38 samples for planktic foraminiferal biostratigraphic and quantitative analyses at decimeter intervals, with closer sampling across the K/P boundary interval. Samples were disagregated in tap water with diluted H2O2, washed through a 63μm sieve and dried at 50°C. The quantitative planktic foraminiferal analysis was based on representative splits (using a modified Otto microsplitter) of approximately 300 specimens larger than 63μm. In order to find rare species and minimize the Signor and Lipps (1982) effect, we intensively scanned the residue in size fractions larger than 100, 150 and 250μm (mainly from the uppermost Maastrichtian samples). All the representative specimens were picked and mounted on microslides for a permanent record and identification. Preservation of the planktic foraminifera is generally good. Faunal counts for >63μm size fraction are listed in Tables 1 and 2.

BIOSTRATIGRAPHY AND QUANTITATIVE ANALYSIS

We used the lower latitude biozonation suggested by Molina et al. (1996), a slight modification of previous biozonations (Bolli 1966; Pardo et al. 1996), and identified the *Plummerita hantkeninoides, Guembelitria cretacea, Parvularugoglobigerina eugubina* and *Parasubbotina pseudobulloides* Biozones (text-fig. 2). The *G. cretacea* Biozone spans the interval from the last appearance datum of Plummerita hantkeninoides at the K/P boundary and the first appearance datum of *G. eugubina*. The bases of the *P. hantkeninoides, Pv. eugubina* and *P. pseudobulloides* Biozones are placed at the first appearance of the eponymous species. Text-figure 2 shows the datum events and biozonations and a comparison with other studies (Bolli 1966; Blow 1979; Smit 1982; Keller 1988a, 1993; Canudo et al. 1991; Berggren et al. 1995; Pardo et al. 1996). The ranges of planktic foraminifera are shown in text-figures 3 and 4 and relative abundance in the size fraction >63μm is shown in text-figure 5.

We identified 67 Cretaceous species typical of low latitude assemblages. In the size fraction >63μm, these assemblages were largely dominated by biserial species (*Heterohelix, Pseudotextularia, Pseudoguembelina*), mainly *Heterohelix* with an abundance of 65-75%. *Globigerinelloides, Hedbergella, Rugoglobigerina* and *Guembelitria* were frequent, *Globotruncana* and *Globotruncanita* were common and *Abathomphalus, Contusotruncana, Schackoina, Planoglobulina* and *Racemi-*

SPECIES RANGES OF PLANKTIC FORAMINIFERA > 63 µm
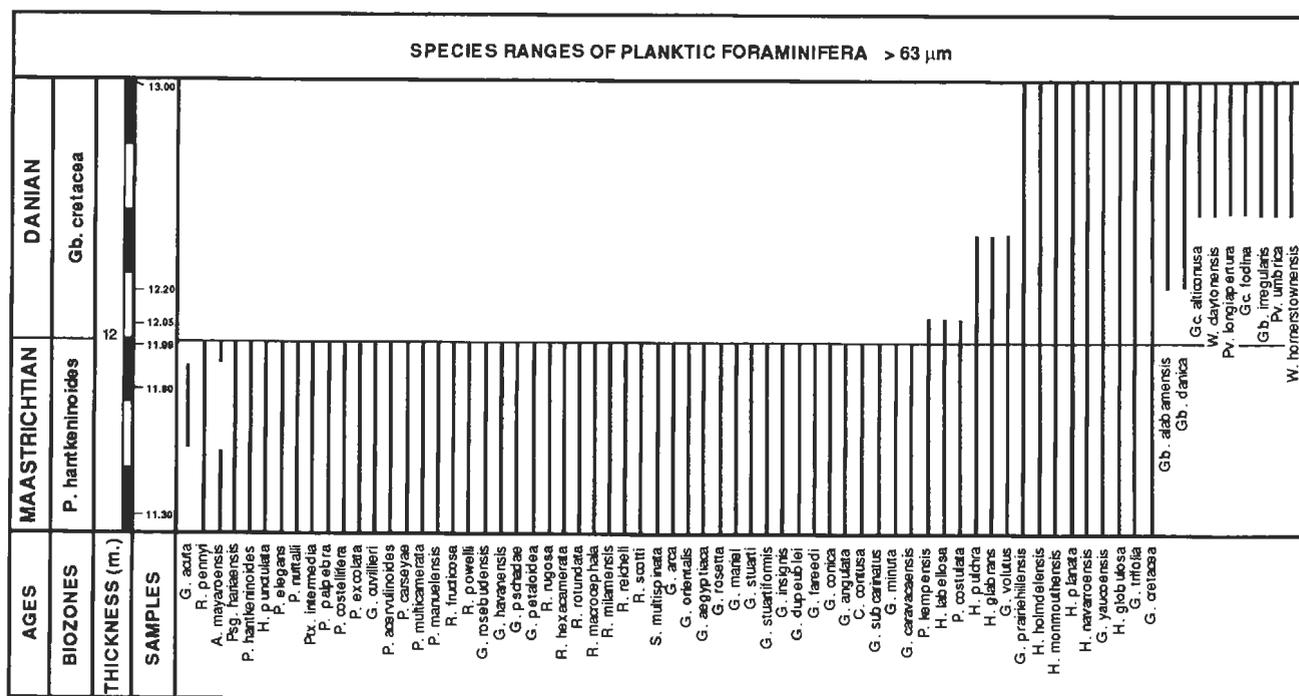
TEXT-FIGURE 3
Species extinction pattern at El Kef based on six samples intervals that are equivalent to the El Kef blind sample test.

guembelina were rare. Most of the species were present during the whole late Maastrichtian, although some taxa disappeared below the K/P boundary and could indicate very slight changes in the faunal assemblages in the uppermost part of the *P. hantkeninoides* Biozone.

The species that disappeared below the K/P boundary in the uppermost 12 meters of the Maastrichtian were *Archaeoglobigerina cretacea* (d'Orbigny 1840), *A. blowi* Pessagno (1967), *Contusotruncana patelliformis* (Gandolfi 1955), *C. plicata* (White 1928), *Abathomphalus intermedius* (Bolli 1951) and *Gublerina acuta* de Klasz (1953). These 6 species represent only about 8.9% of identified Cretaceous species. This percentage may be even less if we take into account the "Signor-Lipps" effect. At least *C. patelliformis* and *A. intermedius* disappeared at the K/P boundary in Agost, Caravaca, Aïn Settara, Zumaya and San Sebastián (Molina et al. 1996, 1998; Arenillas et al. 1998; Arz and Arenillas 1998; Arz et al. 1999; Dupuis et al. in press) and, therefore, these species could be excluded. Furthermore, the planktic foraminiferal assemblages are highly stable throughout the Upper Maastrichtian at all population rates (text-figs. 5, 6 and 7).

A total of 46 species (68.6% of all species) disappeared at the El Kef K/P boundary, which represent about 70% of the specimens in the population larger than 150µm (text-fig. 6), though only about 10% in the population larger than 63mm (text-figs. 5 and 6). This simultaneous disappearance constitutes the greatest and most sudden extinction event in the history of planktic foraminifera. Most of these species were large, complex, tropical-subtropical and deep-intermediate dwelling forms (Keller 1993, 1996). In order to minimize the "Signor-Lipps" effect, we double-checked this coincidence by scanning the residue of the uppermost Cretaceous and lowermost Tertiary samples in the

size fraction larger than 63, 100, 150 and 250µm (mainly the uppermost samples of the Maastrichtian). Certain rare species could appear to become extinct before their true extinction as may have occurred with *C. patelliformis* and *A. intermedius*.

A total of 15 Cretaceous species (22.4% in population) were present in the lowermost Danian (*G. cretacea*, *Pv. eugubina* and *P. pseudobulloides* Biozones) and could be considered Cretaceous survivors: *Heterohelix glabrans* (Cushman 1938), *H. planata* (Cushman 1938), *H. navarroensis* Loeblich (1951), *H. globulosa* (Ehrenberg 1840), *H. pulchra* (Brotzen 1936), *H. labellosa* Nederbragt (1991), *Pseudoguembelina kempensis* (Esker 1968), *P. costulata* (Cushman 1938), *Hedbergella holmdelensis* Olsson (1964), *H. monmouthensis* (Olsson 1960), *Globigerinelloides yaucoensis* (Pessagno 1960), *G. volutus* (White 1928), *G. prairiehillensis* Pessagno (1967), *Guembelitria cretacea* Cushman (1933) and *G. trifolia* (Morozova 1961, sensu Blow 1979). They were cosmopolitan, small, simple surface dwellers and gradually disappeared during the early Danian. All were frequent or common in the late Maastrichtian and exhibited a great continuity in occurrence into the early Danian.

After a comparative study of other subtropical and temperate latitude continuous sections we established five quantitative stages in the population larger than 63µm across the K/P boundary:

Stage 0 - Typical faunal association of the uppermost Maastrichtian, dominated by biserial species (*Heterohelix*). The tropical-subtropical species represent only about 10% of the specimens larger than 63µm but 70% of the specimens larger than 150µm
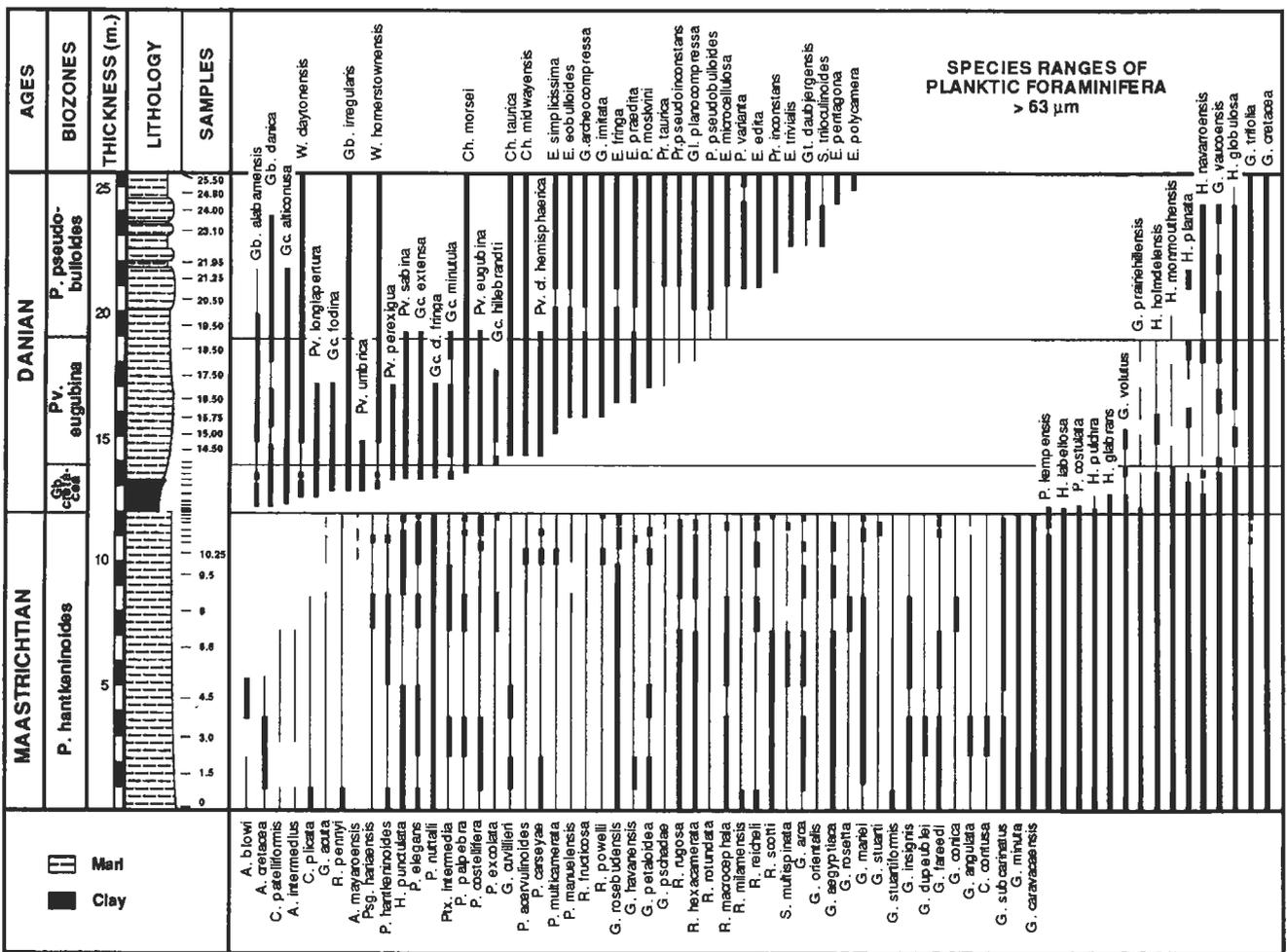
TEXT-FIGURE 4
Species ranges of planktic foraminifera in the El Kef section. Thick line means present in the quantitative split and thin line found in the residue.

Stage 1 - Predominance of *Guembelitria* and other probable Cretaceous survivors (*Hedbergella* and *Heterohelix*) of the K/P boundary event. All planktic foraminifera are smaller than 150μm, except some probably reworked Cretaceous specimens. This stage spans the lower part of the *G. cretacea* Biozone.

Stage 2 - Predominance of *Parvularugoglobigerina* and *Globoconusa*. All planktic foraminifera are smaller than 150μm, except in the uppermost part. This stage spans the upper part of the *G. cretacea* Biozone and the lower part of the *Pv. eugubina* Biozone.

Stage 3 - Predominance of *Chiloguembelina* and *Woodringina*. This stage spans the upper part of the *Pv. eugubina* Biozone and the lower part of the *P. pseudobulloides* Biozone.

Stage 4 - Predominance of *Eoglobigerina, Parasubbotina, Subbotina, Praemurica* and *Globanomalina*. We did not study this stage at El Kef, but it is dominant in most of the lower Danian in other sections.

These quantitative stages were initially observed and proposed in several Spanish sections (Zumaya, San Sebastián, Osinaga and Músquiz) by Arenillas et al. (1998), Arz and Arenillas

(1998) and Arz et al. (1999). Having the partial or total identification of these stages one can recognize and quantify hiatuses across the K/P boundary since these stages do not involve problematic taxonomic assignments. They can also be recognized at other sections in the Tethys region (Agost, Caravaca, Ain Settara, Elles). Text-figure 6 shows the stratigraphical position of these quantitative stages at the El Kef section.

At El Kef, stage 1 was characterized by a major increase of *Guembelitria* with a maximum peak in abundance of 89% (Table 2, text-fig. 6). This stage spanned 1.5m in the lower part of *G. cretacea* Biozone and coincided with the dark clay layer, with a sudden decrease of %CaCO$_3$ and P/B ratio (text-fig. 7) and with the negative δ^{13}C (Keller and Lidinger 1989). The P/B ratio is about 95-99% in the upper Maastrichtian at Aïn Settara, but decreases to around 65% just above the K/P boundary and only 1-5% in the middle part of the *G. cretacea* Biozone. The P/B ratio is expressed as the percentage relationship between the number of the planktic foraminiferal specimens and the number of the total foraminiferal specimens. Considering the total amount of planktic and benthic foraminifera, the abundance of *Guembelitria* and other "survivor" Cretaceous species seems to be much less in stage 1 (text-fig. 6).
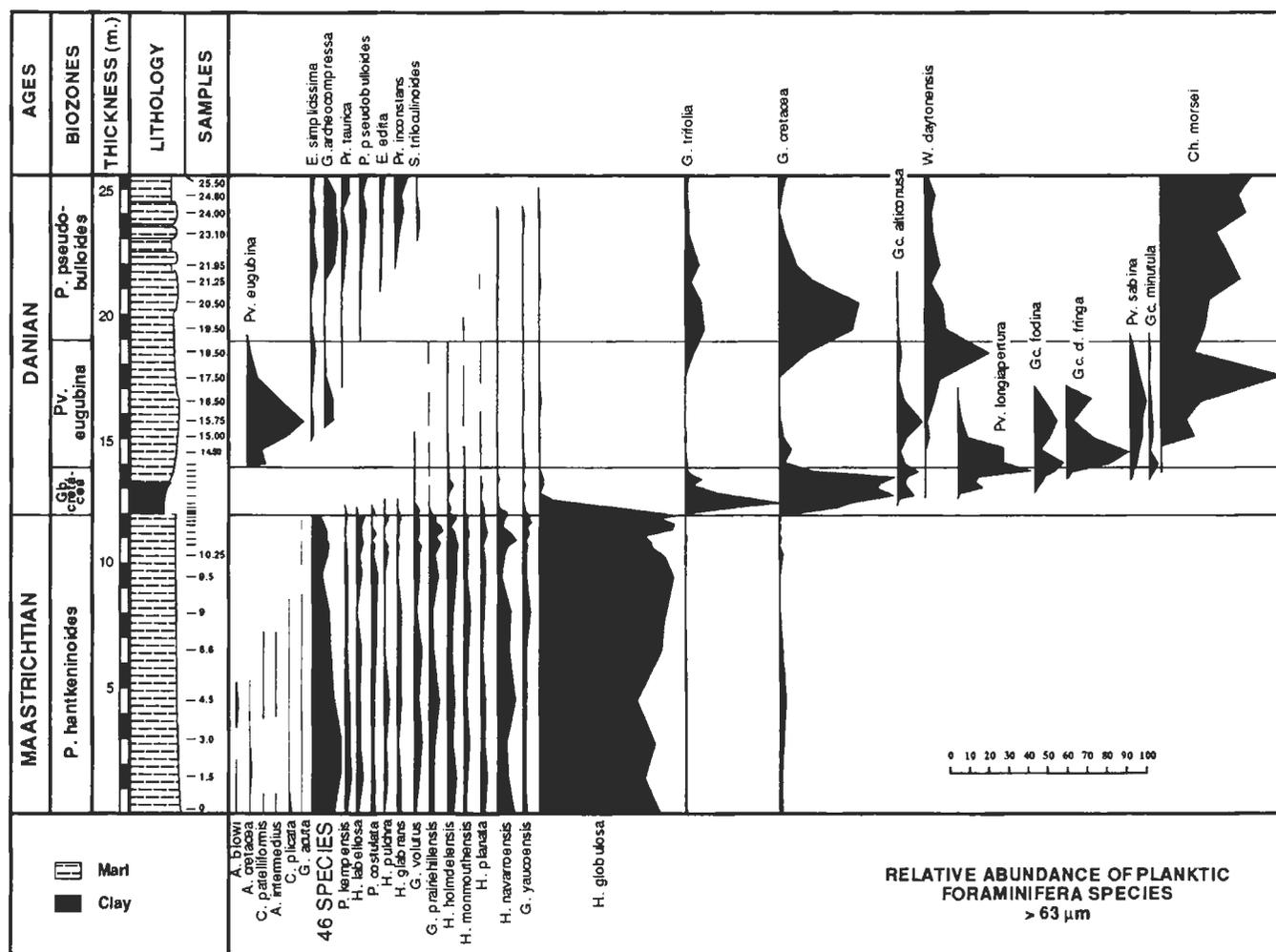
TEXT-FIGURE 5
Relative abundance of planktic foraminifera species across the K/P boundary at the El Kef section in the size fraction bigger than 106µm.

The P/B ratio and % CaCO$_3$ increased in stage 2 and coincided with the proliferation of *Parvularugoglobigerina* and *Globoconusa* (text-fig. 7). The first radiation of new opportunist species begins here (Molina et al. 1996, 1998; Arenillas et al. 1998; Arz and Arenillas 1998) along with the first appearance of new species of guembelitriids, woodringinids and chiloguembelinids (D´Hondt 1991; MacLeod 1993) and globoconusids and parvularugoglobigerinids (Luterbacher and Premoli Silva 1964; Olsson and Liu 1993; Arenillas and Arz 1996; Arenillas et al. 1998). Paleocene species replaced the Cretaceous species that could not successfully adapt to the new environmental conditions (MacLeod 1993; Molina et al. 1996, 1998). A second radiation of new tertiary species is initiated in the stage 3 (Liu and Olsson 1992; Olsson et al. 1992; Arenillas and Arz 1996; Arenillas et al. 1998), with the appearance of species with perforate cancellate and spinose wall texture (*Eoglobigerina*, *Parasubbotina* and *Subbotina*), perforate cancellate and non-spinose wall texture (*Praemurica*), perforate smooth wall texture (*Globanomalina*) and pustulose wall texture (*Globastica*).

EXTINCTION IN THE TERMINAL CRETACEOUS

The El Kef blind test is an admirable attempt to resolve the controversy concerning the extinction of planktic foraminifera at the K/P boundary (Lipps 1997; Ginsburg 1997a,b). In many ways, however, it simply managed to underline the central problems in the debate between Smit and Keller. A similar controversy has occurred at Agost and Caravaca (Spain), with each side supporting a more catastrophic (Smit 1982, 1990; Molina et al. 1996, 1998; Kaiho and Lamolda 1999) or a more gradual mass extinction model (Canudo et al. 1991; Pardo et al. 1996). At these sections, Smit (1982, 1990) suggested a catastrophic mass extinction of nearly all Cretaceous taxa at the K/P boundary. The presence of many Cretaceous species in lowermost Danian sediments was ignored based on the assumption that all these specimens were reworked. On the contrary, at the same El Kef section, Keller (1988) concluded that the K/P boundary extinctions did not appear to have occurred instantaneously and species extinctions were gradual and selective. In this case, Keller assumed that a great part of the Cretaceous specimens found in the lowermost Danian were Cretaceous survivors and
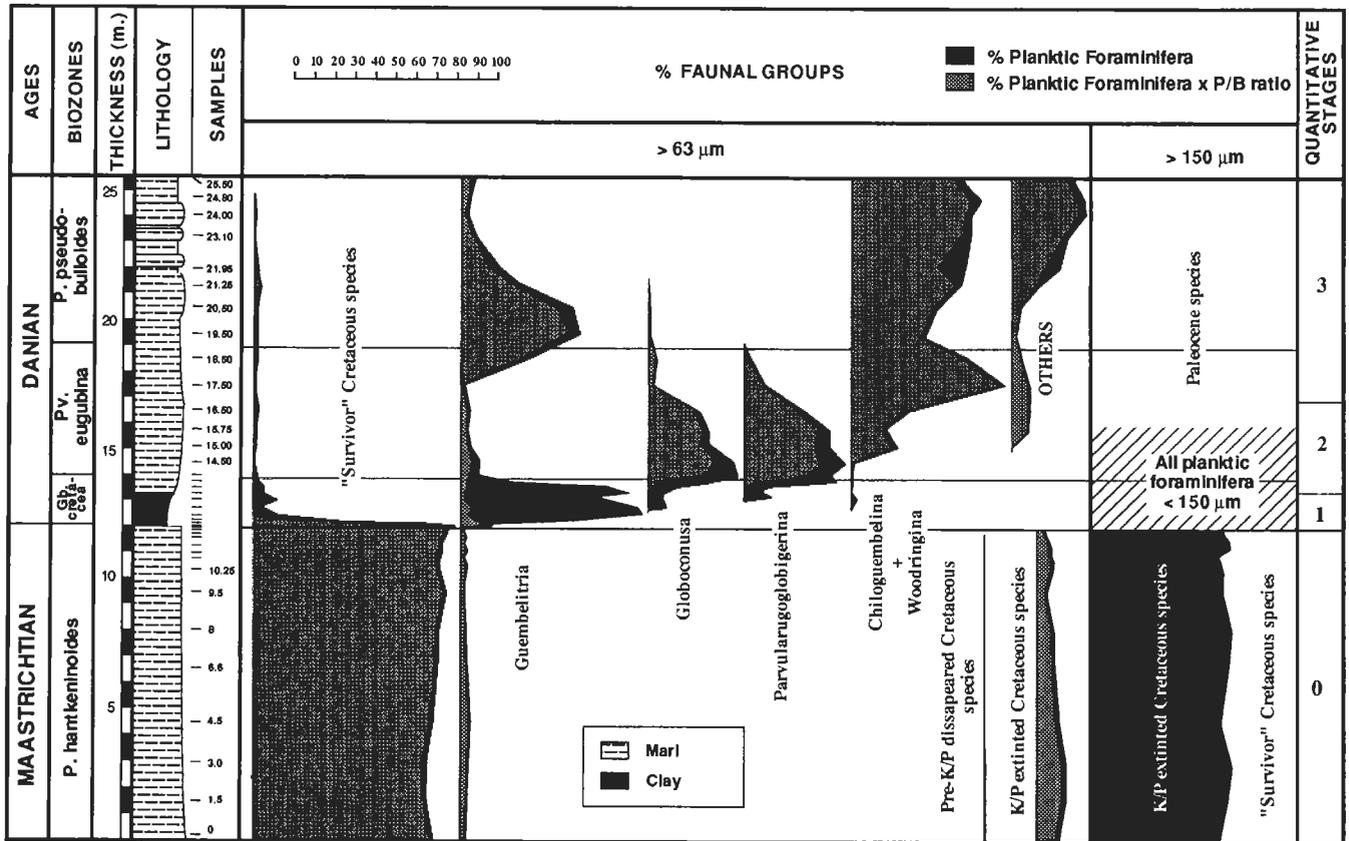
TEXT-FIGURE 6
Relative abundance of planktic foraminifera faunal groups in the size fractions bigger than 63μm and 150μm.

identified several species that went extinct below the K/P boundary. A literal reading of her results suggests that few species went extinct at the K/P boundary.

Although the last appearance of a species is not necessarily its true extinction, a local disappearance could be the result of pre-boundary environmental changes. Therefore, the possible local disappearance of some species in the uppermost Maastrichtian at El Kef could have been the result of environmental restrictions from global eustatic changes or an increase in worldwide volcanic intensity (Keller 1988, 1989a,b). Keller et al. (1995) suggest a sea-level regression and subsequent rise combined with a shallowing of the local minimum oxygen zone. However, could these apparent pre-K/P disappearances be the product of pre-boundary environmental changes or, on the contrary, are they a clear example of Signor-Lipps effect?

In 1988 Keller reported that 12 Cretaceous species (22%) became extinct before the K/P boundary, 31 species (58%) disappeared near the K/P boundary and at least 10 species (19%) survived into the early Paleocene. However, again at El Kef (El Kef 1 - stratotype and El Kef 2), Keller et al. (1995) proposed a more gradual extinction pattern with 24 species (43%) disappearing below the K/P boundary, 7 species (12%) at the K/P boundary and 24 species (45%) above. The Cretaceous species in the uppermost sample of the Maastrichtian decreased from 77% in Keller (1988) to only 58% in Keller et al. (1995). Simi-

larly, 19% disappeared after the K/P boundary in Keller (1988) and 31% in Keller et al. (1995). These data are contradictory and we feel that this variation is not viable (as proposed by Keller et al. 1995) since a Lazarus effect may be rejected in two sections as close to one another as are El Kef 1 and 2. The only possible explanation of this biostratigraphic incongruity is the Signor-Lipps effect.

If we compare Keller's studies and combine the ranges of all the Cretaceous species identified, it appears that she finds most of the Cretaceous species in the uppermost samples of the Maastrichtian. Nevertheless, it is very difficult to compare the biostratigraphic differences between Keller (1988) and Keller et al. (1995) because the taxonomic assignment was different. If we only compare the species with the same nomenclature, only *R. fructicosa* was not found by Keller in the uppermost sample of Maastrichtian. For example, "*G. volutus*" is considered a Cretaceous survivor taxa in 1988 and as a pre-K/P extinct taxa in 1995. The rest of the possible pre-K/P extinct species proposed by Keller et al. (1995) do not coincide in name with the species proposed by Keller (1988) and it is thereby impossible to make a rigorous comparison. However, we found all the Cretaceous species of the last Maastrichtian 60-70cm in the top-most Cretaceous sample (KF 12.00), except for *Gublerina acuta* (text-fig. 3). Some specimens found in this sample and considered by Keller et al. (1995) as pre-K/P disappeared species are shown on Plate 1: *Gublerina cuivillieri* de Kikoine

(1948), *Planoglobulina multicamerata* (de Klasz 1953), *Pseudotextularia intermedia* (de Klasz 1953), *Pseudotextularia elegans* (Rzehak 1891), *Globigerinelloides volutus* (White 1928), *Globotruncana aegyptiaca* Nakkady (1950), *Abathomphalus mayaroensis* (Bolli) and *Plummerita hantkeninoides* (Brönnimann).

Keller (1997) indicates that the evaluation and determination of reworking of rare species in the upper Maastrichtian is very difficult since great part of the last appearances are single specimens and may be reworked. This apparent difficulty could be used to justify the existence of pre-K/P disappearances. However, we found a great continuity in the occurrence of almost all the species across the upper Maastrichtian, which partially avoids the problem of potential reworking (text-fig. 4, Table 1).

Species continuity is not the only criterion used to evaluate indigenous or reworked specimens. If species abundance is stable it may be as indigenous as other more frequent species. We found a notable stability in the abundance of all species and faunal groups in terminal Maastrichtian (text-figs. 5, 6 and 7) and, for this reason, we suggest that most Cretaceous species became extinct at the K/P boundary. Moreover, if the apparent local disappearance of several species is the result of pre-K/P environmental and global paleoceanographic changes (Keller et al. 1995), the relative abundance of the different species and faunal groups would have been immediately affected. However, since this did not occur, the Signor-Lipps effect is very probably present in Keller's studies.

BLIND TEST

The El Kef blind test has received several criticisms due to its limitations and uncertainties (Masters 1997) and its initial weak test design (Kouwenhoven 1997). According to Masters (1997), the blind test results were doomed to failure because of the narrowness of the considered interval, the lack of taxonomic consistency among the four testers and the inability to discriminate between survivors and reworked specimens. In fact, the blind test clearly reveals taxonomic problems: Canudo (1997) identifies 47 species, Masters (1997) 54, Olsson (1997) 44 and Orue-etxebarria (1997) 61. There are 84 different Cretaceous species names (Smit and Nederbragt 1997) but nomenclatorial coincidence in only 14. Counting the species identified by Smit (1982, 1990), Keller (1988) and Keller et al. (1995) at the same El Kef section, there are almost 100 different names. The lack of unanimity in taxonomic assignments is also evident in Keller's studies; in the last 50-60cm of the upper Maastrichtian in the same section, Keller (1988) found 10 Cretaceous species not mentioned by Keller et al. (1995) whereas Keller et al. (1995) found 16 Cretaceous species not mentioned by Keller (1988).

The blind test also suffered from an absence of an initial agreement on standard taxonomy. Although taxonomic incoherence is an important problem (Huber et al. 1994 vs. Keller and MacLeod 1994), it is probably not the main hurdle. Synonymous and intraspecific variability may be difficult to establish, i.e. a micropaleontologist can be more or less defined as a splitter or lumper depending on the number of morphospecies identified. The authors of this paper, with 67 Cretaceous identified species, and Orue-etxebarria, with 61, may be considered as the most taxonomic "splitters". Olsson (44 species) and Canudo (47 species) are the most taxonomic "lumpers". Since a splitter taxonomist may be more rigorous in identifying rare forms than a lumper, it is important that most splitters concur in having

found all (or almost all) the Cretaceous morphospecies across the last meter of the Maastrichtian (text-fig. 3). However, the K/P controversy is not between splitter and lumper taxonomists. Irrespective of the number of species identified or the species names used, the controversy is due to some authors suggest a high number of forms disappeared below the K/P boundary. Moreover, these supposed pre-K/P disappearances generally affect rare forms. We consider that the only explanation for the apparent disappearance is the Signor-Lipps effect.

Each of the participants in the blind test showed a pattern more or less compatible with either Smit (1982) or Keller (1988). However, many of the morphospecies are quite rare and may not all be found without an exhaustive search (Orue-etxebarria 1997). For this reason, Smit and Nederbragt (1997) indicate that, when the results of all four testers are taken together, species recognized by two or more testers occur in all Cretaceous samples. Keller (1997) affirms that the low taxonomic agreement among the testers illustrates that taxic census data cannot be compared on a species by species basis. Although it does not seem too difficult to establish the synonyms between the species proposed by the different testers (Smit and Nederbragt 1997), it is true that there is no guarantee that all four testers applied the same species name to same morphotype (Keller 1997).

Keller (1997) proposed that the comparison of extinction patterns of all taxa is more instructive than comparing species extinctions using the same species names. However, the comparison of extinction patterns does not solve the problem, because the proposed pattern can depend on a previous interpretation or an unsatisfactory methodology. If we only consider comparing extinction patterns the results are contradictory, i.e., Olsson, Orue-etxebarria and Smit support a catastrophic mass extinction and Masters, Canudo and Keller support a gradual mass extinction. To solve the problem, we must compare the extinction of forms by forms, or of morphospecies by morphospecies but not by the patterns of extinction of each author. The final pattern of K/P extinction will be the result of the confirmation of the ranges of planktic foraminiferal morphospecies across the K/P boundary.

We also considered the species ranges of planktic foraminifera based on six samples equivalent to the El Kef blind sample test (see text-fig. 3). In this case, the species extinction pattern was the following: 1 (1.6%) species probably disappeared in the late Maastrichtian, 46 (74.1%) species extinct at the K/P boundary and 15 (24.2%) ranged into the earliest Danian. This pattern is very compatible with Smit (1982, 1990), Olsson (1997) and Orue-etxebarria (1997). We agree with Smit and Nederbragt (1997) that the blind test demonstrates the lack of noticeable step-wise extinction below the K/P boundary. The pre-K/P boundary extinctions are non-existent in the uppermost centimeters of the Maastrichtian at El Kef section, with the exception of *G. acuta* (text-fig. 7). At least in terms of this objective, our data indicate that the blind test helps to solve the controversy.

SURVIVORS IN THE BASAL TERTIARY

One of the main problems in the K/P debate is the possibility of reworked Cretaceous specimens in lowermost Danian strata. Depending on the taphonomic interpretation, these specimens can be considered reworked or indigenous-survivors. Historically, many micropaleontologists assumed that, except *Guembelitria cretacea*, all the Cretaceous specimens in the basal Paleocene are reworked and did not survive the K/P boundary extinction event (Smit 1982, 1990; Huber 1991). At
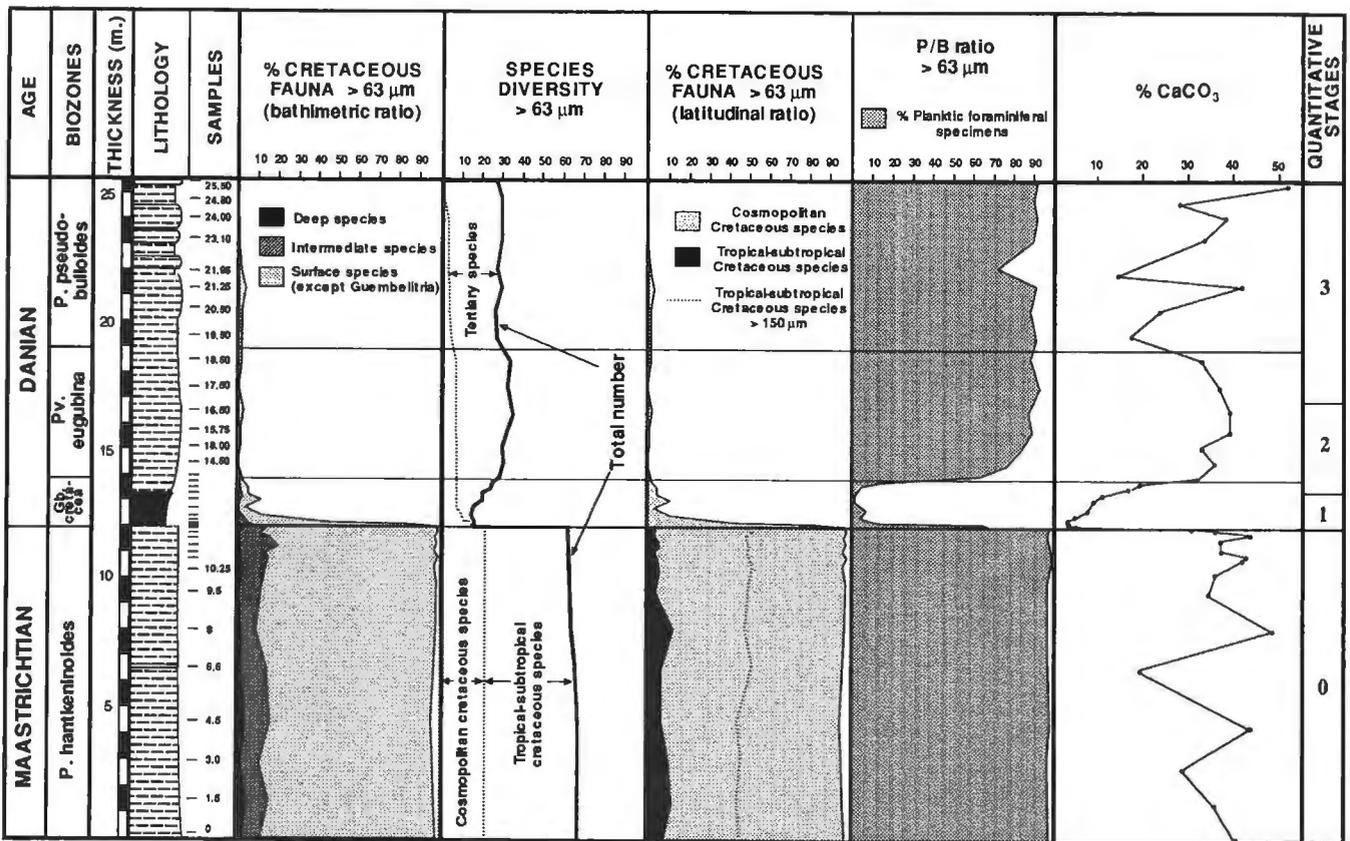
TEXT-FIGURE 7
Relative abundance of Cretaceous planktic foraminiferal fauna, species diversity, P/B ratio and %CaCO₃ changes across the K/P boundary at the El Kef section in the size fraction bigger than 63μm (and 150μm).

El Kef, there is almost no sign of reworking as evidenced by currents or turbiditic sediments. However, reworked Cretaceous specimens can be relatively frequent in the lowest samples of Danian in other sections (Huber 1991, 1996; Kaiho and Lamolda 1999). It is very difficult to determine which specimens are reworked at El Kef due to the lack of a simple visual criterion. To minimize the potential problem, we only ignored the presence of very isolated, broken and/or poorly preserved specimens, assuming that they were reworked and not listing them in tables or text-figures. We also ignored Cretaceous species not found in the lowermost Danian of nearby sections (Arz and Arenillas 1998; Arz et al. 1999).

Some large and complex Cretaceous species can be found in the first samples of the Danian at El Kef and other sections, including globotruncanids, globotruncanitids, rugoglobigerinids and planoglobulinids (Keller 1988, 1989a; Canudo et al. 1991; Keller et al. 1993, 1995; Molina et al. 1996, 1998; Apellaniz et al. 1997; Arz and Arenillas 1998; Arz et al. 1999). Most of these species are broken and/or poorly preserved specimens and are a lot less abundant than in the Maastrichtian. There are large and complex Cretaceous specimens in other Danian samples but these are isolated and usually preserved differently. In addition, these Cretaceous specimens are not present in any studied section in the lowermost Danian (Molina et al. 1998; Arz and Arenillas 1998; Arz et al. 1999) and we can assume that all of them are reworked.

Smaller cosmopolitan species, such as guembelitrids, hedbergellids, heterohelicids and globigerinellids species, are abundant in these lowest samples of the Danian (Maurrasse et al. 1979; Keller 1988) and could be Cretaceous survivors. According to Smit (1982), the only survivors were *Guembelitria cretacea* and probably *Hedbergella monmouthensis* and *Globigerinelloides messinae* (= *G. volutus*). However, it has been shown that species in Paleocene sediments initially considered reworked (Smit 1990) exhibit a Paleocene δ¹⁸O and δ¹³C isotopic signal (Barrera and Keller 1990, 1994; Keller et al. 1993; Keller 1993).

The Cretaceous species present in the earliest Danian with a Paleocene isotopic signal were most probably survivors. They include: *H. globulosa, H. navarroensis, G. cretacea, G. trifolia, H. holmdelensis* and *H. monmouthensis* (Barrera and Keller 1990, 1994; Keller et al. 1993; Keller 1993; Huber 1996; MacLeod and Huber 1996). Furthermore, Keller et al. (1995) included more species based on their constant presence in the lowermost Danian: *G. aspera* (=*G. prairiehillensis*), *G. yaucoensis, H. dentata* (=*H. planata*), *H. striata* (=*H. globulosa*), *P. costulata, H. complanata* (=*H. planata*), *G. subcarinatus, Ch. waiparaensis* (=*Heterohelix?*) and *G. danica.* Other survivor candidates include *H. pulchra, H. labellosa, P. kempensis* and *G. volutus* (Molina et al. 1996, 1998; Arenillas et al. 1998; Apellaniz et al. 1997; Arz and Arenillas 1998; Arz et al. 1999; Dupuis et al. in press). However, only *G. cretacea* and

TABLE 1
Relative abundance of uppermost Maastrichtian planktic foraminifera at El Kef in the size fraction bigger than 63μm.

SPECIES	MAASTRICHTIAN SAMPLES > 63 μm														
	0.00	1.50	3.00	4.50	6.60	8.00	9.50	10.25	10.65	11.00	11.30	11.60	11.80	11.97	12.00
Guembelitria cretacea	1.2	1.5	2.8	3.5	2.0	0.9	0.6	2.3	0.3	1.3	0.9	1.3	0.3	0.9	0.9
Gb. trifolia	0.6	0.6	0.6	0.6	0.6	0.3	0.3	x	x	0.9	x	0.5		0.3	0.3
Heterohelix planata	1.8	2.9	1.5	1.8	0.9	1.5	1.9	1.7	1.0	2.5	3.3	2.4	1.8	1.5	1.9
H. globulosa	61.5	54.2	59.3	50.4	61.4	62.9	68.9	64.1	58.7	58.6	54.7	68.0	69.1	61.9	69.2
H. pulchra	0.6	1.5	0.9	2.1	0.6	0.6	0.3	1.2	1.3	0.6	0.3	0.3	0.3	1.8	1.2
H. punctulata	0.3	0.5	1.2	0.9	x	x	0.3	0.6	1.3	1.3	0.3	x	0.9	1.2	0.3
H. glabrans	1.5	1.5	0.3	1.8	1.4	1.8	0.3	0.3	1.0	0.3	0.9	1.1	0.9	1.5	0.6
H. navarroensis	9.7	6.4	4.9	9.7	6.9	7.4	2.5	4.7	6.2	10.0	7.0	3.2	4.8	4.9	5.5
H. labellosa	0.6	2.0	0.9	1.8	2.3	0.3	2.5	2.3	2.6	3.1	2.4	1.3	1.8	4.6	2.5
Pseudotextularia nuttalli	1.2	2.0	2.8	1.8	1.1	2.4	1.3	0.9	0.3	0.9	0.6	0.3	0.9	0.6	0.6
P. elegans	0.3	x	0.9	1.2	x	0.6	x	1.2	0.3	0.6	0.3	0.5	x	0.3	0.3
P. intermedia	x	x	0.3	x	x	0.3	0.3	x	x	x	x	x	x	x	x
Gublerina acuta	x	x	x	x	x	x		x	x	x		x	x		
G. cuvillieri	x	0.3	x	0.3	x	x	x	x	x	x	x	x	x	x	x
Pseudoguembelina kempensis	0.6	1.5	1.2	1.2	0.6	0.3	0.6	0.9	0.3	0.6	x	0.3	x	0.3	0.3
P. palpebra	x	x	0.3	x	x	0.3	x	x	x	x	0.2	x	x	0.3	x
P. costulata	1.5	1.2	0.9	1.8	2.0	2.1	2.5	0.6	1.3	0.3	2.1	0.3	0.6	0.3	0.3
P. costellifera	x	0.9	0.3	x	x	x	x	x	0.3	x	0.3	0.3	x	0.3	x
P. excolata	x	x	x	x	x	0.3	x	x	x	x	x	x	0.3	x	x
P. hariaensis	x	x	x	x	x	0.6	x	x	x	0.3	x	x	x	x	x
Planoglobulina acervulinoides	x	x	x	x	x	x	x	0.3	x	x	x	x	x	x	x
P. carseyae	0.3	0.6	x	x	x	x	x	0.3	x	x	0.3	x	x	x	x
P. multicamerata	x	x	x	x	x	x	x	0.3	x	x	x	x	x	x	x
P. manuelensis	x	x	x	x	x	x		x	x	x	x	x	x	x	x
Racemiguembelina fructicosa	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
R. powelli	x	x	x	x	x	x	x	0.3	x	x	x	x	x	x	0.3
Globigerinelloides yaucoensis	2.1	1.2	1.2	1.8	1.7	3.5	1.7	1.5	2.6	1.9	3.0	2.1	4.2	3.0	3.7
G. rosebudensis	0.3	0.3	0.6	0.6	0.6	0.3	0.6	x	0.7	0.3	0.3	x	0.3	x	0.3
G. prairiehillensis	2.4	2.0	2.8	5.3	2.6	1.8	5.0	3.2	6.5	4.7	7.9	6.7	3.0	3.3	2.8
G. volutus	0.9	2.6	3.4	2.4	4.6	1.2	2.8	2.3	3.6	1.9	3.3	3.0	3.3	3.3	2.5
G. subcarinatus	0.3	0.3	0.3	x	0.9	0.9	0.3	0.9	0.3	0.3	0.9	0.3	0.3	0.3	x
Hedbergella monmouthensis	0.6	1.5	1.9	0.9	1.4	2.9	0.9	1.5	1.3	1.3	2.1	1.1	1.2	1.2	1.9
H. holmdelensis	3.0	4.9	2.5	3.8	2.0	3.5	4.4	5.3	5.9	5.0	4.0	1.9	3.0	5.5	3.1
Globotruncanella caravacaensis	x	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	x	0.3	0.3	0.9	0.3	0.3
G. havanensis	x	0.3	x	x	x	x	x	x	x	0.3	x	x	x	x	x
G. petaloidea	0.9	0.6	x	0.9	x	x	x	0.6	x	x	0.9	x	x	x	x
G. pschadae	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
G. minuta	1.2	1.5	0.3	0.9	1.7	0.6	0.3	1.5	1.3	0.9	0.9	1.6	0.9	1.5	0.3
Archaeoglobigerina cretacea	x	0.3	0.3	x											
A. blowi	x	x		0.3											
Schackoina multispinata	x	x	x	0.3		x	x	x	x	x		0.3	x	x	x
Plummerita hantkeninoides	0.3	x	x	x	0.3	0.3	x	x	x	0.3	x	x	x	x	x
Rugoglobigerina reicheli	0.6	x	x	x	x	0.6	x	x	0.3	0.3	x	0.3	x	0.3	x
R. rugosa	0.6	3.5	2.5	1.2	1.1	x	0.6	0.6	1.0	0.6	0.9	0.8	0.3	x	x
R. hexacamerata	0.6	0.6	1.2	0.3	0.9	x	0.3	0.6	0.7	0.6	x	0.3	0.6	x	x
R. rotundata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
R. milamensis	0.3	x	x	x	x	x	x	x	x	x	x	x	x	x	0.3
R. scotti	0.9	0.3	0.3	1.2	0.3	x	x	x	x	x	x	x	x	x	x
R. pennyi	0.3	x	x	x	x	x	x	x	x	x	x	x	x	x	x
R. macrocephala	0.3	0.6	0.3	x	0.6	0.3	x	x	x	x	x	0.5	x	x	x
Globotruncana arca	x	0.3	0.6	x	0.3	x	0.3	x	0.3	x	x	x	x	0.3	0.3
G. aegyptiaca	0.9	0.6	0.6	0.3	0.3	x	0.6	x	0.3	0.3	0.9	0.8	x	x	x
G. orientalis	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
G. rosetta	x	x	x	x	x	0.3	x	x	x	x	x	x	x	x	x
G. mariei	x	x	0.3	0.3	0.6	0.3	x	x	x	x	0.3	x	x	0.3	x
Globotruncanita stuarti	x	x	x	x	x	x	x	x	x	x	0.3	0.3	x	x	x
G. stuartiformis	0.3	x	x	x	x	x	x	x	x	x	x	x	x	x	x
G. insignis	0.3	0.6	0.6	x	0.3	0.3	x	x	x	x	x	x	x	x	x
G. fareedi	0.3	0.3	0.3	x	0.3	x	x	x	x	x	0.3	x	0.3	x	0.3
G. conica	x	x	x	x	x	0.3	x	x	x	x	x	x	x	x	x
G. dupeublei	x	x	x	0.3	x	x	x	x	x	x	x	x	x	x	x
G. angulata	x	x	0.3	x	x	x	x	x	x	x	x	0.3	x	x	x
Contusotruncana contusa	x	x	0.3	x	x	x	x	x	x	x	x	x	x	x	x
C. plicata	0.3	x	x	x	x	x									
C. patelliformis	x			x	x										
Abathomphalus mayaroensis								x		x	x				x
A. intermedius	x			x	x										
TOTAL	330	345	324	341	350	340	320	343	306	321	329	373	335	329	325
P/B	97.9	96.3	95.9	98.0	98.3	96.8	95.4	96.1	99.1	98.3	96.5	95.9	96.2	97.5	97.0
%CaCO₃	40.4	36.6	28.4	42.9	19.7	48.8	34.0	35.6	41.2	41.5	37.3	37.0	42.9	36.8	30.8

TABLE 2
Relative abundance of lowermost Danian planktic foraminifera at El Kef in the size fraction bigger than 63µm.

SPECIES	12.05	12.10	12.20	12.40	12.70	13.00	13.25	13.50	13.75	14.00	14.50	15.00	15.75	16.50	17.50	18.50	19.50	20.50	21.25	21.95	23.10	24.00	24.80	25.50
Parvularugoglob. longiapertura					0.3	13.0	7.8	10.4	37.3	23.4	23.3	5.3	1.6	0.7										
Pv. perexigua								0.3	2.0	9.6	13.2	6.4	1.6	1.7										
Pv. umbrica						0.7		0.3	1.2	0.3	x													
Pv. eugubina										9.9	7.6	20.2	29.6	16.6	5.0	1.0								
Pv. sabina								1.8	1.5	3.4	5.3	7.0	7.6	9.5	5.0	1.9								
Pv. cf. hemisphaerica											0.3	1.9	0.5	0.5	0.5	0.4								
PARVULARUGOGLOBIGERINA					0.3	13.7	7.8	12.8	42.0	46.6	49.7	40.8	40.9	29.0	10.5	3.3								
Globoconusa fodina						2.2	3.9	5.9	10.6	14.4	3.1	8.1	10.7	6.3										
Gc. cf. fringa								1.2	3.2	21.2	32.4	12.3	3.3	12.5										
Gc. extensa								0.6	2.6	1.3	3.3	1.4	0.8	0.2	0.5	0.1								
Gc. alticonusa				x	8.9	5.3	3.9	5.6	10.3	3.4	1.1	4.5	12.3	3.4	0.3	1.4	0.2	0.5	0.4					
Gc. minutula								0.3	2.3	4.5	0.6	1.7	1.8	1.4	x	0.7								
Gc. hillebrandti										0.5	x	1.4	0.3	0.7	0.3	0.1								
GLOBOCONUSA				x	8.9	7.5	7.8	13.6	29.0	45.3	40.6	29.4	29.2	24.5	1.1	4.4	0.2	0.5	0.4					
Globastica daubjergensis																					x	1.7	5.3	x
GLOBASTICA																					x	1.7	5.3	x
Eoglobigerina simplicissima												0.9	1.0	0.2	0.8	1.6	0.4	x	1.3	3.2	0.8	2.2	0.7	1.3
E. eobulloides													0.6	x	0.3	0.7	x	x	0.4	0.7	x	x	0.2	0.8
E. pentagona																							0.2	0.2
E. fringa														0.2	0.3	0.4	1.0	x	0.4	1.7	0.5	0.5	0.7	0.6
E. trivialis																					1.1	1.4	2.2	0.2
E. praeedita														1.0	1.4	0.4	x	0.5	2.2	1.0	0.3	1.0	1.7	0.8
E. edita																			0.2	0.5	0.5	1.0	1.5	2.1
E. polycamera																							x	0.4
E. microcellulosa																	x	x	0.8	1.2	1.1	0.5	x	0.2
EOGLOBIGERINA												0.9	1.6	1.4	2.8	3.1	1.4	0.5	5.1	8.3	4.3	6.6	6.2	6.2
Subbotina triloculinoides																					0.3	0.5	x	x
SUBBOTINA																					0.3	0.5	x	x
Globanomalina imitata												2.3	3.4	5.0	3.7	0.6	1.1	1.1	2.2	5.9	1.9	2.7	0.8	
G. archeocompresa												4.7	4.1	0.8	0.1	x	0.3	0.4	5.8	7.3	6.3	6.6	0.6	
G. planocompresa															x	x	0.4	0.6	0.7	2.1	1.2	2.4	1.3	
GLOBANOMALINA												7.0	7.5	5.8	1.7	0.6	1.8	2.1	8.7	15.3	9.4	11.7	2.7	
Parasubbotina moskvini															0.5	0.6	0.2	0.3	1.9	2.2	2.7	3.2	0.5	1.3
P. varianta																			0.2	0.5	0.5	0.7	x	1.3
P. pseudobulloides															0.5	0.6	x	0.3	0.6	1.0	2.1	3.4	1.5	3.9
PARASUBBOTINA															0.5	0.6	0.2	0.6	2.7	3.7	5.3	7.5	2.0	6.5
Praemurica inconstans																				0.2	2.4	4.9	4.4	7.4
Pr. taurica															x		x		x	1.0	1.9	0.7	3.4	3.0
P. pseudoinconstans																x		x	2.4	0.7	1.6	4.9	2.4	3.4
PRAEMURICA															x	x	x	x	2.8	1.9	5.9	10.5	10.2	13.8
Chiloguembelina morsei									0.6	x	0.3	17.4	12.3	20.3	63.5	17.3	22.4	25.9	41.3	38.2	29.2	45.6	40.1	48.0
Ch. midwayensis										0.3	0.5	0.8	0.2	0.3	0.3	x	0.6	1.1	2.8	1.7	3.8	2.9	1.9	1.1
Ch. taurica										x	0.5	2.2	1.3	1.7	2.2	2.1	1.7	2.4	4.1	6.0	15.4	5.9	4.9	5.1
Woodringina claytonensis					0.7	0.7		x				x	2.2	1.8	7.2	32.8	10.6	9.8	3.2	8.8	4.9	3.9	6.6	1.1
W. hornerstownensis						1.5		0.3	0.3	x	1.4	0.3	1.0	0.8	1.0	4.4	1.7	0.8	2.8	2.2	6.2	1.0	3.7	0.8
CHILOG. + WOOD.					0.7	2.2		0.3	0.9	x	1.4	23.7	17.0	28.3	77.6	53.9	36.1	41.1	53.8	56.9	59.5	59.3	62.2	56.1
Guembelitria danica			1.2	3.3	9.2	6.1	7.8	4.7	5.3	1.4	0.3	x	0.5	0.2	x	1.8	6.1	2.4	4.3	0.2	0.3			
Gb. irregularis					1.7	5.3	10.8	2.1	1.5	1.1	1.4	0.9	0.3	1.4	0.3	9.6	4.8	2.2	3.0	0.5	0.5		0.2	0.2
Gb. alabamensis			0.3		1.3	0.7		0.6	x	0.3	0.3	0.3	0.2	0.3	0.3	0.4	0.4		x					
Gb. cretacea	11.8	12.5	30.0	36.9	57.5	50.0	51.9	58.0	17.6	3.6	6.1	2.2	1.0	1.0	0.3	14.2	37.8	40.7	17.6	9.8	3.5	0.2	1.7	4.3
Gb. trifolia	5.1	4.5	23.4	49.5	17.3	4.6	9.8	4.4	2.6	1.7	0.8	1.1	0.8	0.7	0.3	5.1	10.8	9.0	3.4	8.0	2.7	3.2	2.7	3.2
GUEMBELITRIA	16.9	17.0	54.9	89.7	87.0	66.7	80.3	69.8	27.0	7.8	8.6	4.5	2.9	3.5	1.2	31.1	59.9	54.3	28.3	18.5	7.0	3.6	4.6	7.5
Heterohelix planata	1.0	1.6	0.3	0.3	0.3	1.5		x		x	x	x	0.3		x	0.1			0.4		0.3			
H. globulosa	65.2	61.3	38.1	7.6	1.0	2.3	2.9	2.4	0.3	x	x	0.3	x	1.2	0.3	0.4	0.8	0.5	1.9	0.5	0.3	0.2	x	
H. pulchra	0.2	x		x																				
H. glabrans	1.5	0.3		0.3																				
H. labellosa	0.7	0.5																						
H. navarroensis	5.4	5.6	0.9	0.6	x			1.5	x		x	x	x	x	x	0.3	x	0.3	0.6	0.2	0.3	0.2		
Pseudoguembelina kempensis	x	0.3																						
P.costulata	1.0	0.8	0.3																					
Globigerinelloides yaucoensis	2.3	1.3	0.3	0.6	0.3	0.7	1.0	0.3	x	0.3	x	x		0.5	x	0.3	0.2	0.3	x		0.2	x	0.2	
G. prairiehellensis	1.8	1.3	x	x	x			x		x	x	x		x	x		x							
G. volutus	2.0	4.0	2.5	0.3	x				0.3	0.3	x		0.3											
Hedbergella monmouthensis	0.5	0.3	0.9	0.6	0.7	0.7		0.3	0.3	x	x	x	x	x	x		x							
H. holmdelensis	1.0	0.3	1.5	x	0.7	3.0		0.3	x	x	x	0.3	0.3	x		x								
CRETACEOUS	83.1	83.0	44.8	10.3	3.0	8.9	3.9	4.8	0.9	0.6	x	0.9	0.6	1.7	0.3	1.1	1.0	1.1	3.5	1.1	0.6	0.6		
TOTAL	388	375	320	303	294	130	101	336	340	354	356	356	381	409	360	677	473	366	460	398	369	408	405	464
P/B	68.9	65.2	13.1	4.5	7.2	1.5	1.3	5.0	14.5	63.2	77.2	83.9	89.8	87.8	92.8	89.0	91.0	89.6	91.7	72.4	90.4	92.5	90.6	92.1
%CaCO₃	5.0	3.7	3.2	4.8	7.9	9.3	10.7	17.0	19.2	31.4	35.6	32.7	39.5	39.4	37.6	33.7	17.3	23.6	41.1	14.8	33.4	38.9	28.7	51.6

G. trifolia are certain survivors, because their relative and "absolute" abundance seems to increase into the lowermost Danian and they clearly play a role in the phylogeny of new Danian taxa (Olsson and Liu 1993; Arenillas and Arz 1996; Smit and Nederbragt 1997; Berggren and Norris 1997; Molina et al. 1998; Arenillas et al. 1998).

According to Smit and Nederbragt (1997), the differences in isotopic signals between foraminiferal tests of the Maastrichtian and Danian do not provide an unequivocal solution. All surviving Cretaceous species are smaller than 150µm (text-fig. 6), except some reworked specimens, and can be considered small and immature. D'Hondt and Zachos (1993) found significant

isotopic differences between small immature and large mature specimens. Even if there is post-K/P survivorship, these small specimens will always yield different stable isotope ratios (Smit and Nederbragt 1997). Therefore, most Cretaceous specimens found into the Danian sediments must be considered only as possible Cretaceous survivors, except for guembeletriids. The only certainty is that all the supposed Cretaceous survivors are always smaller in the lower Danian than in the upper Maastrichtian (Smit 1982, 1990; Keller 1988, 1989a,b; Lamolda 1990; Canudo et al. 1991; Keller et al. 1993, 1995; Molina et al. 1996, 1998).

The absolute abundance of survivor species was also decimated just above the K/P boundary, except for guembelitrids (Smit et al. 1988; Smit 1990; Smit and Nederbragt 1997). To better estimate the abundance of the foraminiferal population across the K/P boundary, Smit et al. (1988) try to estimate the "absolute" abundance expressed as the number of specimens per gram of sediment, corrected for sedimentation rate. These results depend on the difficult measurement of sedimentation rate in each interval. However, the "absolute" abundance provides better information about faunal changes across the K/P boundary and shows some remarkable differences in relation to relative abundance (Smit and Nederbragt 1997). The results of "absolute" abundance by Smit et al. (1988) are similar to our results when we considered the P/B ratio and recalculated the relative abundance of species and faunal groups (text-fig. 6). Although the relative abundance of the different survivor species indicate very few changes at the K/P boundary, their populations were clearly decimated just above the K/P boundary. These data (decrease of planktic foraminiferal size and the P/B relative and "absolute" population) are proof in themselves that great faunal changes occurred just at the K/P boundary.

MODEL AND CAUSE OF EXTINCTION

The different interpretations of K/P biostratigraphy are the result of several problems including the "Signor-Lipps" effect, the possibility of reworking and the existence of one or more hiatuses (Signor and Lipps 1982; Keller et al. 1993; Molina 1994, 1995; MacLeod 1994; Huber 1996; MacLeod and Huber 1996; Smit and Nederbragt 1997). These problems are usually used to support one or another hypothesis regarding extinction patterns (Arz et al. 1998; Arz and Arenillas 1998) and have led to tautological arguments (Arenillas et al. 1998). For example, specialists who favor a more catastrophic hypothesis appeal to pre-K/P "Signor-Lipps" effect and post-K/P reworking problems to reject the apparent gradual extinction pattern across the K/P boundary. Specialists who favor a more gradual hypothesis attribute the apparent catastrophic extinction pattern to a hiatus effect just at K/P boundary and the post-K/P "Signor-Lipps" effect. The El Kef blind test showed that all interpretations are feasible, at least theoretically.

However, one question remains, Is the planktic foraminiferal record adequate to estimate an extinction model across the K/P event? We would reply in the affirmative but only if the micropaleontological record is correctly interpreted. We should also consider the psychological factor (Kouwenhoven 1997). The participants in the El Kef blind test may have been psychologically preconditioned since several were involved in the K/P debate and had published their hypotheses on K/P extinction patterns (Lamolda et al. 1983; Orue-etxebarria 1985; Canudo et al. 1991; Liu and Olsson 1992; Olsson and Liu 1993). The interpretation of the results may have been influenced by the ideas of each analyst. Obviously a stricter methodology is required (Kouwenhoven 1997) and any future test should follow a rigorous procedure (Ginsburg 1997c). However, although the different taxonomic, biostratigraphic and taphonomic problems hamper a more correct interpretation, the quantitative analysis could help to reinterpret the results and minimize these problems.

The K/P-studies should tend to eliminate tautological reasonings and minimize the methodological and interpretative problems. Although there may be several valid interpretations we suggest the following objective results:

1. If we minimize the Signor-Lipps effect, there are no great pre-K/P changes either in the number of extinctions or assemblages turnover at El Kef. Our data indicate a great stability in the terminal Maastrichtian planktic foraminiferal assemblages, with only 1 taxon having become extinct in the last meter of the Maastrichtian (text-fig. 3).

2. Presence of Cretaceous specimens in the lowermost part of the Danian, either reworked or indigenous. Cretaceous specimens can be found in the first Danian samples, but it is not clear whether they are reworked or indigenous.

PLATE 1

SEM micrographs of some Upper Maastrichtian species examined in this study. Scale bars = 100μm.

1-2 *Gublerina cuivillieri* Kikoine, sample KF 12.00. *Plummerita hantkeninoides* Biozone.

3-4 *Planoglobulina multicamerata* (De Klasz), sample KF 12.00. *Plummerita hantkeninoides* Biozone.

5-6 *Pseudotextularia intermedia* (De Klasz), sample KF 12.00. *Plummerita hantkeninoides* Biozone.

7-8 *Pseudotextularia elegans* (Rzehak), sample KF 12.00. *Plummerita hantkeninoides* Biozone.

9-10 *Globigerinelloides volutus* (White), sample KF 12.00. *Plummerita hantkeninoides* Biozone.

11-12 *Globotruncana aegyptiaca* Nakkady, sample KF 12.00. *Plummerita hantkeninoides* Biozone.

13-14 *Abathomphalus mayaroensis* (Bolli), sample KF 12.00. *Plummerita hantkeninoides* Biozone.

15-16 *Plummerita hantkeninoides* (Brönnimann), sample KF 12.00. *Plummerita hantkeninoides* Biozone.
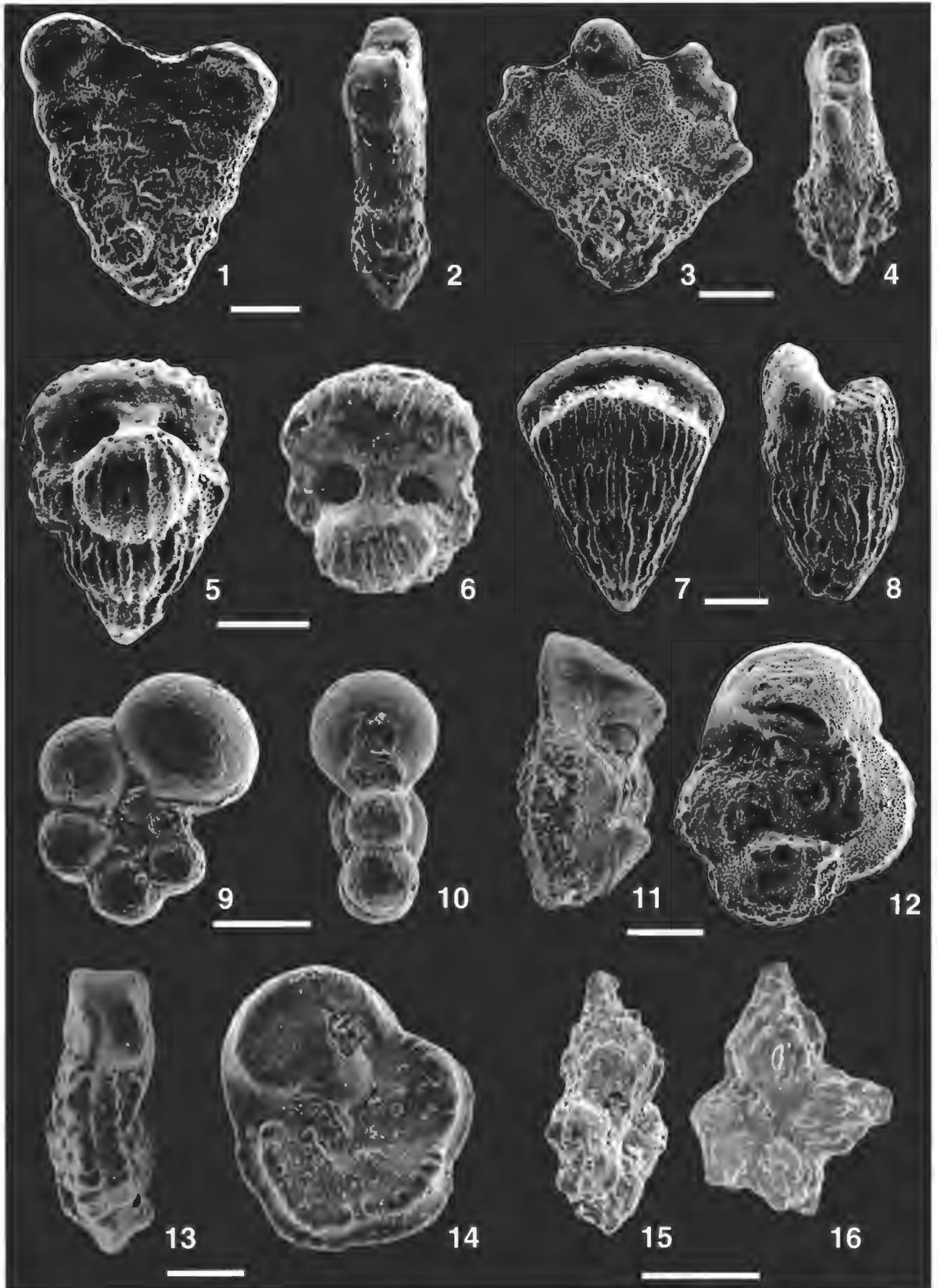
3. The possible Cretaceous survivors are always smaller in the lower Danian than in the upper Maastrichtian. All the specimens are smaller than 150µm and even 100µm in the basal Danian (text-fig. 6). This is recognized by all the micropaleontologists at all continuous K/P sections.

4. The planktic foraminiferal evolutionary radiation occurs above the K/P boundary and never below (text-figs. 3, 4 and 5).

We consider that point four is another independent proof of a catastrophic mass extinction at the K/P boundary (Arenillas et al. 1998; Arz and Arenillas 1998). If the mass extinction was gradual, the evolution of new species should have occurred during the whole Cretaceous-Paleocene transition, ecologically replacing extinct species and recolonizing vacant habitats. Consequently, the evolutionary pattern would be gradual both in the late Maastrichtian and early Danian. However, the evolutionary model is an adaptative radiation and occurs above the K/P boundary (D'Hondt et al. 1996; Arenillas et al. 1998; Arz and Arenillas 1998). In this sense, the gradual extinction pattern of the surviving Cretaceous species can be independent of the pre-K/P extinctions and be the long term result of an extraterrestrial impact or competition among new evolving species (Arenillas and Arz 1996; Molina et al. 1996, 1998).

The presence of smaller Cretaceous species in the earliest Danian can be explained using two different hypotheses. The first considers that all specimens, except guembelitriids, are reworked. We did not find large relative quantitative changes in the relative abundance of each taxon in the Maastrichtian and in the first centimeters of the Danian. Possibly the planktic foraminiferal assemblages found in these first samples of Danian were reworked with a similar relative abundance but a different absolute abundance. If there were multiple survivors, they did not play a role in the phylogeny of new Danian taxa (Olsson 1997). Only survivor species of *Guembelitria* and probably *Hedbergella* are phylogenetically linked to new

Danian taxa (Hemleben et al. 1991; Liu and Olsson 1992; Olsson et al. 1992; Arenillas and Arz 1996; Berggren and Norris 1997).

The second hypothesis considers these species as survivors and applies several concepts from the mass extinction theory (Kauffman and Harries 1996a,b; Harries et al. 1996) to early Danian planktic foraminifera (Koutsoukos 1996; Molina et al. 1998; Arenillas et al. 1998; Arz and Arenillas 1998). The species that became extinct at the K/P boundary were mainly deep dwellers with a K-strategy, whereas the survivors were the surface dwellers of r-strategy. Some of the opportunist species such as guembelitriids were disaster species that bloomed immediately after the K/P boundary in the *G. cretacea* Zone (stage 1, text-figs. 5, 6 and 7). Others, such as hedbergellids, heterohelicids and globigerinellids may have been opportunist pre-adapted survivors and ecological generalists. Disaster species and opportunist species are specifically adapted to stressful environments and ecological generalists enjoy more random possibilities of survival during a catastrophe since they are very abundant.

However, even if the Cretaceous survivors can be explained by the first or the second hypothesis, our data show that the planktic foraminiferal mass extinction pattern across the K/P boundary was sudden. The planktic foraminiferal mass extinction across the K/P boundary at El Kef involves 6 (8.9%) species extinctions in the last 12 meters of the upper Maastrichtian, 46 (68.7%) species extinct at the K/P boundary and 15 (22.4%) ranging into the lowermost Danian. We observed a sudden mass extinction at the K/P boundary and a less evident gradual mass extinction across the K/P boundary, mainly in the lowest Danian. After the K/P catastrophic mass extinction, an evolutionary radiation of new Paleocene species began just above the K/P boundary. Irrespective of the number of Cretaceous survivors found, this pattern is much more compatible with the catastrophic pattern of Smit than the gradual pattern suggested by Keller.

PLATE 2
SEM micrographs of some Lower Danian species examined in this study. Scale bars = 100µm.

1-3 *Parvularugoblobigerina eugubina* (Luterbacher and Premoli Silva), sample KF 15.00. *Parvularugoglobigerina eugubina* Biozone

4-5 *Parvularugoblobigerina longiapertura* (Blow), sample KF 13.75. *Guembelitria cretacea* Biozone.

7-8 *Globoconusa alticonusa* (Li et al.), sample KF 12.70. *Guembelitria cretacea* Biozone.

9-10 *Guembelitria cretacea* (Cushman), sample KF 12.70. *Guembelitria cretacea* Biozone.

11-12 *Globoconusa fodina* (Blow), sample KF 13.75. *Guembelitria cretacea* Biozone.

13-15 *Globoconusa cf. fringa,* sample KF 14.00. *Parvularugoglobigerina eugubina* Biozone

16-18 *Globoconusa minutula* (Luterbacher and Premoli Silva), sample KF 14.00. *Parvularugoglobigerina eugubina* Biozone

19-20 *Globanomalina archeocompressa* (Blow), sample KF 25.00. *Parasubbotina pseudobulloides* Biozone.

21-22 *Parasubbotina pseudobulloides* (Plummer), sample 25.00. *Parasubbotina pseudobulloides* Biozone.

23-24 *Chiloguembelina morsei* Kline, sample KF 24.00. *Parasubbotina pseudobulloides* Biozone.

25-26 *Praemurica inconstans* (Subbotina), sample KF 25.50. *Parasubbotina pseudobulloides* Biozone.

According to Keller, the existence of pre-K/P boundary extinctions would be incompatible with an impact-induced extinction. These previous extinctions could be more compatible with a gradual effect caused by massive volcanism or paleoceanographical changes since they represent a slight acceleration of the extinctions (Keller 1988, 1989b; Canudo et al. 1991; Keller et al. 1993, 1996). However, this pre-K/P extinction pattern has not been sufficiently documented by Keller. On the contrary, our data suggest relatively few pre-K/P disappearances. Furthermore, the K/P catastrophic mass extinction exactly coincides with the layer containing the Ir anomaly and other extraterrestrial impact evidence at El Kef and several sections worldwide such as Agost, Caravaca, Zumaya and Aïn Settara (Smit 1990; Schmitz 1994; Molina 1994, 1995; Molina et al. 1996, 1998; Apellaniz et al. 1997; Dupuis et al. in press). This K/P extinction pattern identified by us in several sections is compatible with the catastrophic effects caused by the impact of a large extraterrestrial body (Smit 1990; Molina et al. 1996, 1998), since an unusual event requires an unusual cause.

CONCLUSIONS

We studied the planktic foraminiferal biostratigraphy and assemblages turnover across the K/P boundary at El Kef and suggest a new interpretation of the El Kef blind test. This section is one of the most continuous K/P boundary sections known and the possible hiatus effect is minimal. The debate about the planktic foraminiferal extinction model across the K/P boundary is the result of several problems including the "Signor-Lipps" effect and the possibility of reworking. This is evident from the blind test and is the reason it apparently failed to solve the controversy. However, the blind test and our independent test demonstrate the lack of a step-wise extinction below the K/P boundary. We considered species ranges based on six sample intervals, equivalent to the El Kef blind sample test, and found a catastrophic mass extinction pattern: 1 (1.6%) species disappearing in last meter of the Maastrichtian, 46 (74.1%) species extinct at the K/P boundary and 15 (24.2%) ranging into the earliest Danian.

Irrespective of the different interpretations, we suggest four objective results:

- There are no significant pre-K/P quantitative changes either in number of extinctions or assemblages turnover at the El Kef.

- Cretaceous specimens are present in the lowermost Danian, but it is not clear whether they are reworked or indigenous.

- Apparent Cretaceous survivors are always smaller in size and lower in absolute abundance in the lower Danian than in the upper Maastrichtian.

- The planktic foraminiferal evolutionary radiation always begins above the K/P boundary and never below.

These results indicate that the pre-K/P "Signor-Lipps" effect and post-K/P reworking problems are more important in the K/P debate than the hiatus effect at the K/P boundary and the post-K/P "Signor-Lipps" effect. At El Kef, we have only found 6 (8.9%) species disappearing below the K/P boundary in the last 12 meters of the upper Maastrichtian, but 46 (68.6%) species extinct at the K/P boundary and 15 (22.4%) possible Cretaceous survivors ranging into the lowermost Danian. Similar patterns have been identified by us in the most continuous marine sections worldwide known to date. This model of catastrophic mass extinction constitutes the largest and most sudden extinction event in the history of planktic foraminifera and is very compatible with the possible catastrophic effects caused by the impact of a large extraterrestrial bolide.

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