THE CRETACEOUS/PALEOGENE (K/P) BOUNDARY AT AÏN SETTARA, TUNISIA: SUDDEN CATASTROPHIC MASS EXTINCTION IN PLANKTIC FORAMINIFERA

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ABSTRACT

The quantitative study and high resolution sampling of an essentially continuous and expanded Cretaceous/Paleogene (K/P) boundary section in Tunisia allow us to test the model of extinction in planktic foraminifera. The extinction at the Aïn Settara section occurred over a short period of time similar to the Tunisian sections at El Kef and Elles and the Spanish sections at Agost, Caravaca and Zumaya. At Aïn Settara only 3 species disappeared in the latest Maastrichtian, 45 became extinct precisely at the K/P boundary and 18 disappeared in the earliest Danian. The species that became extinct at the K/P boundary constitute about 20% of the individuals in the population larger than 63 microns and 68% of the species, which suddenly became extinct in a catastrophic event precisely coinciding with the layer containing evidence for an asteroid impact. Most of these species are large, complex and low latitude deeper to intermediate dwelling forms. This extinction event is clearly the most important catastrophic mass extinction recorded in the history of planktic foraminifera. This pattern of extinction is superimposed on a controversial gradual pattern of extinction of 21 species that apparently began in the latest Maastrichtian and ended in the early Danian. The Maastrichtian species that seem to become extinct gradually are generally small, cosmopolitan and simple surface dwellers. The catastrophic mass extinction of the 45 species coincident with the K/P boundary is compatible with the effect of the impact of a large asteroid, whereas the gradual extinction of 18 species in the basal Danian could also be attributed to the long term disruptive effect of the impact.

INTRODUCTION

There is a wide consensus among specialists in planktic foraminifera that the Cretaceous/Paleogene (K/P) turnover is a mass extinction because it affected more than 50% of the species. This mass extinction event has been pointed out by many specialists since the early studies of the fossil record of planktic foraminifera (Berggren, 1962, 1969, 1971; Luterbacher and Premoli Silva, 1964; Bolli, 1966; Premoli Silva, 1977; Maurrasse and others, 1979; Blow, 1979). Detailed biostratigraphic studies of the Gubbio section (Italy) allowed Luterbacher and Premoli Silva (1964) to describe several new species as well as the new *Globigerina eugubina* Biozone between the Maastrichtian and Danian, which is characterized by a planktic foraminiferal association completely different from those found in the uppermost Maastrichtian assemblages.

When Alvarez and others (1980) proposed the theory that the K/P boundary mass extinction was caused by a large bolide impact, it was assumed that the planktic foraminifera model of extinction was very sudden and catastrophic. This theory was corroborated by Smit and Hertogen (1980) who documented that at the Caravaca section (Spain) the impact severely affected the planktic foraminifera and only one species survived (*Guembelitria cretacea*). The K/P planktic foraminiferal fossil record was studied in detail by Smit (1977, 1979); it yielded a new assemblage between the Maastrichtian and Danian that led to the definition of a high resolution biozone (*G. cretacea* Biozone). Initially, Smit considered most of the Maastrichtian taxa found in the lowermost Danian to be reworked specimens. However, Smit subsequently (1982, 1990, 1994) admitted that some Maastrichtian species survived and that the final extinctions may have extended over a certain period of time, although he maintained that the K/P mass extinction event was sudden, catastrophic and the consequence of a large extraterrestrial bolide impact (Smit, 1990, 1997).

Paleontologists have often questioned the catastrophic nature of the impact at the K/P boundary and they argue that the pattern of the mass extinction in the terminal Maastrichtian is gradual (Keller, 1988, 1989a,b, 1994, 1996; Keller and others, 1993, 1995, 1998). They conclude that 2/3 of the species declined prior to becoming extinct below or at the K/P boundary and about 1/3 of the species survived well into the Danian. Consequently, Keller and others (1995) argue that the gradual pattern of extinction cannot be attributed to a global biotic effect of the asteroid impact.

The main reason for these two opposite hypotheses may be methodological as was pointed out by Signor and Lipps (1982) and Molina (1994, 1995, 1997). For example, it is evident that the fossil record of dinosaurs is very scarce compared with the fossil record of many microfossil groups and hence is much more affected by the Signor-Lipps effect (incomplete ranges are due to insufficient sampling). However, microfossils such as planktic foraminifera have a very abundant and continuous fossil record and therefore are very suitable to confirm, or disprove, the cause and effect relation between large impact and catastrophic mass extinction.

In an attempt to further clarify the pattern of extinction at the K/P boundary, a blind sample test was suggested, and in 1992 a group of scientists re-sampled the El Kef section in Tunisia. Six unlabeled samples were studied by four investigators and the results recently published (Lipps, 1997; Ginsburg, 1997a,b; Smit and others, 1997; Canudo, 1997; Masters, 1997; Olsson, 1997; Orue-Etxebarria, 1997) were inconclusive as the data supported neither pattern of extinction (Keller, 1997; Smit and Nederbragt, 1997). The different interpretations of the blind test seemingly showed that the test failed to resolve the controversy.
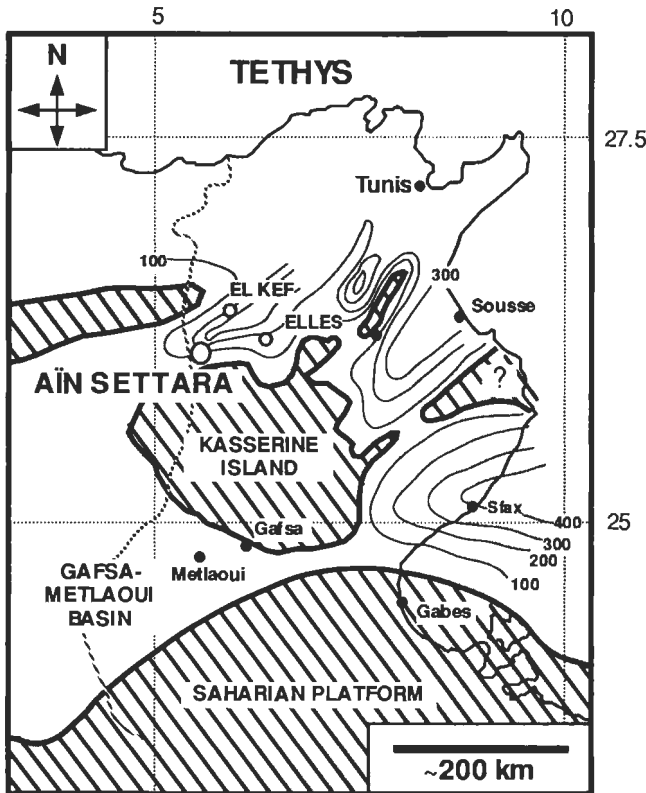
FIGURE 1. Paleolatitudinal and paleogeographic location of the Aïn Settara section (modified from Denham and Scotese, 1987).

Our recent studies of several continuous sections from Spain and Tunisia (Arenillas, 1996; Arz, 1996; Molina and others, 1996, 1998; Arenillas and others, 1998; Arz and Arenillas, 1998; Arz and others, 1999a,b; Dupuis and others, in press) support the main pattern of sudden and catastrophic mass extinction at the K/P boundary. In the present study, we present further corroborative evidence in a detailed quantitative study of planktic foraminifera from the Aïn Settara section in Tunisia. The outcrop contains an expanded, continuous and well-exposed section across the K/P boundary. The planktic foraminifera are quite well-preserved, the assemblages are very diversified, and the section is very similar to the El Kef section. Thus, the results can be correlated to that area and shed further light on the controversy.

MATERIALS AND METHODS

The Aïn Settara section is located in Central Tunisia, in the region between Kalaat Senan, Tajerouine and Kalaa Khasba, 50 km south of the El Kef K/P boundary stratotype (Fig. 1). The K/P boundary lies within the lower part of the marly El Haria Formation, at about 180 m above the top of the Abiot Formation and 400 m below the base of the Metlaoui Formation (Bourollet, 1956). The El Haria Formation includes several units, two of which are relevant to this study: the Sidi Nasseur Marls that include the base the boundary clay and the infrajacent Aïn Settara Marls. The K/P boundary is exposed in a 100 m high steep flank of a deeply incised gully. It occurs at about 80 m above the gully, and is horizontally traceable for more than 200 m. There is almost no vegetation on this steep slope and there-

fore exposure is excellent (see detailed map in Dupuis and others, in press).

Samples were collected at cm-intervals across the critical K/P boundary interval and at m-intervals below and well above the boundary as indicated in Tables 1 and 2.A total of 41 samples were analysed for this study. Between meter 83 and 84, a total of 16 samples were taken, and their numbers correspond to the centimeter intervals. All the samples were disaggregated in tap water and dilute H_2O_2, then washed through a 63-micron sieve and dried at 50°C. Preservation of planktic foraminifera is quite good, although the original calcite shells are recrystalized. Bioturbation was observed immediately below the red boundary layer, and evidence of dissolution is conspicuous just a few centimeters above.

Population counts were based on representative splits, obtained with a modified Otto microspliter, of 300 or more specimens in the size fraction larger than 63 microns. All the representative specimens were picked and mounted on microslides for a permanent record and identification. The remaining sample was intensively scanned for rare species in order to avoid or minimize the Signor-Lipps effect (Signor and Lipps, 1982). Faunal counts for the picked fraction are listed in Tables 1 and 2.

BIOSTRATIGRAPHY

The microfossil content of the Aïn Settara section is very similar to the well known Tunisian section at El Kef and quite similar to the Spanish sections at Caravaca and Agost. As shown in Figure 2, we have used the classical system of biozonation, indicating the sequence of planktic foraminiferal datum events used to establish our biozones at Aïn Settara. Figure 2 also shows a comparison with other related biozonations for reference. Following the lower latitude biozonation used by Molina and others (1996), we have identified five biozones across the K/P boundary at Aïn Settara: *Abathomphalus mayaroensis* Biozone, *Plummerita hantkeninoides* Biozone, *Guembelitria cretacea* Biozone, *Parvularugoglobigerina eugubina* Biozone and *Parasubbotina pseudobulloides* Biozone.

The *A. mayaroensis* Biozone was defined by the total range of *A. mayaroensis* and characterized the upper Maastrichtian in low latitude regions as well as the Tethyan palaeogeographic realm. However, it has been found that *A. mayaroensis* is very rare or absent in high latitude regions (Blow, 1979) in relatively shallow-water deposits such as El Kef in Tunisia or Ben Gurion in Israel (Keller, 1988; Abramovich and others, 1998) and is problematic as an index species in terminal the Maastrichtian (Molina and others, 1998). For these reasons, we have used the *P. hantkeninoides* Biozone (Ion, 1993) to further characterize the terminal Maastrichtian with a more detailed biozonation. The *P. hantkeninoides* Biozone is defined by the total range of the nominate taxon (Plate 1), whose first appearance datum (FAD) defines the upper limit of the *A. mayaroensis* Biozone, and it was later used by Keller and others (1995), Pardo and others (1996) and Molina and others (1996, 1998). The large tropical Maastrichtian taxa suddenly disappear at the stratigraphic level that corresponds to the top of this biozone.

Table 1.   Relative abundance of uppermost Maastrichtian planktic forminifera at Aïn Settara.

Species	Cretaceous samples > 63 μm									
	82	82.5	83	−30 −32	−20 −22	−12 −14	−10 −12	−5 −7	−1 −3	0 −1
Guembelitria cretacea	1.3	1.8	1.0	1.0	0.6	0.6	3.6	0.6	2.5	4.4
G. trifolia	0.3	0.9	0.3	1.0	1.2	1.2	0.6	0.3	0.9	0.3
Heterohelix planata	2.7	4.5	5.3	4.5	3.5	12.0	4.9	4.6	3.1	2.5
H. globulosa	40.5	40.9	45.4	62.4	58.5	39.7	42.7	48.0	37.1	37.3
H. pulchra	3.7	2.1	6.9	4.8	5.6	5.1	4.2	4.9	4.7	5.4
H. punctulata	0.3	1.2	0.3	1.3	1.2	0.6	0.3	2.0		0.6
H. glabrans	1.7	0.6	1.6	1.9	0.6	0.9	2.6	2.6	2.5	1.9
H. labellosa	3.4	3.3	2.0	2.6	4.4	3.9	1.0	2.3	1.6	3.8
H. navarroensis	14.6	19.1	10.6	0.6	2.0	15.9	12.4	9.5	21.4	16.5
Pseudotextularia nuttalli	0.7	0.3	x	0.3	0.9	0.6	0.3	0.6	0.3	x
P. elegans	0.3	0.3	0.6	0.3	x	0.9	0.6	1.6	0.3	0.6
P. intermedia	x	x		x		x	x		x	x
Gublerina acuta		x								
G. cuvillieri	0.3	x	x	x	x		x	x		x
Pseudoguembelina kempensis	2.4	3.3	3.3	1.0	3.8	3.3	2.9	3.3	3.1	2.2
P. palpebra	0.3	x	0.3	0.3	x	0.6	0.6	0.3		0.6
P. costulata	1.0	0.9	2.0	1.0	1.7	3.9	3.9	1.3	3.4	1.3
P. costellifera	1.3	0.3	x	x		0.6	0.6	0.6	0.9	0.6
P. excolata		x	x	x	x	0.3	0.3	0.3	x	0.3
P. hariaensis	x	x		x	x	x	x	x	x	x
Planoglobulina acervulinoides	x	x		x	x	x	x	x	x	x
P. carseyae	x	x	x	x	0.3	0.3	0.3	x	x	0.3
P. multicamerata	x	x		x	x	x	x	x	x	x
P. manuelensis		x			x	x			x	x
Racemiguembelina fructicosa	x	x	x	x	x	x	x	x	x	x
R. powelli	x	x	x	0.3	x	x	0.3	0.3	x	x
Globigerinelloides yaucoensis	2.0	2.1	1.6	2.2	1.2	2.1	3.2	2.3	2.5	3.2
G. rosebudensis	0.3	x	x		0.6	0.3	x		x	0.3
G. prairiehillensis	3.7	3.9	3.3	3.2	1.5	1.5	1.9	1.0	1.2	1.6
G. volutus	4.7	1.8	1.3	0.3	0.3	3.0	0.3	2.9	1.6	1.3
G. subcarinatus	0.7	1.2	0.6		0.9	0.6	0.6	0.6	1.2	0.6
G. multispina	x	x	x				x	x		0.3
Hedbergella monmouthensis	2.0	1.5	2.3	2.9	2.9	1.5	2.9	1.0	1.9	2.8
H. holmdelensis	3.4	0.9	2.6	1.6	1.2	1.8	2.6	2.9	3.8	2.2
Globotruncanella caravacaensis	1.7	1.2	1.3	0.3	0.3	0.3	x	0.3	0.6	0.3
G. havanensis		x	x	x	x	x	x	0.6	x	x
G. petaloidea	x	x	x	x	x	x	0.3	x	x	x
G. pschadae	x	x		x	x	x		x	x	x
G. minuta	4.1	3.6	3.3	2.9	3.2	0.9	2.6	1.3	3.1	2.8
Archaeoglobigerina cretacea	x									
A. blowi	x	0.3	x	0.3		0.6	0.3	1.0	0.6	0.3
Schackoina multispinata	x			0.3	x	0.3	x		x	x
Plummerita hantkeninoides	0.3	0.3	0.6	0.3	0.3	x	x	x	x	x
Rugoglobigerina reicheli	0.7	0.9	0.3	0.6	0.6	0.3		0.6		0.9
R. rugosa	0.3	0.3	x	0.6	0.3	0.9	1.0	0.3	0.3	x
R. hexacamerata	x	x	0.3	x	x	x	x	0.6	x	0.3
R. rotundata	x	x			x	x		x	0.3	0.3
R. pennyi	x	x	0.3	x	x	0.3				
R. macrocephala	x	x	0.6	x	0.6	0.3	0.6	x	0.3	x
R. scotti	x	x	0.3		0.3	x	0.3	x	x	x
Globotruncana arca	x	x	x	x	0.3	0.3	x	x	x	x
G. aegyptiaca	0.3	0.3	x	x	x	0.3	0.3	0.3	x	x
G. rosetta	x	x	x		0.3	x	x		x	x
G. mariei	0.3	x	x	x	0.3	x	x	x	0.3	x
Globotruncanita stuarti	x	x	x	x	x	x	x	x	x	x
G. stuartiformis	x	x	x	x	x	x	x	0.3	x	x
G. insignis	x	x	x	x			x		x	x
G. fareedi	x	0.9	1.0	0.3	x	0.3	x	x	x	x
G. conica	x		x	x	x		x	x	x	x
G. falsocalcarata	x	0.6	x		x			x	x	x
G. angulata	x	x		x		x	x		x	x
G. dupeublei	x	x	x	x	x	x	0.3	x		x
Contusotruncana contusa	x	x	x	x	x	x	x	x		x
C. plicata										
C. patelliformis	x			x		x		x		x
C. walfischensis		x				x	x			x
Abathomphalus mayaroensis										x
Total number counted	294	330	302	310	340	334	307	304	318	315

PERIODS	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	Parasubbotina pseudobulloides	P1b	P1b S.triloculinoides G. compressa	Parasubbotina pseudobulloides	P1c Globigerina pseudobulloides / P1b Eoglobigerina taurica	P1a Globorotalia (Turborotalia) pseudobulloides Globorotalia (Turborotalia) archeocompressa	Globigerina pseudobulloides
		Pr. inconstans			P1a Pv. eugubina- Subbotina triloculinoides				
		Pv. eugubina							
		Pb. pseudobulloides	Parvularugoglob. eugubina	P1a(2) / P1a(1) / P1a	Pα Parvularugog. eugubina	Parvularugog. longiapertura	P1a G. eugubina	Pα Globorotalia (Turborotalia) longiapertura	Globigerina eugubina
		Pv. longiapertura							
		Pr. taurica							
		Pv. eugubina	Guembelitria cretacea	P0	P0 G. cretacea	G. cretacea	P0 G. cretacea	M18 Rugoglob. hexacamerata	Unzoned
		Pv. longiapertura / Gb. alticonusa							
CRETACEOUS	MAASTRICHTIAN	P. hantkeninoides / A. mayaroensis	Plummerita hantkeninoides	Plummerita hantkeninoides	Abathomphalus mayaroensis	Abathomphalus mayaroensis	Abathomphalus mayaroensis	M17 Abathomphalus mayaroensis	Abathomphalus mayaroensis
		P. hantkeninoides	Abathomphalus mayaroensis	Abathomphalus mayaroensis					
		A. mayaroensis							

FIGURE 2. Comparison of uppermost Maastrichtian and lowermost Danian planktic foraminiferal biozonations with the biozonations use in this paper.

The *G. cretacea* Biozone spans the interval between the last appearance datum (LAD) of *P. hankeninoides* and/or *A. mayaroensis* precisely at the K/P boundary and the FAD of *Pv. eugubina*. The K/P boundary stratotype was defined in the XXVIIIth International Geological Congress in Washington in 1989 at the base of the boundary clay at the El Kef section (Tunisia) and is recognized by an Ir anomaly, an increase in Ni-rich spinels, an increase in total organic carbon (TOC), a decrease in $\delta^{13}C$, the presence of microtektites, shocked quartz, and the first appearance of the Danian planktic foraminifera. Similarly, most of this evidence that characterizes an impact has also been recognized at the base of the boundary clay of the Aïn Settara section. Dupuis and others (in press) have also detected the Ir anomaly and a very concentrated horizon of Ni-rich spinels just above the yellowish-red horizon of Jarosite and FeO. The layer with geochemical anomalies at Aïn Settara is very good evidence of the extraterrestrial bolide impact and is just below a 55-cm thick interval of dark clay. The terminal Maastrichtian is characterized by gray marls, but the topmost centimeter is a dark gray clay horizon probably due to diagenetic contact. The *G. cretacea* Biozone is comparatively very well expanded (60 cm thick) and is lithologically characterized by a few millimeters of a yellowish-red horizon of Jarosite and FeO at its base. This horizon is overlapped by thin lenses of brownish-black clay, grey silt and heterogeneous brownish-black clay (Dupuis and others, in press). The dissolution and the reworking of planktic foraminifera

are only notable in these basal layers. Most of the *G. cretacea* Biozone is characterized by black clays which contain a very well-preserved autochthonous fauna. The Danian planktic foraminifera first appeared in the lower part of this biozone.

The *Pv. eugubina* Biozone defines the interval between the *Pv. eugubina* FAD and the *P. pseudobulloides* LAD. At Aïn Settara, this biozone is 4.5 m thick. For high resolution biostratigraphy, it is useful to differentiate between *Pv. eugubina* and *Parvularugoglobigerina longiapertura*. When these species have been considered synonymous (Olsson and others, 1999), the *Pv. longiapertura* morphotype FAD has been frequently used to identify the P0/P1a or P0/Pα boundary (Fig. 2). In this case, P0 (= *G. cretacea* Biozone) is 15 cm thick. However, these species are distinguished by the apertural form which is high-arched in *Pv. longiapertura* and low-arched in *Pv. eugubina* (Plate 2). In this sense, following Blow (1979), Canudo and others (1991) used *P. longiapertura* as a marker of the zone because this species has a very distinct and stable morphology characterized by a compressed test and high slit-like aperture and thus could be a more suitable index taxon. *Pv. longiapertura* appears earlier in the Aïn Settara, Agost, Caravaca and Zumaya sections than *Pv. eugubina* (Canudo and others, 1991; Molina and others, 1996, 1998). Although this alternative biozone could also be used (Apellaniz and others, 1997), nonetheless we decided to continue the use of the classical better known *Pv. eugubina* Biozone.

TABLE 2. Relative abundance of lowermost Danian planktic forminifera at Aïn Settara.

Species	+3/+5	+8/+10	+15/+17	+20/+22	+30/+32	+40/+42	+45/+47	+50/+52	+55/+57	84	84.2	84.5	84.7	85	86	87	88	89	90	92	93.8
										Paleocene samples > 63 μm											
Parvularugoglob. longiapertura			1.1	8.0	35.8	49.8	35.3	24.8	33.6	26.4	18.7	21.3	15.1	13.6	7.4	3.1					
P. perexigua				0.3	1.7	2.9	0.3	2.4	2.9	7.7	8.8	20.3	10.3	19.5	9.3	12.9					
P. umbrica				3.5	2.6	1.8	1.2	0.6		0.4	0.4	0.3	x	0.3							
P. eugubina										2.8	9.1	2.7	9.6	7.7	2.6	15.1	1.5	0.3	0.5		
P. sabina						0.3	0.6	0.3	1.2	0.4	1.8	2.7	7.7	8.8	2.6	6.9	0.4	1.2	3.1		
P. cf. hemisphaerica														1.1	1.3	2.2					
PARVULARUGOGLOBIGERINA			1.1	8.3	41.0	55.6	38.0	29.6	38.3	37.7	38.8	47.3	42.7	51.0	23.2	40.2	1.9	1.5	3.6		
Globoconusa fodina				1.0	0.8	2.3	9.9	21.8	18.4	11.4	15.0	10.1	17.0	4.4	20.0	7.9			R		
Gc. cf. fringa							0.9	3.0	1.7	2.4	8.8	6.4	11.4	7.0	7.4	6.0			R		
G. extensa					1.0	2.7	4.2	6.7		0.4	8.8	6.8	4.0	x	3.2	2.2	0.4	x	x	R	
G. alticonusa			3.0	1.0	3.1	4.5	6.9	8.4	6.1	8.9	2.2	4.4	2.6	2.2	15.8	14.8	0.4	0.3	0.5	R	
G. minutula							2.4	1.4		4.9	6.2	2.0	1.5	1.7	1.6	1.2	1.5	0.6	0.8		
Gc. hilebrandti										0.4	6.9	0.3	3.3								
GLOBOCONUSA			3.0	2.0	3.9	7.8	20.4	39.8	34.3	20.4	47.9	30.0	39.8	15.3	48.0	32.0	2.3	0.9	1.3		
Eoglobigerina simplicissima														x		1.2	0.7	0.9	x	0.3	0.6
E. eobulloides														x		x	1.1	1.3	x	1.0	0.6
E. pentagona																			x	x	1.7
E. fringa															x		0.7	0.3	x	0.6	2.3
E. trivialis																		x	x	0.3	1.7
E. praedita															x	x	1.5	1.3	1.0	2.0	7.9
E. edita																			0.2	3.2	5.6
E. microcellulosa																		x	x	0.3	x
EOGLOBIGERINA														x		1.2	4.0	3.8	1.2	7.7	19.4
Subbotina triloculinoides																				x	
SUBBOTINA																				x	
Globanomalina imitata														x		x	2.7	1.2	4.9	6.5	2.3
G. archeocompresa															x	0.3	1.9	0.3	2.6	8.1	3.3
G. planocompresa																		x	2.0	2.6	4.2
GLOBANOMALINA														x		0.3	4.6	1.5	9.5	17.2	9.8
Parasubbotina moskvini														x		0.3	1.1	1.2	0.8	0.6	2.9
P. varianta																		x	x	x	4.2
P. pseudobulloides																		1.2	x	1.3	3.9
PARASUBBOTINA														x		0.3	1.1	2.4	0.8	1.9	11.0
Praemurica inconstans																			0.8	0.3	3.3
Pr. taurica																x	x	1.2	1.0	2.9	2.3
P. pseudoinconstans																	0.4	1.5	x	0.6	1.6
PRAEMURICA																x	0.4	2.7	1.8	3.8	7.2
Chiloguembelina morsel												x	x	4.4	13.9	8.5	23.3	23.2	20.1	16.6	15.4
Ch. midwayensis														x		2.2	3.8	9.3	7.7	7.8	3.9
Ch. taurica														8.4	3.2	3.5	3.0	5.7	10.1	15.3	11.2
Woodringina claytonensis										x	x	x	0.4	x	x	0.3	3.4	3.3	8.2	2.3	3.6
W. hornerstownensis												x	x	1.4	1.6	1.9	6.1	4.5	13.7	7.8	5.6
CHILOG. + WOOD.										x	x	x	0.4	14.2	18.7	16.4	39.6	46.0	59.8	49.8	39.7
Guembelitria danica		0.9	1.5	1.3	3.1	3.6	1.8	2.4	0.6	1.2	0.7	1.0	0.4	0.7	0.3	0.3	4.9	3.3			
G. irregularis				0.7	0.4	1.6	1.8	0.6	0.9	0.8	0.4	0.3	0.4	x	x	0.3	1.1			x	x
G. alabamensis		0.6	1.1	0.7	0.4	1.0	x	0.6	0.3	1.2	x	0.3	x	0.3	0.3	0.9	x	1.2	x	2.6	1.4
G. cretacea	7.1	15.3	56.4	46.6	25.7	20.5	27.5	24.2	18.7	19.9	5.1	9.5	9.2	5.9	1.3	0.9	19.1	28.8	8.5	2.9	0.3
G. trifolia	5.1	7.9	9.8	11.1	3.5	2.3	3.6	0.9	2.9	1.2	0.7	1.7	2.9	2.2	1.3	1.9	4.9	3.3	7.0	9.1	0.3
GUEMBELITRIA	12.2	24.7	68.8	60.4	33.1	29.0	34.7	28.7	23.4	24.3	6.9	12.8	12.9	9.1	2.9	4.3	30.0	36.6	15.5	14.6	2.0

TABLE 2. Continued.

Species	Paleocene samples > 63 µm																				
	+3/+5	+8/+10	+15/+17	+20/+22	+30/+32	+40/+42	+45/+47	+50/+52	+55/+57	84	84.2	84.5	84.7	85	86	87	88	89	90	92	93.8
Heterohelix planata	2.0	2.2	1.1	x		0.3	0.9	x	0.6	x		1.0	0.4	x	0.3	x	1.5				
H. globulosa	57.0	41.6	7.9	15.8	8.9	3.9	2.4	2.1	1.2	2.4	4.7	5.4	1.8	2.6	1.9	2.8	6.1	2.4	1.8	1.3	
H. pulchra	3.4	2.5	1.1	1.0			0.3	0.3													
H. glabrans	0.7	1.3	0.7	0.3	x																
H. labellosa	2.0	0.9	1.1				2.0														
H. navarroensis	9.9	9.5	4.5	6.0	5.4	1.0		0.3	0.9	1.6	0.7	2.4	0.7	1.5	1.6	0.9	4.2	1.2	5.1		
Pseudoguembelina kempensis	0.7	0.6	0.7																		
P. costulata	1.0	0.6	x	0.3																	
Globigerinelloides yaucoensis	0.3	0.6	2.3		0.4	0.3	0.3	x	x	0.8	x		x	x	x	x		0.3	0.2	0.3	
G. prairiehellensis	2.0	1.3	1.5	0.3	x		0.6	x	x				x	0.4			1.5	0.3	0.5		
G. volutus	0.7	1.6	1.1	0.3	0.4		x	x	x	1.2	x	0.7	x		0.3		1.1				
G. subcarinatus	0.3	1.3	0.4																		
Hedbergella monmouthensis	4.1	4.7	1.5	3.0	1.9	0.3	0.3	x	0.3	1.2	0.4	0.7	x	1.1	0.6	x	0.4	0.3			
H. holmdelensis	1.7	2.3	1.1	1.3	3.1	0.6	x	0.3	x	1.2	x	0.3	x		0.3	x	1.5				
Globotruncanella caravacaensis	1.0	0.9	x	x		0.3	x	x	0.6	x	0.4	x	x		0.3	0.3					
G. minuta	x	0.3	x	0.7	1.9	0.6	x	x	x	x	x										
CRETACEOUS	87.7	75.2	26.9	10.0	48.24	28.3	6.9	3.0	3.5	9.3	6.6	13.2	3.3	5.8	6.1	4.5	17.3	4.5	3.3	1.6	
Total number counted	293	293	264	298	257	307	334	334	342	246	273	295	271	272	310	317	262	331	387	307	304

The *Parasubbotina pseudobulloides* Biozone defines the interval between the *P. pseudobulloides* FAD and *G. compressa* FAD (Blow, 1979; Molina and others, 1996). This biozone is well established and has been used in most of the classical biozonations. Recently, however, the FAD of *P. pseudobulloides* has been argued to be diachronous (MacLeod and Keller, 1991a,b) and hence Canudo and others (1991) use the LAD of *P. longiapertura* as an alternative datum event. Because this alternative also has taxonomic and biostratigraphic problems, we decided to follow the classical biozonation of Bolli (1966). The lower part of this zone is also characterized by the recurrence of planktic foraminifera that reach again larger sizes and can be found in the fraction larger than 150 microns.

EXTINCTION PATTERN

The upper Maastrichtian assemblages from the Aïn Settara section are well diversified (Figs. 3 and 4) and are quantitatively dominated by small biserial species (heterohelicids and pseudguembelinids), specially *Heterohelix globulosa* (approximately 50% in abundance) and *Heterohelix navarroensis* (15%) and, in lesser quantities, *Heterohelix planata*, *Heterohelix pulchra*, *Heterohelix labellosa*, *Heterohelix glabrans*, *Pseudoguembelina costulata* and *Pseudoguembelina kempensis* (Fig. 5). The triserial species (guembelitriids) are common at Aïn Settara, with *Guembelitria cretacea* being generally more abundant than *Guembelitria trifolia*. Planispiral (globigerinelloids) and simple trochospiral (hedbergellids and globotruncanellids) species are also common, namely *Globigerinelloides yaucoensis*, *Globigerinelloides prairiehillensis*, *Globigerinelloides volutus*, *Globigerinelloides subcarinatus*, *Hedbergella holmdelensis*, *Hedbergella monmouthensis*, *Globotruncanella caravacaensis* and *Globotruncanella minuta*. These taxa are all relatively small and morphologically simple, indicating that the Maastrichtian assemblages at Aïn Settara are quantitatively dominated by cosmopolitan species.

Conversely, large, complex and tropical-subtropical taxa are less abundant than the cosmopolitan ones, but they dominate in number of species. Simple and double-keeled trochospiral species (globotruncanids, abathomphalids) are generally rare, although some species such as *Globotruncana arca*, *Globotruncana aegyptiaca* or *Globotruncanita fareedi* are quite common. Rugose trochospiral (rugoglobigerinids and plummeritids) species, such as *Rugoglobigerina reicheli*, *Rugoglobigerina rugosa*, *Rugoglobigerina macrocephala* and *Plummerita hantkeninoides*, are more common than the keeled faunal group. The complex biserial (pseudotextularids) species, such as *Pseudotextularia nutalli* and *Pseudotextularia elegans*, are also common. Other species recorded are rare and belong to keeled high trochospiral (contusotruncanids) species, tubulospinose (schackoinids) species and complex biserial and multiserial (planoglobulinds, racemiguembelinids and gublerinids) species.

The classic index species *A. mayaroensis* is very rare in the uppermost Maastrichtian and is apparently absent above meter 65, although there is an uncertain recurrence in the uppermost Maastrichtian sample (Figs. 3 and 4). The absence of a deep-dwelling species such as *A. mayaroensis* could be due to a sea level fall that prevented this species
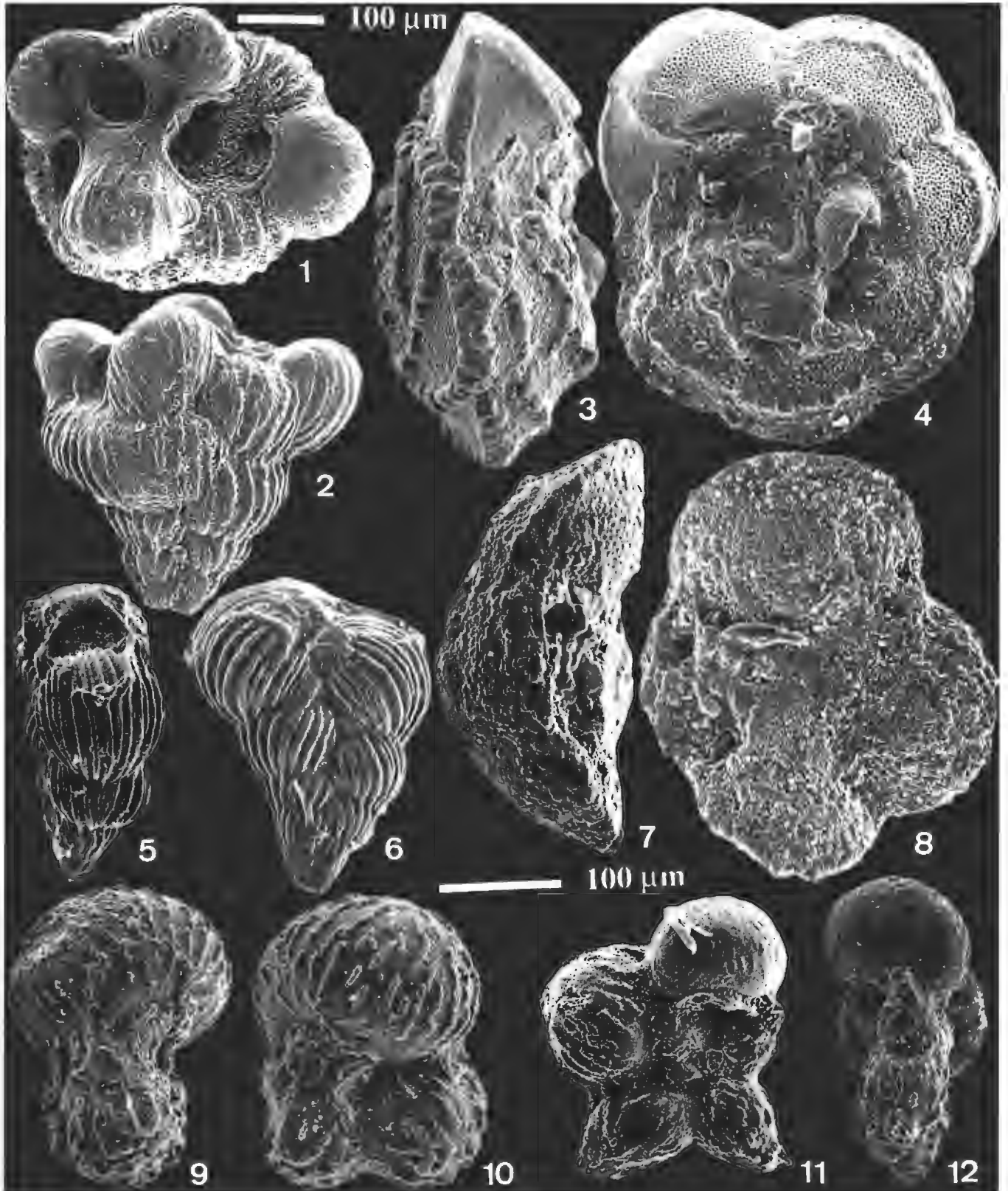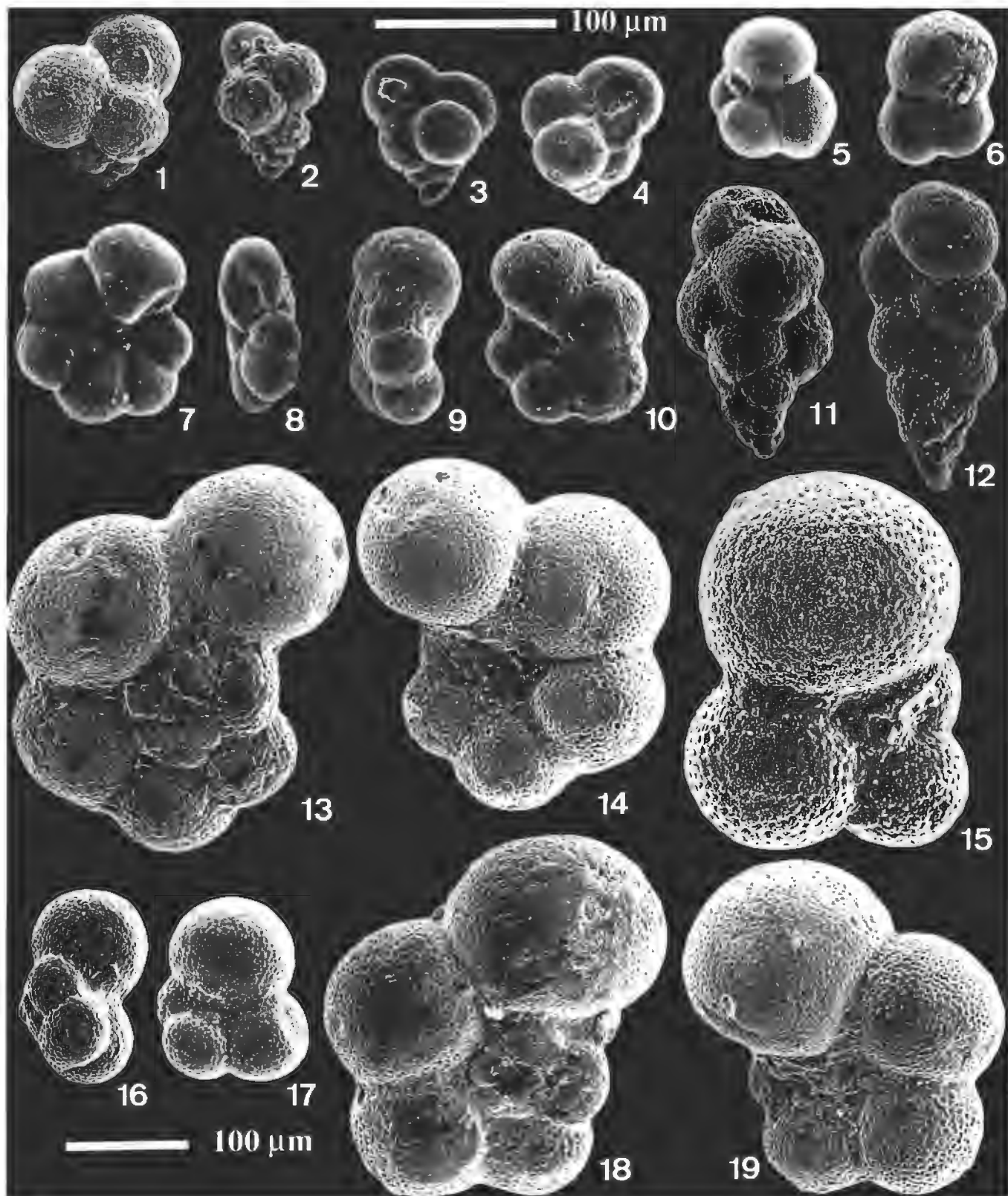
PLATE 1

SEM micrographs of some examined Upper Maastrichtian species. Upper scale bar corresponds to micrographs 1 and 2. Lower scale bar corresponds to the rest of the micrographs. **1** and **2** *Racemiguembelina powelli* Smith and Pessagno, 82.5 sample. **3** and **4** *Globotruncana arca* (Cushman), −0-3 sample. **5** and **6** *Pseudoguembelina costellifera* Masters, −0-3 sample. **7** and **8** *Globotruncanella pschade* (Keller), −0-3 sample. **9** and **10** *Rugoglobigerina macrocephala* Brönnimann, −0-3 sample. **11** and **12** *Plummerita hantkeninoides* (Brönnimann), 82.5 sample.

PLATE 2

SEM micrographs of some examined Lower Danian species. Upper scale bar corresponds to micrographs 1 to 12. Lower scale bar corresponds to the rest of the micrographs. **1** *Guembelitria trifolia* (Morozova), 82.5 sample. **2** *Guembelitria cretacea* Cushman, 88 sample. **3** and **4** *Globoconusa conusa* Khalilov, +20+22 sample. **5** *Globoconusa fodina* (Blow), +50+52 sample. **6** *Globoconusa minutula* (Luterbacher and Premoli Silva), 86 sample. **7** and **8** *Parvularugoglobigerina longiapertura* (Blow), +30+32 sample. **9** and **10** *Parvularugoglobigerina eugubina* (Luterbacher and Premoli Silva), 86 sample. **11** *Guembelitria irregularis* Morozova, +30+32 sample. **12** *Chiloguembelina morsei* Kline, 90 sample. **13** and **14** *Praemurica inconstans* (Subbotina), 93.8 sample. **15** *Subbotina triloculinoides* (Plummer), STW 97. **16** and **17** *Eoglobigerina simplicissima* Blow, 92 sample. **18** and **19** *Parasubbotina pseudobulloides* (Plummer), 93.8 sample.
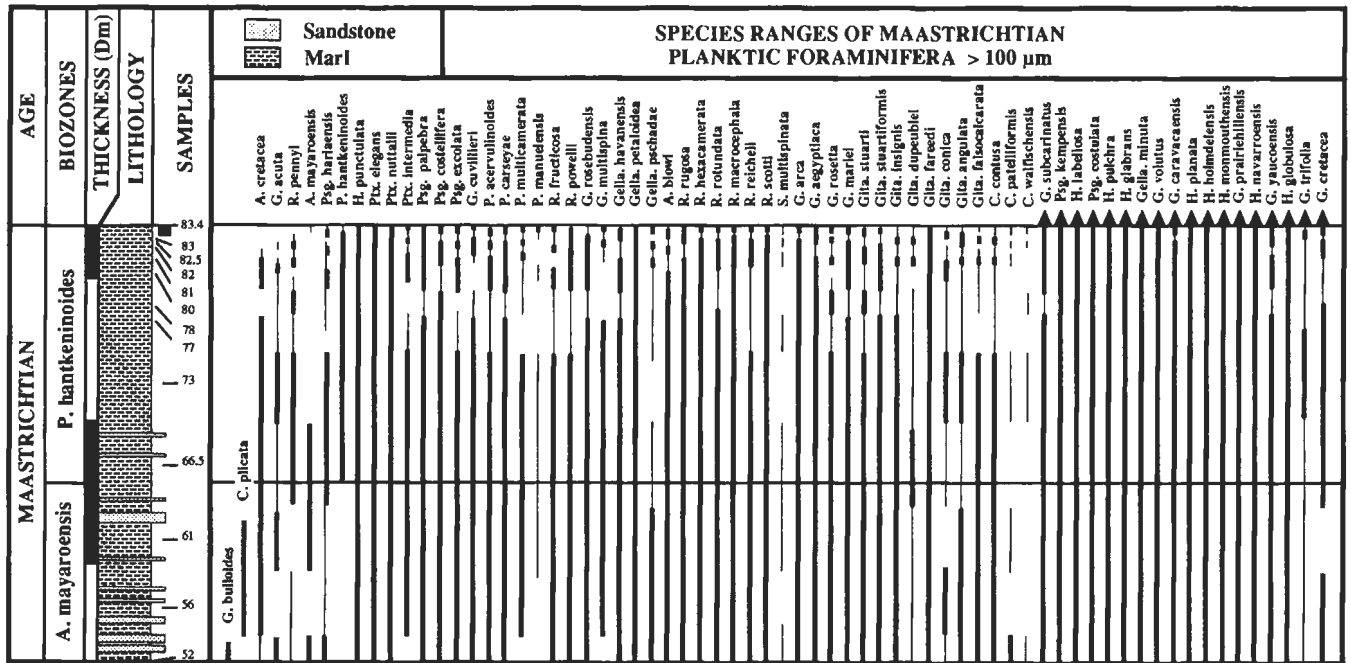
FIGURE 3. Species ranges of planktic foraminifera in the uppermost Maastrichtian at the Aïn Settara section in the size fraction bigger than 100 μm. Thick line means present in the quantitative split, and thin line indicates those found in the residue.

from reproducing in a shallow environment (Canudo and Molina, 1992; Arz, 1996; Arenillas and others, 1996). This possibility could also explain the absence of *Abathomphalus intermedius* and the scarcity of other deep dwellers as well, namely *Gublerina cuvillieri*, *Planoglobulina carseyae*, *Planoglobulina multicamerata*, *Planoglobulina manuelensis*, *Globotruncanita falsocalcarata*, etc.

The stratigraphic distribution of the assemblages within the upper Maastrichtian indicated only small changes with most of the species present in the *A. mayaroensis* and *P. hantkeninoides* Biozones. Environmental conditions must have been quite stable because very few species disappeared within the interval from the middle part of the *A. mayaroensis* Biozone to the K/P boundary (Arz, 1996). Extinct species include *Globotruncana bulloides* and *Contusotruncana plicata* in the *A. mayaroensis* Biozone and *Gublerina acuta*, *Archaeoglobigerina cretacea* and *Rugoglobigerina pennyi* in the upper part of *P. hantkeninoides* Biozone. These pre-K/P disappearances could be either the result of a slight acceleration of extinctions in the terminal Maastrichtian, a normal process of background extinction or the remaining Signor-Lipps effect.

Since *P. hantkeninoides* is the only new species in this interval, it is evident that extinctions were more frequent than new appearances in the late Maastrichtian (Fig. 3). Quantitative study within the uppermost Maastrichtian also shows little variation among the relative abundance of the different species (Fig. 5). The total percentage of population reduction at the K/P boundary is approximately 20% (counted in the size fraction larger than 63 microns), but they represent about 68% of the species. Our study of the 66 species identified in uppermost *Plummetita hantkeninoides* Biozone shows that 45 disappear at a level coincident with the layer that constitutes the K/P boundary. The extinct taxa

are the large and complex forms adapted generally to deep water environments (Hart, 1980; Keller, 1988).

The sudden extinction not only coincides with the layer that characterizes the K/P boundary, but it also appears at the level that shows an Ir anomaly and Ni-spinels (Dupuis and others, in press). We were able to establish this by high resolution study of the uppermost Maastrichtian and lowermost Paleogene samples with special attention to those closest to the boundary layer. This methodology is necessary to minimize the Signor-Lipps effect, because the rare species could appear to become extinct before their real moment of extinction. The stratigraphic ranges of some large, complex, tropical and deep-dwelling forms are apparently discontinuous in the terminal Maastrichtian, but most of them are present up to the K/P boundary. Our data indicate that extinction affected the following genera: *Globotruncana*, *Globotruncanita*, *Contusotruncana*, *Abathomphalus*, *Rugoglobigerina*, *Plummerita*, *Schackoina*, *Pseudotextularia*, *Gublerina*, *Planoglobulina* and *Racemiguembelina*. Based on numerical values of their frequency, the pattern of mass extinction for these genera can be defined as catastrophic and coincident with the K/P boundary. In addition, the K/P extinction event affected 66% of the pseudoguembelinid species, 60% of the globotruncanellid species, 33% of the globigerinelloid species and only 14% of the heterohelicid species (Tables 1 and 2).

In the lowermost Danian, a total of 18 species are found that could be considered possible Maastrichtian survivors, because the section, except for the lowermost 5 centimeters of the Danian, shows almost no evidence of reworking such as current structures or other forms of displacement. We do not consider this of significance, taking into account that the *G. cretacea* biozone is about 50 centimeters thick. To eliminate the potential problem of reworking, when a method-
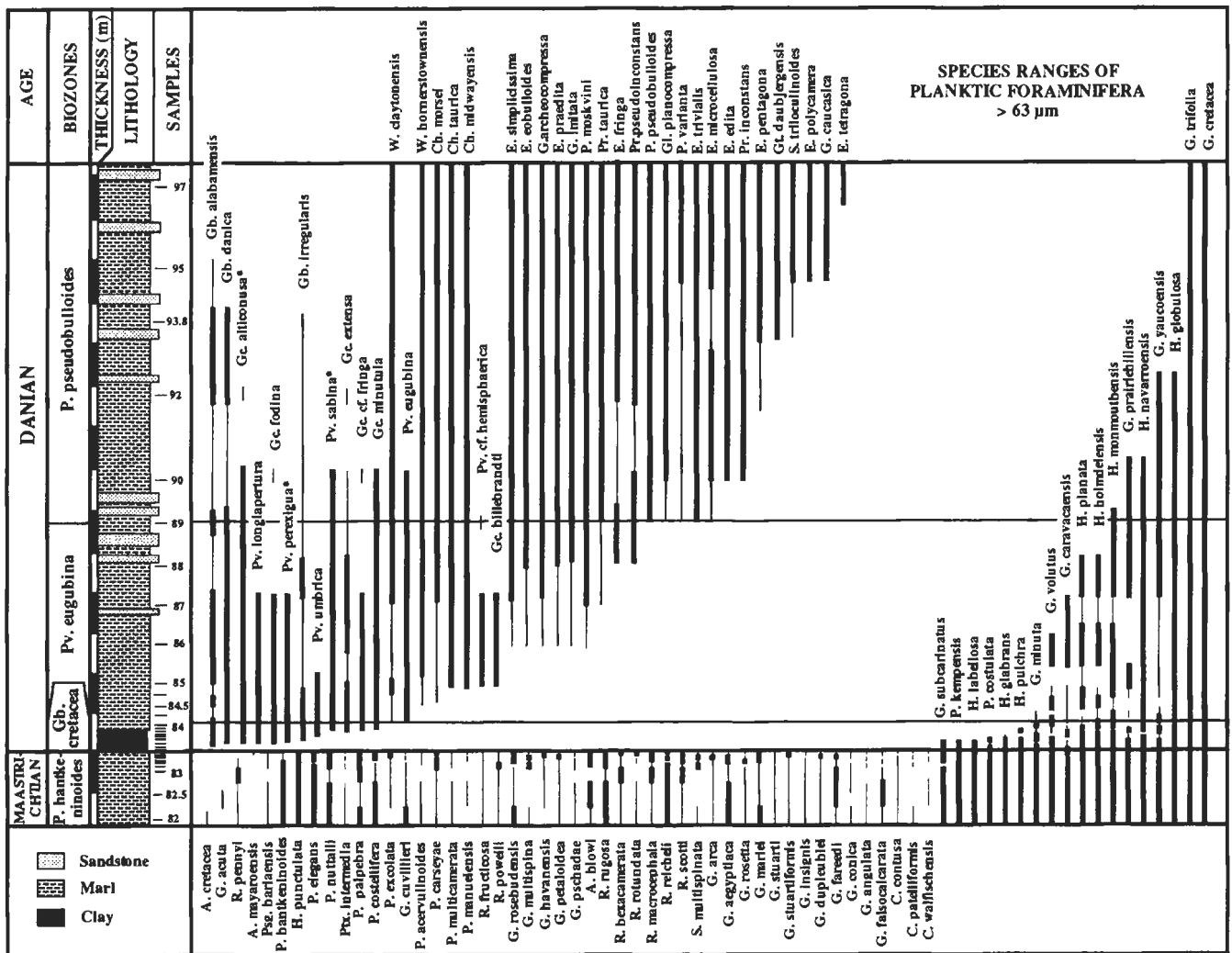
FIGURE 4. Species ranges of planktic foraminifera across the K/P boundary at the Aïn Settara section in the size fraction greater than 63 μm. Thick line means present in the quantitative split and, thin line indicates those found in the residue.

ology of high resolution sampling is used, we considered the isolated and differently preserved specimens in a sample as very probably reworked, and we therefore did not list them. The 18 taxa considered as possible Maastrichtian survivors are cosmopolitan, small and generally surface dwellers that declined gradually within the early Danian, except for *Guembelitria trifolia* and *G. cretacea* which are recorded at still younger levels and become extinct above the interval studied (Fig. 4). The "survivor fauna" is dominated by guembelitriids, with a lower abundance of heterohelicids, hedbergellids and globigerinelloids. At Aïn Settara, the guembelitriids are much more abundant in the lower part of the *G. cretacea* Biozone than in the upper Maastrichtian (Figs. 5 and 6), whereas, the rest of the possible survivor species are less abundant in the lowermost Danian than in the Maastrichtian (Fig. 6). Only *Hedbergella holmdelensis*, *Hedbergella monmouthensis* and *Heterohelix globulosa*, which dominated the uppermost Maastrichtian planktic foraminiferal populations, are initially as abundant in the lowermost Danian as in the Maastrichtian.

The pattern of extinction of the remaining "survivor fau-

na" is as follows: six species (*G. subcarinatus, Psg. kempensis, H. labellosa, Psg. costulata, H. pulchra* and *H. glabrans*) disappear in the *G. cretacea* Biozone; five species (*G. minuta, G. volutus, G. caravacaensis, H. planata* and *H. holmdelensis*) disappear in the *P. eugubina* Biozone; five species (*H. monmouthensis, G. prairiehillensis, H. navarroensis, G. yaucoensis* and *H. globulosa*) disappear in the lowermost *P. pseudobulloides* Biozone; and finally two species (*G. cretacea* and *G. trifolia*) continue higher up into the Danian. The post-K/P extinctions begin with the species belonging to the genera more affected by the K/P extinction event (*Globotruncanella* and *Pseudoguembelina*) and the deep-intermediate dwellers (*H. pulchra, H. glabrans* and *H. planata*).

Our data indicate a simultaneous decline of the survivor species and an increase of the Danian species (Fig. 4, Table 2). The latter are initially opportunistic cosmopolitan species dominated first by guembelitriids and finally by parvularugoglobigerinids and globoconusids (Fig. 6). All these taxa, such as *Pv. longiapertura, Pv. eugubina, Pv. sabina, Pv. perexigua, Globoconusa fodina* and *Globoconusa alticon-*
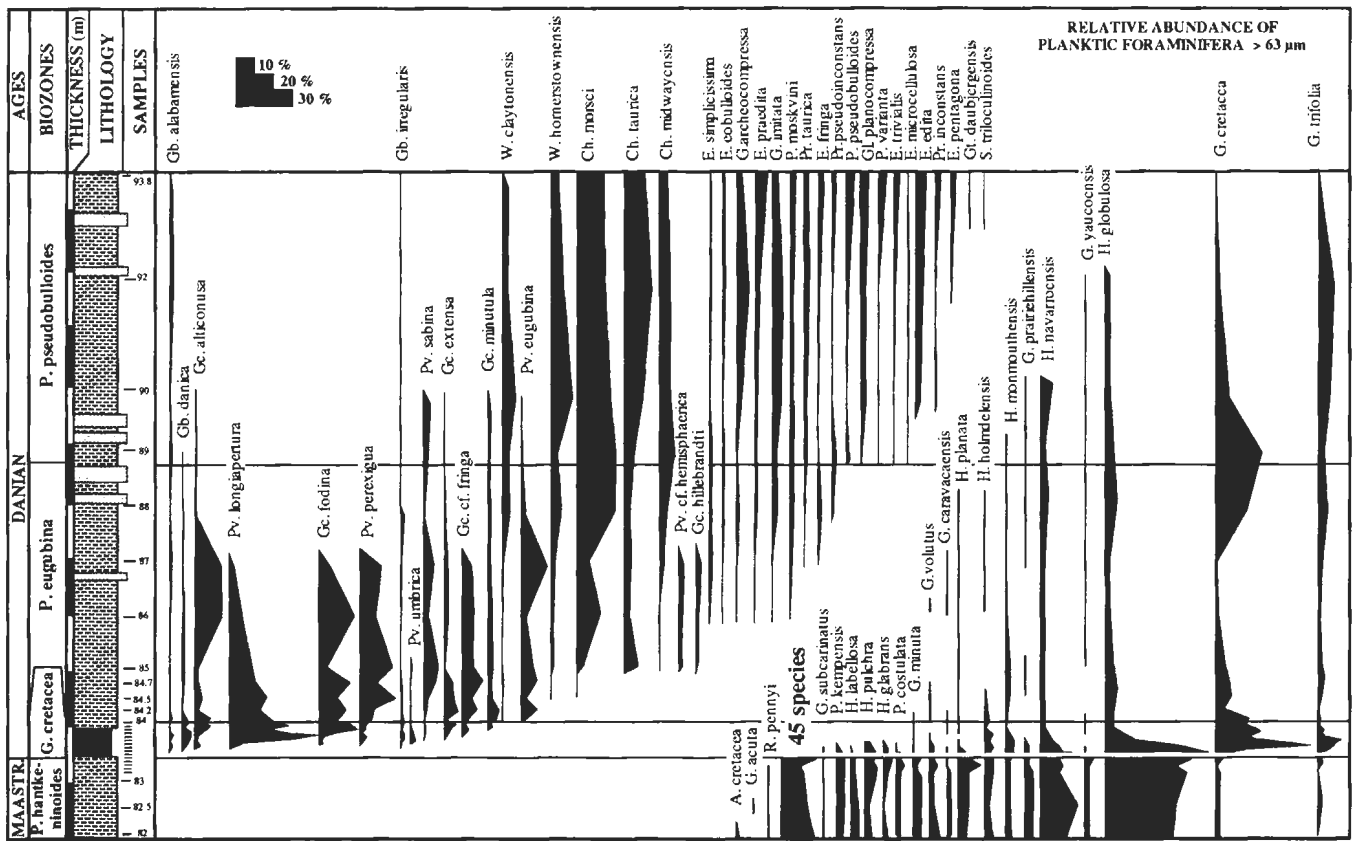
FIGURE 5. Relative abundance of planktic foraminifera species across the K/P boundary at the Aïn Settara section in the size fraction bigger than 63 μm.

usa, are small cosmopolitan surface dwellers that originate in the G. cretacea and Pv. eugubina Biozones and are short lived, becoming extinct in the lower part of the P. pseudobulloides Biozone. Biserial species, such as Woodringina hornerstownensis, W. claytonensis, Chiloguembelina morsei, Ch. taurica and Ch. midwayensis, became dominant after the disappearance of most of parvularugoglobigerinids and globoconusids (Fig. 6). New species continued to evolve across the Pv. eugubina–P. pseudobulloides Biozone boundary where they reached normal size and began to colonize the intermediate and deep environments. These new species include taxa with a perforate, cancellate wall texture (Eoglobigerina, Parasubbotina, Subbotina and Praemurica) and a perforate, smooth wall texture (Globanomalina). These newly evolved Danian species increase in abundance across the P. pseudobulloides Biozone, although these new Danian assemblages continue being largely dominated by chiloguembelinids and woodringinids at least up to the top of the section (Fig. 6).

DISCUSSION

The debate concerning planktic foraminiferal extinction models across the K/P boundary is still controversial and reflects mainly the different methodologies used to obtain the data and the different interpretations of these data (Molina, 1994, 1995, 1997). The earliest studies of the K/P transition (Bolli, 1966) were carried out on scattered samples. In other cases, when K/P-sections were sampled in detail,

the real pattern of extinction could not be established because of hiatuses (MacLeod and Keller, 1991a). In all these cases, the results provided questionable catastrophic patterns of extinction (MacLeod and Keller, 1991a,b). In order to establish the true magnitude of the extinction, a suitable section and appropriate methodology, including detailed sampling, are necessary.

The continuity and thickness of the K/P section are the two most important factors. When Alvarez and others (1980) proposed the impact hypothesis which offered a mechanism to explain the cause of the Cretaceous-Paleogene extinction, their concept was based mainly on the Gubbio (Italy) section which was initially studied in detail by Luterbacher and Premoli-Silva (1964). However, the Italian section was too condensed to establish the real model of extinction (Arenillas, 1998). At present, El Kef, Elles and Aïn Settara (Tunisia) and Agost, Caravaca and Zumaya (Spain) are considered some of the most expanded and continuous sections known world wide (MacLeod and Keller, 1991a,b) and, thus, these sections may serve for further analysis of the pattern of planktic foraminiferal extinction. Other factors also had to be taken into consideration: the section must be neither too shallow (to have a diversified planktic fossil record) nor too deep (to avoid dissolution effects) and located in a region of low paleolatitudes where the fauna was most diversified.

The Aïn Settara section is suitable for such study because, such as other Tunisian and Spanish sections, it is one of the
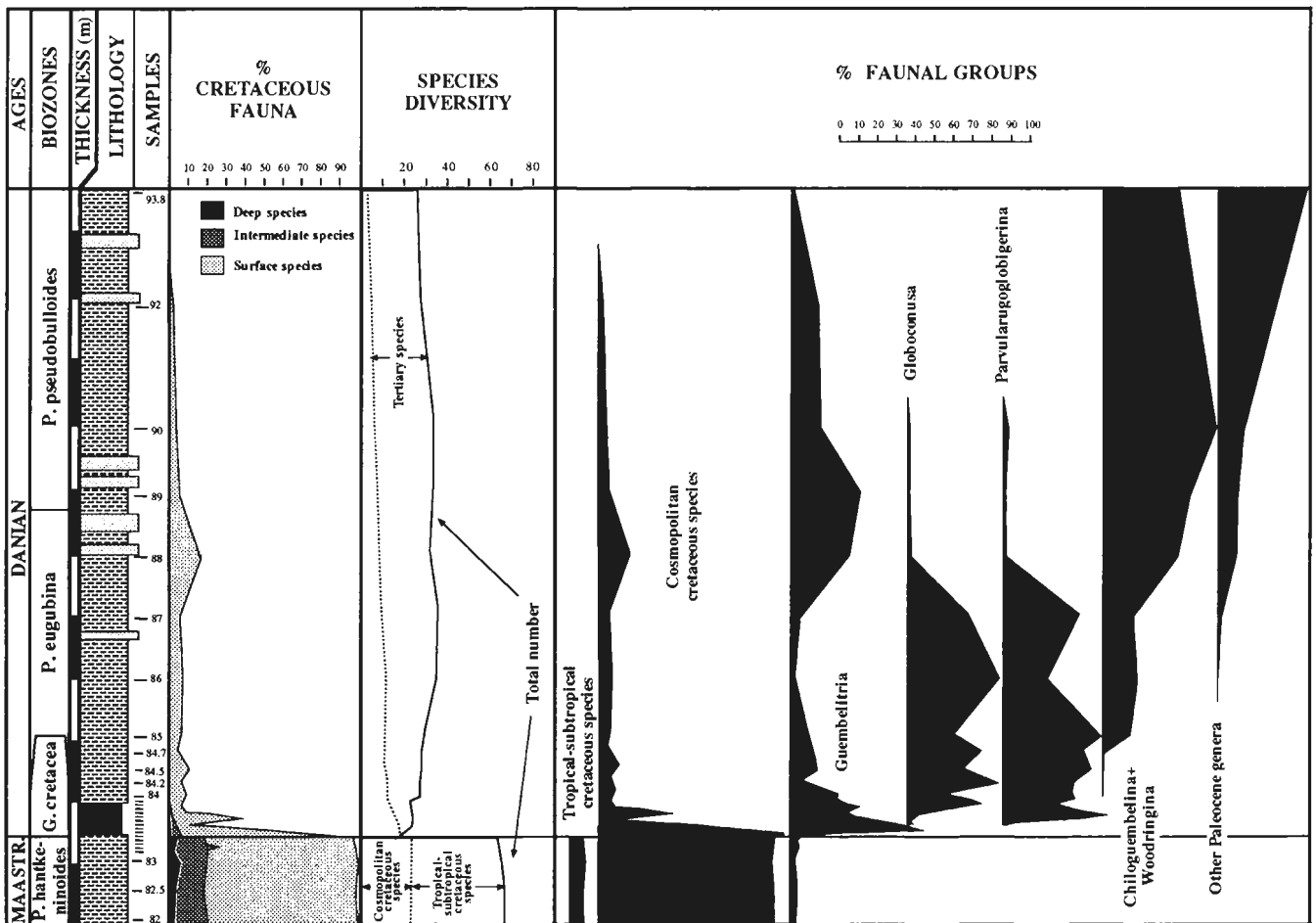
FIGURE 6. Relative abundance of Cretaceous planktic foraminiferal fauna, species diversity and planktic foraminifera faunal groups across the K/P boundary at the El Kef section in the size fraction bigger than 63 μm.

most expanded marine sections known to date (Dupuis and others, in press). The section is comparable to the El Kef stratotype or Elles sections in Tunisia and is more expanded than Agost, Caravaca and Zumaya in Spain (Keller, 1988; Keller and others, 1995, 1998; Molina and others, 1998). All the planktic biozones have been found, and the pattern of origination of the new Danian species is gradual and similar to the pattern identified at El Kef, Elles, Agost, Caravaca and Zumaya. These two criteria indicate that the Aïn Settara is a very continous section. The Aïn Settara section is rich in planktic foraminifera and, therefore, provides a very good opportunity to test the extinction patterns of Maastrichtian planktic foraminifera and the subsequent evolution of Danian species. The methodology used is based on high resolution sampling, quantitative study, and thorough scanning of the residue to find rare species. For these reasons, we think that the results of our study help to elucidate the controversy about whether the mass extinction across the K/P boundary was catastrophic or gradual.

The paleontological controversy about the K/P event originated in the last decade between Smit and Keller and is centered on two relevant aspects: the pattern of the extinction below the K/P boundary and the surviving Maastrichtian species that extend into the Danian. Smit (1977, 1979,

1982, 1990) studied expanded sections (Caravaca, Agost and El Kef), detailed the planktic foraminiferal pattern of extinction across the K/P boundary, and developed the idea that the asteroid impact event at the K/P boundary suddenly exterminated all but one species (G. cretacea). Although he took closely spaced samples across the K/P boundary, he concluded that the extinction of planktic foraminifera was abrupt without any previous warning in the sedimentary record (Smit and Hertogen, 1980). Smit assumed this extinction model based mainly on a taphonomic interpretation whereby Maastrichtian specimens present above the K/P boundary were considered to be reworked. These data were questioned by Keller (1988) who believed that the evidence shows that species extinction extended across the K/P boundary at El Kef with 14 species disappearing just below the boundary and 10 species surviving well into the Danian. These results suggested that the extinctions appear unrelated to an impact event (Keller, 1989a,b). However, she also based her gradual extinction model on a different taphonomic interpretation.

Similar gradual patterns of disappearance have been described in other continuous sections such as Agost and Caravaca in Spain (Canudo and others, 1991) and Ben Gurion in Israel (Abramovich and others, 1998). However, further

studies in the Agost section (Pardo and others, 1996) argued in favor of a less gradual pattern of extinction, and Molina and others (1996) emphasized that the main pattern of extinction was very sudden and catastrophic because only a few species disappeared within the terminal Maastrichtian. These findings were in contrast to those discussed for the sections at El Kef (Keller, 1988; Keller and others, 1995) and the Brazos River (Keller, 1989a,b). At Aïn Settara (Figs. 5 and 6, Table 1) and other low latitude sections such as Elles, Agost and Caravaca (Molina and others, 1996, 1998; Arenillas and others, 1998; Arz and others, 1999b), our quantitative data do not show noticeable changes in the terminal Maastrichtian, and no large species decrease in abundance. Few local quantitative changes prior to the K/P boundary were noted in the Spanish sections at Zumaya and Sopelana (Lamolda and others, 1983; Lamolda, 1990) and in the Tunisian section at El Kef (Brinkhuis and Zachariasse, 1988), but these are not significant (Arz and others, 1999a; Arenillas and others, in press).

Keller and others (1995) suggested a more notable gradual pattern of disappearance at El Kef with 24 species (43%) disappearing just below the K/P boundary, 7 species (12%) at the K/P boundary and 24 species (45%) above the K/P boundary. According to the results of the El Kef blind test (Canudo, 1997; Masters, 1997; Olsson, 1997; Orue-Etxebarria, 1997) and our data from the El Kef section, it is evident that the "Signor-Lipps" effect is present in Keller's studies (Arenillas and others, in press). Our data from Aïn Settara indicate that only 5 species disappeared and only 1 appeared in the late Maastrichtian. Nevertheless, only 3 species dissapeared in the upper part of the *P. hantkeninoides* Biozone, compared to 24 species in the study by Keller and others (1995). These data are very similar to the results obtained at Elles, Agost, Caravaca, Zumaya and San Sebastián (Molina and others, 1996, 1998; Arz and others, 1998, 1999a,b; Arenillas and others, 1998; Arz and Arenillas, 1998). The data show such a low decline of the fauna prior to the K/P boundary that the pattern could be interpreted as the normal process of background extinction.

In our opinion, the differences among the patterns of extinction found in all these sections may be primarily due to latitudinal effect. In this since, some authors indicate that the decline prior to the K/P boundary is mainly due to a gradual decrease in temperature at all latitudes across the K/P boundary, beginning below the boundary (Schmitz and others, 1992; Barrera, 1994). Such a temperature decline at the close of the Maastrichtian may explain why the pattern of catastrophic extinction is not evident in higher latitudes, as the cooler waters had different assemblages that apparently were not affected (Keller, 1993; Keller and others, 1993; MacLeod and Keller, 1994). A cooling would also explain why sections of lower latitudinal regions show a more evident pattern of catastrophic extinction (Molina and others, 1996; Pardo, 1996; Pardo and others, 1997; Arz and others, 1998). However, most of the apparent gradual extinction pattern prior the K/P boundary identified in low latitudes (Keller, 1988, 1989a,b, 1996; Keller and others, 1993, 1995) may be further explained by means of the Signor-Lipps effect.

Another factor to be considered is taxonomic assignment; without a standardized taxonomy, there is no reliable way to compare the studies of different authors (Aubry, 1999). However, the taxonomic effect is probably not the cause of the problem. Irrespective of the number of species identified and their taxonomic assignment, the controversy is caused because some authors show that all or nearly all "forms" range to the K/P boundary while others show that a high number of "forms" disappeared below the K/P boundary. The only explanation for these opposing results is the Signor-Lipps effect. Our data from the Aïn Settara section show the disappearances of *G. acuta*, *A. cretacea* and *R. pennyi* in the upper part of the *P. hantkeninoides* Biozone prior to the K/P boundary, and we believe that these extinctions are not significant and could be due to the normal pattern of background extinction or even the remaining Signor-Lipps effect.

To minimize the Signor-Lipps effect in terminal Maastrichtian sediments, we have used high resolution sampling coupled with a thorough search for rare species in all samples and particularly in the highest of the Maastrichtian. This careful methodology has allowed us to establish that 45 species suddenly became extinct at the K/P boundary at Aïn Settara (Figs. 3 and 4). This planktic foraminiferal extinction event affected only about 20% of the specimens in the fraction larger than 63 microns, but about 68% of the species which clearly implicates this as the most important extinction event in the history of planktic foraminifera. This pattern of extinction includes the sudden disappearance of 12 (66%) genera of uppermost Maastrichtian planktic foraminifera. The species that became extinct were the deep dwellers and the majority of the intermediate dwellers, whereas the cosmopolitan surface dwellers suffered less. Perhaps, the cosmopolitan species were less affected in high latitude regions and recolonized the low latitude areas immediately after the impact event (Molina and others, 1996, 1998).

The question of how many species survived the K/P boundary extinction event is still a hotly debated issue. Smit (1982, 1990) suggested that only *Guembelitria cretacea* survived, and Keller (1988, 1989a,b, 1994) and MacLeod and Keller (1994) reported that about 1/3 of the species survived. As pointed out earlier, the assumption that almost all planktic foraminifera became extinct at the K/P boundary was based on a taphonomic interpretation that the specimens found in the basal Danian were reworked. However, it is common to find Maastrichtian specimens in the basal Danian of the Aïn Settara section as well as in other sections worldwide (Maurrasse, 1980; Keller, 1988, 1989a,b; Canudo and others, 1991), however, no simple visual criteria exist for discerning whether they are indigenous or reworked. A suitable methodology, based on isotopic analyses of the most abundant Maastrichtian species present in lowermost Danian sediments, allowed Barrera and Keller (1990) and Keller and others (1993) to suggest that some species present in Danian sediments also have Danian stable isotopic signals which implies that they are true Maastrichtian survivors. A number of the 18 species that we regard as possible survivors include those that have been isotopically analysed by Keller and others (1993, 1995), Huber (1996) and MacLeod and Huber (1996). In contrast, Kaiho and Lamolda (1999), who also have isotopically analysed the possible survivors at the Caravaca section, concluded that they are

reworked. The existence of reworked Maastrichtian specimens is relatively common in the basal samples of the Danian (Huber, 1991, 1996). The criteria used in this paper to determine whether species are possible survivors is based on their consistent presence in several samples and geographic distribution in other sections (Arz, 1996; Molina and others, 1996, 1998; Arz and others, 1999a,b).

We do not consider all Maastrichtian specimens present in earliest Danian samples as survivors. Reworked taxa occur particularly in samples from the basal few centimeters of the *G. cretacea* Biozone, which includes some larger globotruncanids, globotruncanitids and/or other complex Maastrichtian specimens. These specimens are isolated, display different state of preservation, and occur scattered in younger levels. Taxa that appear in several samples and are common have been tabulated as autochthonous in Table 2, excluding those that have different preservation states. Species such us *H. labellosa, Psg. kempensis, Psg. costulata* and *G. subcarinatus* are common only in the first samples of the Danian, precisely where the problems of reworking can be more frequent; for this reason, their status is unresolved and needs further confirmation in other sections.

The data from the Aïn Settara section indicate that, after the K/P boundary event, small species begin to appear following a model of "explosive" adaptive radiation (Fig. 4). This gradual but rapid evolutionary event occurred simultaneously with the gradual decline of possible Maastrichtian survivors. The Danian species were ecologically replacing the Maastrichtian species that were not able to successfully adapt to the new environment (MacLeod, 1993). We surmise that, during the *P. pseudobulloides* Biochron, the evolution of new Danian species began to colonize the vacant intermediate-deep environments, and their tests attained again a larger size. The gradual post-K/P pattern of dual extinction and origination could be interpreted as being related to the long term effect of the extraterrestrial impact (Molina and others, 1996, 1998) as is suggested by the impact hypothesis (D'Hondt, 1994a,b; D'Hondt and others, 1996). Furthermore, assuming that several Maastrichtian taxa survived, biological causes (competition, endemism) are likely to have played a role in the post-K/P extinction and origination (Molina, 1994, 1995; Arenillas, 1996; Arenillas and Arz, 1996).

Perhaps, the few pre-K/P extinctions are only local disappearances and are the product of a Lazarus effect in the Tethyan region caused by global geological changes, such as a decrease in temperature that began in the latest Maastrichtian (Schmitz and others, 1992; Barrera, 1994) which may have been associated with a sea level fall (Brinkhuis and Zachariasse, 1988). The biological constraints that affected the post-K/P assemblages could have been controlled by both terrestrial geological causes and the long term disruptive effect of the extraterrestrial bolide impact. However, we consider that the terrestrial causes do not adequately explain either the catastrophic mass extinction at the K/P boundary or the model of "explosive" adaptive radiation just after the K/P boundary event. It is quite generally accepted that an asteroid impacted the Earth at the K/P-boundary time and that the layer is a record of short and long-term sedimentologic processes that differ depending on the proximity to the impact site (Maurrase and Sen, 1991;

D'Hondt, 1994b; Schmitz, 1994; López-Oliva and Keller, 1996; Arz and others, 1998). Furthermore, the catastrophic mass extinction coincides exactly with the base of the yellow-red layer containing the impact evidence at Aïn Settara (Dupuis and others, in press) and other sections (Molina and others, 1998). For these reasons, we suggest that the pattern of extinction and origination across the K/P boundary is more compatible with the impact hypothesis than other geological causes.

CONCLUSIONS

The Aïn Settara section in Tunisia is one of the most continuous and expanded marine records of the K/P boundary known so far in a pelagic marine environment. The planktic foraminiferal assemblages are very rich, diversified and well-preserved. Six biozones have been recognized across the K/P boundary: *Abathomphalus mayaroensis* Biozone and *Plummerita hantkeninoides* Biozone (late Maastrichtian), *Guembelitria cretacea* Biozone, *Parvularugoglobigerina eugubina* Biozone and *Parasubbotina pseudobulloides* Biozone (early Danian).

Our quantitative study of high resolution sampling across the K/P boundary has allowed us to test the model of extinction in planktic foraminifera at the boundary. The data indicate that the extinction occurred over a short period of time similar to the Tunisian sections of El Kef and Elles and the Spanish sections of Agost, Caravaca and Zumaya. At Aïn Settara only 3 species disappeared within the uppermost Maastrichtian deposits, whereas 45 became extinct precisely at the K/P boundary and 18 apparently crossed the boundary and disappeared in the lowest Danian. The species that became extinct at the K/P boundary only constitute about 20% of the individuals in the population larger than 63 microns, but these 45 species that suddenly became extinct represent 68% of the taxa. This sudden extinction is a catastrophic event that coincides with the layer containing evidence of an asteroid impact. Most of the extinct species are large, complex and low-latitude deeper- to intermediate-dwelling forms, and this event is considered the most important catastrophic mass extinction in the history of planktic foraminifera.

The pattern of sudden extinction is superimposed on a controversial gradual pattern of extinction of 21 species that apparently began in the late Maastrichtian and ended in the early Danian. The Maastrichtian species that seem to have became extinct gradually are small cosmopolitan simple surface dwellers and constitute about 80% of the individuals in the populations. We believe that the sudden catastrophic mass extinction of 45 species in coincidence with the K/P boundary is very compatible with the effect of a large extraterrestrial bolide impact and that the controversial extinction of 18 species in the early Danian could be related to the long term effect of the impact. The other 3 species that disappeared in the late Maastrichtian were probably the result of the normal process of background extinction.

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