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Benthic foraminiferal turnover across the Cretaceous/Paleogene boundary at Agost (southeastern Spain): paleoenvironmental inferences

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Abstract

We studied Upper Cretaceous and Lower Paleogene benthic foraminifera from the Agost section (southeastern Spain) to infer paleobathymetrical changes and paleoenvironmental turnover across the Cretaceous/Paleogene (K/P) transition. Benthic foraminifera indicate uppermost bathyal depths at Agost during the *Abathomphalus mayaroensis* Biochron (from about 400 kyr before the K/P boundary) through the early *Plummerita hantkeninoides* Biochron (about 120–150 kyr before that boundary). The depth increased to middle bathyal for the remainder of the Cretaceous, and remained so for the Danian part of the studied section (*Parasubbotina pseudobulloides* Biochron, at least 200 kyr after the K/P boundary). There were no perceivable bathymetrical changes at the K/P boundary, where ~5% of the species became extinct, and the species composition of the benthic foraminiferal fauna changed considerably. Below the boundary, infaunal morphogroups constitute up to 65–73% of the faunas. Directly above the boundary, in the black clays of the lower *Guembelitria cretacea* Biozone, benthic foraminifera are rare. Several opportunistic taxa (e.g. the agglutinant *Haplophragmoides* sp.) have short peaks in relative abundance, possibly reflecting low-oxygen conditions as well as environmental instability, with benthos receiving food from short-lived, local blooms of primary producers. Above the clays through the end of the studied interval, epifaunal morphogroups dominate (up to 70% of the assemblages) or there is an even mixture or epifaunal and infaunal morphogroups. Infaunal groups do not recover to pre-extinction relative abundances, indicating that the food supply to the benthos did not recover fully over the studied interval (about 200 kyr after the K/P boundary). The benthic foraminiferal faunal changes are compatible with the direct and indirect effects of an asteroid impact, which severely destabilized primary producers and the oceanic food web that was dependent upon them.

Keywords: K/P boundary; benthic foraminifera; paleoenvironment; paleobathymetry; paleoproductivity

1. Introduction

The Cretaceous/Paleogene (K/P) boundary, commonly called the Cretaceous/Tertiary (K/T)

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boundary, marks one of the largest mass extinction events in the Phanerozoic. Most researchers accept that at the time of the mass extinction a large meteorite impacted the Yucatan Peninsula in Mexico, creating the Chicxulub crater (e.g. Alvarez et al., 1980; Smit and Hertogen, 1980; Hildebrand et al., 1991; Fig. 1). Such an impact would have caused major coastal flooding and slumping along the continental margins, explaining sedimentological and mineralogical observations in the North Atlantic and around the Gulf of Mexico (e.g. Norris et al., 2001; Soria et al., 2001), as well as enrichment in Ir and shocked quartz grains in the boundary sediments in terrestrial and marine sections globally (e.g. Alvarez et al., 1980; Smit and Hertogen, 1980; Smit and ten Kate, 1982; Gilmore et al., 1984).

Some researchers invoke alternative or additional causes for the end-Cretaceous mass extinction, such as widespread volcanism (e.g. McLean, 1981, 1985; Officer and Drake, 1983), climate and sea-level changes (e.g. Ginsburg, 1984; Brinkhuis and Zachariasse, 1988), or a combination of these (Hallam, 1987; Keller, 1990; Keller et al., 2001). Recent climate reconstructions (Wilf et al., 2003) suggest global warming, with peak warming about 300–100 kyr before the boundary, followed by cooling during the last 100 kyr of the Mesozoic, and no evidence for either strong cooling or warming after the boundary.

There is no reliable model to predict biotic changes as the result of the impact of a large meteorite and the reverberation of such effects through the global biosphere, and we thus cannot state with confidence whether additional causes are necessary to explain the mass extinction. The main argument against a single causal mechanism for the extinctions are the allegedly gradual or stepwise extinctions prior to the K/P boundary (e.g. Keller, 1989a,b). It is, however, not always easy to compare extinction patterns as observed in the fossil record with true extinction patterns (e.g. Signor and Lipps, 1982), in view of the presence of unconformities, bioturbation, and the observed occurrence of rare species. A less severe extinction, involving rudists (Johnson and Kaufman, 1995) and *Inoceramus* bivalves (MacLeod, 1994), occurred a few million years before the

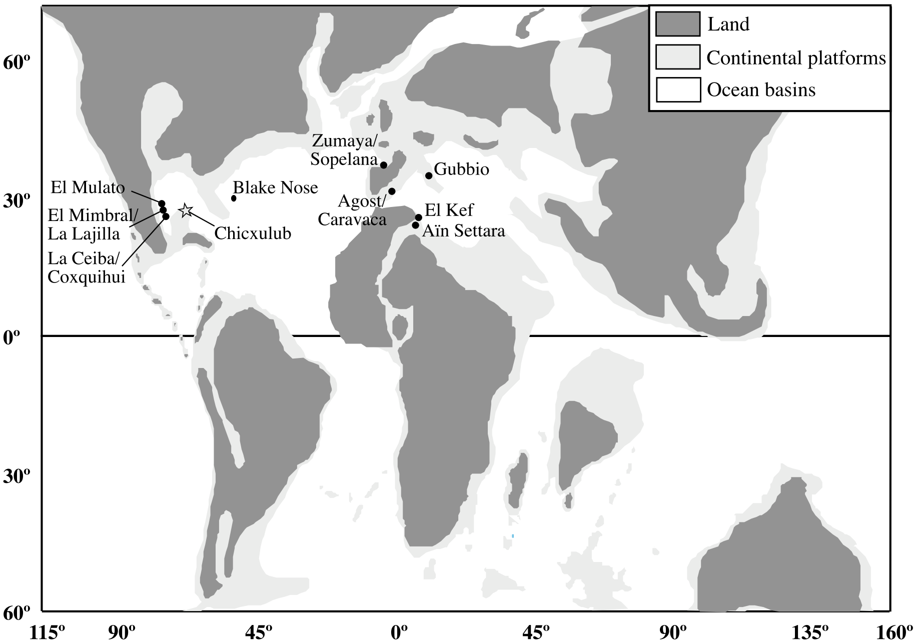

Fig. 1. Paleogeographical distribution of land masses, shallow seas and deep ocean basins at the K/P boundary, showing the Chicxulub structure (Yucatan Peninsula, Mexico) and K/P boundary referred to in the text sections. Modified from Denham and Scotesse (1987).

K/P boundary in the Middle Maastrichtian (e.g. Barrera et al., 1997), but a catastrophic mass extinction pattern at the boundary itself has been demonstrated for such organisms as planktonic foraminifera by most authors (e.g. Molina et al., 1998; Arenillas et al., 2000). In order to document the severity of the mass extinction, we need to obtain more information on its possible selectivity in different floral and faunal groups over different habitats, and to evaluate whether additional, independent causes were implicated in the extinctions, or whether direct and indirect consequences of an impact can explain the observed patterns.

Foraminifera are abundant and well preserved, and are thus an excellent group of organisms to study faunal changes across the K/P transition, as well as to perform detailed biostratigraphical studies. Planktonic foraminifera suffered severe extinction globally across the K/P boundary (e.g. Luterbacher and Premoli-Silva, 1964; Smit, 1990). This extinction was well documented in studies of Tethyan sections in Spain and Tunisia (e.g. Brinkhuis and Zachariasse, 1988; Canudo et al., 1991; Molina et al., 1996, 1998; Kaiho and Lamolda, 1999; Arenillas et al., 2000; Arz et al., 2000).

In contrast, benthic foraminifera, which are used as proxies for paleodepth, ocean productivity and oxygenation (e.g. Van der Zwaan et al., 1999), were not affected by a major, global extinction at the K/P boundary, as reviewed by Culver (2002), and documented by the fact that Cushman (1946) could not differentiate the Danian from the Maastrichtian using benthic foraminifera. Culver (2002) documents that benthic foraminifera were little affected during the mass extinction globally at all depths, in contrast to earlier opinions that shallow-water forms were more seriously impacted by the event than deep-sea forms (e.g. Kaiho, 1992, 1994a; Keller, 1992). Deep-sea benthic foraminifera exhibit a temporary faunal restructuring followed by at least partial recovery, as observed in Spanish (Coccioni et al., 1993; Kuhnt and Kaminski, 1993; Coccioni and Galeotti, 1994) and Tunisian sections (Keller, 1988, 1992; Speijer, 1994; Speijer and Van der Zwaan, 1996; Peryt et al., 2002), as well as in other sections globally (Thomas, 1990a,b; Kaiho, 1992; Culver, 2002).

There have been considerably fewer studies of benthic than of planktonic foraminifera, and few data are available on Upper Maastrichtian through Lower Danian benthic foraminifera from southeastern Spain. A few remarks on K/P benthic foraminiferal assemblages from the Caravaca section in the Betic Cordilleras of southeastern Spain were included in a discussion on planktonic foraminifera (Smit, 1990). The faunas at Caravaca were included in an overview by Keller (1992), and later described in detail by Coccioni et al. (1993) and Coccioni and Galeotti (1994). Faunas from the uppermost Maastrichtian at Caravaca were studied by Widmark and Speijer (1997a,b). There is disagreement as to the paleodepth assignment of this section: it was assigned a middle bathyal depth (600–1000 m) by Coccioni and Galeotti (1994), in agreement with an estimate of ∼800 m by Widmark and Speijer (1997a,b). Keller (1992), however, argued that the paleodepth decreased from upper bathyal in the Maastrichtian to outer neritic at the K/P boundary (600–200 m; Keller, 1992).

The Caravaca section is commonly referred to in biostratigraphical studies, because at that section the earliest Tertiary planktonic foraminiferal association, below the *Guembelitria eugubina* Biozone, was first described (Smit, 1977, 1979, 1982), and so were detailed nannofossil zones (Romein, 1977). In addition, geochemical and stable isotope studies were conducted (e.g. Romein and Smit, 1981; Smit, 1982; Smit and ten Kate, 1982; DePaolo et al., 1983; Shukolyukov and Lugmair, 1998; Arinobu et al., 1999; Kaiho et al., 1999; Mukhopadhyay et al., 2001).

We present a study of benthic foraminifera in the Agost section, about 100 km to the east of the Caravaca section. The sections of Agost and Caravaca have a similar lithology of gray marls and calcareous marls (Canudo et al., 1991), and have been considered as some of the most continuous land-based K/P sections (e.g. Perch-Nielsen et al., 1982). The Agost section was first described by Leclerc (1971), who documented the planktonic foraminiferal faunas and argued that the sedimentation was essentially continuous from Santonian to Eocene. Since then, the Agost section has been studied by numerous authors (e.g. Hillebrandt, 1974; Groot et al., 1989; Smit, 1990; Molina et al., 1996; Pardo et al., 1996) who analyzed the biostratigraphy of planktonic foraminifera. Most of these authors are of the opinion that planktonic foraminifera underwent a catastrophic mass extinction at the K/P boundary (Smit, 1990; Molina et al., 1996, 1998), but some interpret the extinctions as more gradual (Canudo et al., 1991; Pardo et al., 1996).

Benthic foraminifera from Agost were included in the study by Pardo et al. (1996), who observed a lack of severe extinctions of benthic foraminifera and suggested that climatic changes and variations in sea level explain the observed faunal changes. They concluded that paleodepths varied between upper bathyal and outer neritic, similar to depth estimates for nearby Caravaca by Keller (1992). Pardo et al. (1996), however, did not document the taxonomy (their figs. 8 and 9), and they list species with assigned habitats, paleoecology, and upper depth limits (their table 4) without reference to sources to support such assignments. We develop and document a paleobathymetric reconstruction of the uppermost Cretaceous and lowermost Paleogene sediments, describe the benthic foraminiferal turnover across the K/P transition, and infer paleoenvironmental changes.

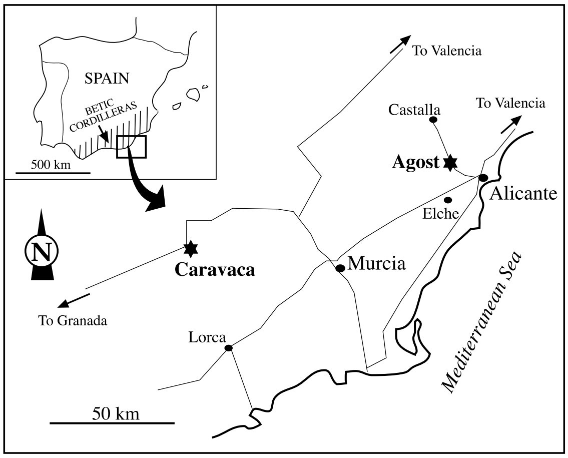

Fig. 2. Location of the Agost section (southeastern Spain).

2. Materials and methods

The Agost section is located in the Betic Cordilleras, southeastern Spain. The outcrop is about 1 km north of Agost village (Alicante region), at km 13 of the road Agost–Castalla (Fig. 2). Agost is ∼100 km to the east of the Caravaca section with a similar lithology (e.g. Canudo et al., 1991). The Maastrichtian sediments consist of pelagic gray massive marls with interbedded calcareous marls; the latter are rare or absent in the uppermost Maastrichtian. These marly sediments, which contain abundant ostracodes and foraminifera, belong to the upper part of the Quipar–Jorquera Formation, originally described by Van Veen (1969). The Quipar–Jorquera Formation is Cenomanian to Eocene in age (Vera, 1983), and shows similar characteristics across the Inner Prebetic.

The K/P boundary lies within Chron 29R (Groot et al., 1989) and is marked by a sharp contact between the Maastrichtian marls and a 12-cm-thick layer of black clays, with a 2–3-mm-thick, red, ferruginous level at its base. This oxidized, Fe-rich level has been called the 'fall-out layer'. It contains goethite and hematite clasts, green (probably glauconitic) clasts, and scarce foraminifera, and it is enriched in Ir, Ni-rich spinels, Co, Cr and sanidine spherules (altered microtektites) (Smit, 1982, 1990). This layer marks the K/P boundary at Agost (Molina et al., 1996). In the black clays the $CaCO_3$ content decreases to less than 1%, there is a shift of bulk $\delta^{13}C$ to more negative values, and there is strong variability in bulk $\delta^{18}O$ values (Romein and Smit, 1981; Smit and ten Kate, 1982; Smit, 1990). Trace element data indicate that anoxic to hypoxic bottom water or pore water conditions occurred, with hypoxia somewhat more extreme at Agost than at Caravaca (Martinez Ruiz et al., 1992, 1999; Kaiho et al., 1999).

The dark clay level is overlain by a 10-cm-thick layer of massive gray clays. Above this level, we identified two dm-thick, tabular bodies of marly limestones, with a dm-thick intercalated layer of calcareous marls. The remainder of the studied section above the K/P boundary consists of massive gray marls containing abundant and well pre-

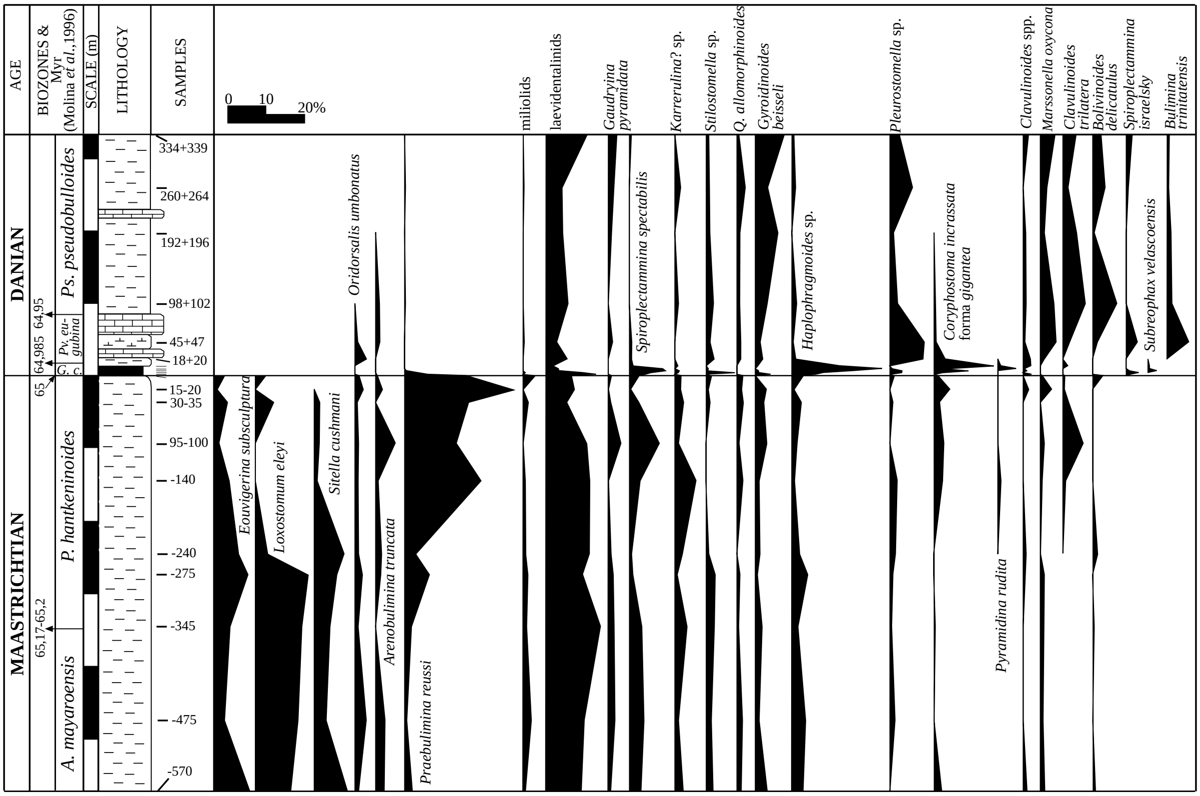

Fig. 3. Occurrence and relative abundance of the most characteristic infaunal benthic foraminiferal species across the K/P transition at Agost. Abbreviation: *G. c.*, *Guembelitria cretacea* Biozone.

served foraminifera, with a 10-cm-thick body of marly limestones 230 cm above the K/P boundary.

For biostratigraphic control we follow Molina et al. (1996), who identified the upper Cretaceous *Abathomphalus mayaroensis* and *Plummerita hantkeninoides* Biozones, and the Danian *Guembelitria cretacea, Parvulorugoglobigerina eugubina*, and *Parasubbotina pseudobulloides* Biozones (Figs. 2 and 3). The time represented in the studied section encompasses about 600 kyr, from 400 kyr before to 200 kyr after the K/P boundary.

We collected 21 samples at decimeter intervals in the upper 6 m of the Maastrichtian and the lower 3.5 m of the Danian, with closer sampling in the uppermost Maastrichtian and the lowermost Danian (Table 1). Samples were disaggregated in water with diluted H_2O_2, washed through a 63-μ sieve, and dried at 50°C. Species richness calculations and quantitative studies were based on representative splits (using a modified Otto micro-splitter) of approximately 200–300 specimens of benthic foraminifera larger than 63 μ. All representative specimens were mounted on microslides for permanent record and identification. Classification at the generic level follows Loeblich and Tappan (1988); when possible, benthic foraminifera were identified at the specific level. The names of the more common species with original authors are listed in Appendix 1. We largely follow the taxonomy of Alegret and Thomas (2001); the Mexican faunas studied by these authors contain around 80% of the benthic foraminiferal species identified at Agost. Appendix 1 includes published references to all species identified. Counts are presented in Table 1.

We consider that the study of the >63-μ fraction is the most appropriate for a detailed analysis of benthic foraminiferal communities; according to Schroeder et al. (1987), the study of larger-size

Table 1
Benthic foraminiferal species counts in the studied samples from Agost

	A−570	A−475	A−345	A−275	A−240	A−140	A−95−100	A−30−35	A−15−20	A−0−2
Alabamina wilcoxensis			2		3	1		1		1
Allomorphina polonica						2		2		
Allomorphina velascoensis									1	
Allomorphina sp.								1		
Ammodiscus cretaceus			1						3	
Ammodiscus latus			1							
Ammodiscus macilentus	2					1	1	1	1	
Ammodiscus sp.		1						1		
Angulogavelinella avnimelechi						1				
Anomalinoides acutus			4	1	1			3		3
Anomalinoides affinis			1	1	2	2	2	6		5
Anomalinoides ammonoides	5	3	11	7	4	4	8	9	3	4
Anomalinoides rubiginosus							1		2	
Anomalinoides spp.	1	1		1				7		8
Arenobulimina truncata	5	5		3	3	1	12		5	1
Astacolus spp.	5		4	2		2	2	2	4	2
Bathysiphon sp. C		3			1	1	1	1		2
Bathysiphon sp. B		1				1		1		1
Bifarina sp.			1							
Bolivinoides draco			3		1	1	2			
Bolivinoides delicatulus	2		1		3					6
Buchnerina sp.			1		1	1		1		1
Bulimina midwayensis				1						
Bulimina sp.				1						
Buliminella grata		2	8							
Buliminella sp.		5	2		1	2		1		2
Cibicidoides aburdurbensis					3					
Cibicidoides dayi					1					
Cibicidoides ekblomi										1
Cibicidoides hyphalus	9	2		1	2	1	7	9		1
Cibicidoides pseudoacutus	1		2							
Cibicidoides velascoensis						1	2	2	9	
Cibicidoides howelli		1			2	5		2	3	3
Cibicidoides proprius	6	9	13	3	1	9	6	7	5	2
Cibicidoides sp.		1			1	1			4	1
Clavulinoides amorpha	2									
Clavulinoides trilatera						1	12	1	1	
Clavul. trilatera juvenile form								3		1
Clavulinoides sp.				1	1				4	
Coryphostoma decurrens	6				2	1	2	2		4
Coryph. incrassata forma *gigantea*	5		1			5	6	4	12	2
Coryphostoma incrassata	5		18							
Coryphostoma plaitum				1	1					
Coryphostoma sp.		3		4	4	2	2	2		1
Dorothia bulleta			2							
Dorothia pupa					2	1			4	1
Dorothia pupa juvenile form						2				2
Dorothia spp.			1							
Ellipsodimorphina sp.										1
Ellipsoidella sp.		1								
Eouvigerina subsculptura	25	5	15	19	13	10	3	8	1	6
Frondicularia jarvisi	1									
Frondicularia sp.	1						1			1
Fursenkoina sp.				2	2	7		7		8

Table 1 (*Continued*).

	A−570	A−475	A−345	A−275	A−240	A−140	A−95−100	A−30−35	A−15−20	A−0−2
Gaudryina pyramidata	1	4	5	3	1		8	1		1
Gaudryina laevigata	1			1		2	3	1		
Gaudryina spp.		2								
Globulina prisca				1						
Globulina spp.								1		
Globobulimina sp.				1	2					
Glomospira sp.		1								1
Glomospirella grzybowski	3	1	2	3	2				1	3
Guttulina sp.	1	1		1		1	1		1	2
Globorotalites michelinianus	17	17	7	9	4	4				
Globorotalites sp.				1		1				
Gyroidinoides beisseli	9	2	7	1	3	3	7	5	7	
Gyroidinoides depressus	5	4	1	2	1		1		3	4
Gyroidinoides globosus									5	1
Gyroidinoides goudkoffi			5		1		1		5	
Gyroidinoides girardanus								1		
Gyroidinoides subangulatus							1		2	
Haplophragmoides small variant	2	7	4	7	1		1	6	1	8
Haplophragmoides large variant	5	1	1	4	3	1	1			
Hemirobulina sp.							2			
Heronallenia lingulata					2			1		
Heterostomella spp.								2	2	
Karrerulina sp.	5	2	9	1	4	12	2	5	4	4
Laevidentalina spp.	24	20	48	23	22	27	27	13	21	16
Lagena spp.		1	1		2	1	5	1		5
Lenticulina spp.	6	2	14	3	6	8	8	7	13	4
Lingulina sp.						1		1		
Loxostomum eleyi	23	22	40	32	7			12		6
Marssonella indentata			1							
Marssonella oxycona	1	1		2		1	2		4	1
Marssonella oxycona juvenile form	1		2						4	
Marssonella spp.		1								
Neoflabellina delicatissima	3	1	4	1			1			
Neoflabellina sp.						1	1			
Nodosarella sp.						3		3		
Nonionella sp.					1			1		1
Nuttallides truempyi	3	6	5	3	5	5	8	4	6	6
Nuttallinella coronula			1							1
Nuttallinella florealis				1	1		5	6	13	3
Oolina spp.								1		1
Oridorsalis plummerae			6		3		5	1		2
Oridorsalis umbonatus	1	6	4	5	2	2	2	1	6	2
Oridorsalis sp.	2									
Osangularia plummerae	2		1	4		6	1	2	1	9
Osangularia spp.					7				1	
Paralabamina hillebrandti				2						
Paralabamina lunata		3		3	4					
Paratrochaminoides sp.									1	
Pleurostomella sp.		2	1	1	3	5		1		3
Praebulimina reussi	5	1	6	15	6	46	34	41	76	37
Praebulimina sp.		4		6	8		1		6	4
Pseudopolimorphina sp.				1						
Pseudouvigerina plummerae	1	2						6	1	1
Pullenia cretacea			1						1	
Pullenia jarvisi	1		4	2	1	3	2		2	4
Pullenia sp.					1					
Pyramidina sp.		1								

Table 1 (*Continued*).

	A−570	A−475	A−345	A−275	A−240	A−140	A−95−100	A−30−35	A−15−20	A−0−2
Pyramidina rudita						1				
Pyrulina sp.				2	1					2
Pyrulinoides sp.	1		2			3		4		
Quadrimorphina allomorphinoides	1	3	1	1		4	1	4	3	3
Quinqueloculina sp.	1	4	4	3	1	1		3		7
Ramulina spp.			2				2			
Recurvoides sp.									1	
Reophax spp.										1
Repmanina charoides				2	7			1		2
Reussoolina sp.							1			
Rhizammina sp.		1				1				1
Saccammina placenta	1		4			1				1
Saccammina spp.	2		3					1		
Saracenaria sp.		1		2		2	2		2	
Sculptobaculites sp.							1			
Sitella cushmani	21	6	13	14	15	2	4	4		
Sliteria varsoviensis			1			3		1		1
Spiroplectammina spp.		1			1			1		
Spiroplectammina spectabilis	7	7	9	2	1	6	18	6	1	6
Stensioeina beccariiformis	9	6	6	6	2	3	5	5	7	1
Stensioeina excolata	6	6	7	4	3	4	2	2	3	1
Stilostomella sp.	4	3	6	5	1			2	1	2
Subreophax sp.		1		1						
Valvalabamina lenticula		1		3	2				1	2
Vulvulina sp.		2								
Vaginulina trilobata	1		2							
Total	257	200	332	232	192	230	236	242	268	231

	Red layer	A+1+2	A+2+3	A+3+4	A+8+10	A+18+20	A+45+47	A+98+102	A+192+196	A+260+264	A+334+339
Alabamina wilcoxensis	1	1			1		4			9	
Ammodiscus cretaceus		1	4	3	1						
Ammodiscus macilentus				1				1			1
Ammodiscus sp.		1	7	3		1		1		1	
Angulogavelinella avnimelechi						4	5				2
Angulogavelinella sp.					2						
Anomalinoides acutus		6	11	18	3	8	12	11	5		
Anomalinoides aegyptiacus							7	4	11	12	5
Anomalinoides affinis					1	3		4			
Anomalinoides ammonoides	5		5	2		6	3	10	8	6	4
Anomalinoides cf. *susanaensis*							1				
Anomalinoides spp.	2	2	3	2		3	3	4		6	
Aragonia velascoensis							2			1	
Arenobulimina truncata							5	4			
Astacolus spp.				1		1	3				
Bathysiphon sp. A								1			
Bathysiphon sp. C		2	1	9	2	1					1
Bathysiphon sp. B					1		1	1			1
Bolivinoides draco				1							
Bolivinoides delicatulus							6	23	1	12	6
Buchnerina sp.								1		1	
Bulimina midwayensis										1	1
Bulimina trinitatensis							22	4	4	1	1
Bulimina sp.			1				1			3	1
Buliminella grata								1			1
Buliminella sp.											1
Cibicidoides aburdurbensis			5	2							

Table 1 (*Continued*).

	Red layer	A+1+2	A+2+3	A+3+4	A+8+10	A+18+20	A+45+47	A+98+102	A+192+196	A+260+264	A+334+339
Cibicidoides dayi									1	3	1
Cibicidoides ekblomi					1	12	16	30	12	26	9
Cibicidoides hyphalus	1	3		3		5	12	17	29	20	9
Cibicidoides velascoensis		1		2		3	6		3		2
Cibicidoides howelli			2	1	1	5				8	1
Cibicidoides proprius				27	4	11	9	4		9	7
Cibicidoides sp.	1	8	1	2		15	2	1	1	4	
Clavulinoides amorpha						2	1	2			
Clavulinoides trilatera					2		6	10	5	3	7
Clavulinoides trilatera juvenile form								9	7	3	2
Clavulinoides sp.	1		2	1	3	3			3		4
Coryphostoma decurrens	1						2				
Coryph. incrassata forma *gigantea*		3	18	9	24	7	2	1			
Coryphostoma incrassata	1	4				2		3	4	4	
Coryphostoma plaitum	2					2			2	3	2
Coryphostoma sp.	1		3	3		5	6	1	6	2	3
Dorothia bulleta											3
Dorothia bulleta juvenile form											3
Dorothia pupa							8	4			
Dorothia pupa juvenile form								5			
Dorothia spp.									2		
Ellipsoidella sp.	3										
Eouvigerina subsculptura		3									
Frondicularia sp.								1		1	
Fursenkoina sp.		3	1							2	
Gaudryina pyramidata							3		2	3	6
Gaudryina spp.							2				
Glandulina sp.							1	3			
Globulina prisca								1			
Globulina spp.						1			6		1
Globobulimina sp.							1			1	
Glomospirella grzybowski			2	10	9			1	4	9	1
Guttulina sp.	1					1	1	4			1
Globorotalites michelinianus						19	49	24			
Globorotalites sp.					3	2	3	17	18	5	
Gyroidinoides beisseli	2	2	3		2	5	5	11	20	13	22
Gyroidinoides depressus	1		4	8	4	5	6		1	13	5
Gyroidinoides globosus			2	1		1	4	2	3		7
Gyroidinoides goudkoffi		4									3
Gyroidinoides girardanus	1		1	2			3		2	2	1
Gyroidinoides subangulatus						1					
Gyroidinoides sp.		1	1	1				2		1	
Haplophragmoides small variant	2	8	10	65	13	1	1			2	
Haplophragmoides large variant	1	2	26	6	6	2		5		2	1
Heronallenia lingulata										1	
Heterostomella spp.			1								
Hyperammina sp.		1	3		1						
Karrerulina sp.		1	2		1			3		4	
Laevidentalina spp.	6	12	8	11	3	14	10	19	17	17	31
Lagena spp.		1			1		2	3	2	3	3
Lenticulina spp.	1	2	3	1	6	7	15	8	6	2	11
Lingulina sp.										1	
Marssonella indentata							3				
Marssonella oxycona						3	11	7	4		7

Table 1 (*Continued*).

	Red layer	A+1+2	A+2+3	A+3+4	A+8+10	A+18+20	A+45+47	A+98+102	A+192+196	A+260+264	A+334+339
Marssonella oxycona juvenile form							7	6		5	4
Neoflabellina sp.							1	1	1		
Nodosarella sp.						1					
Nonionella sp.						1		1	1	7	
Nuttallides spp.								2			1
Nuttallides truempyi			2				2	2	8	5	26
Nuttallinella coronula		1									
Nuttallinella florealis								1			9
Nuttallinella spp.					2		3	8	8	10	
Oolina spp.						1					2
Oridorsalis plummerae	1				1	5	8	3	10	6	
Oridorsalis umbonatus						7	2				
Oridorsalis sp.					3	2			1	2	
Osangularia plummerae	1		2		4	9	6	5	6	6	9
Osangularia spp.		6	3	4	1		3	3	2	4	7
Paliolatella sp.							2		1		
Paliolatella orbygniana									2		1
Paralabamina lunata				5		4	1	2	7	4	
Paratrochaminoides sp.								1			
Pleurostomella sp.		4	7	2		21	34	7	5	23	7
Praebulimina reussi	3	4	1					1		1	
Praebulimina sp.	1	1	1			1	1		2	2	
Pseudouvigerina plummerae		3	1			1			1	3	
Pullenia coryelli									1		
Pullenia cretacea			1				2				
Pullenia jarvisi	1		1			2		2	1	2	2
Pyramidina sp.			1						1	4	
Pyramidina rudita				15	1			8			
Pyrulina sp.							3		1	7	1
Pyrulinoides sp.							1	3			
Quadrimorphina allomorphinoides						4	6	3	3	8	1
Quadrimorphina sp.											6
Quinqueloculina sp.		1					1			1	
Reophax spp.			1								
Repmanina charoides		5	3	11	10						
Rhizammina sp.			1					1			
Saccammina spp.			3	4	1						
Saracenaria sp.			1								
Sculptobaculites sp.						1					
Sliteria varsoviensis				1							
Spiroplectammina spp.				1	4		2			1	
Spiroplectammina dentata						4					
Spiroplectammina israelsky		2	7	4			11			2	5
Spiroplectammina spectabilis	2	7	21	27	2	2	4				1
Stensioeina beccariiformis		12	19	26	27	17	27	6	115	49	25
Stensioeina excolata	3		1	4		4	2	1			
Stilostomella sp.		10	1	2		6	4	7	3	3	2
Subreophax velascoensis			5	2	1						
Subreophax sp.								1			1
Valvalabamina lenticula			3			1			1	6	
Vulvulina sp.											
Vaginulina trilobata							1				
Total	46	128	216	303	152	255	399	343	370	381	288

The number of each sample corresponds to the centimeters below (−) or above (+) the K/P boundary.

Table 2
Habitat preferences of calcareous (Corliss, 1985; Corliss and Chen, 1988) and agglutinated (Jones and Charnock, 1985) benthic foraminiferal morphogroups

EPIFAUNAL CALCAREOUS

Rounded trochospiral
Anomalinoides rubiginosus[a]
Gyroidinoides globosus[a]

Plano-convex trochospiral
Alabamina wilcoxensis
Angulogavelinella avnimelechi
Cibicidoides abudurbensis[b]
Cibicidoides hyphalus[a,b]
Cibicidoides ekblomi
Cibicidoides howelli
Cibicidoides proprius s.l.
Cibicidoides velascoensis[a,b]
Cibicidoides spp.[a]
Globorotalites michelinianus
Globorotalites spp.[a]
Gyroidinoides depressus
Gyroidinoides girardanus[a]
Gyroidinoides subangulatus
Nuttallinella florealis[a]
Nuttallinella coronula
Osangularia plummerae
Paralabamina hillebrandti[a,b]
Stensioeina beccariiformis[b]
Stensioeina excolata
Valvalabamina lenticula

Biconvex trochospiral
Anomalinoides acutus
Anomalinoides aegyptiacus
Anomalinoides affinis
Anomalinoides ammonoides
Anomalinoides spp.
Cibicidoides dayi[a]
Cibicidoides pseudoacutus
Lenticulina spp.[a]
Nuttallides truempyi[2a,c,d]
Oridorsalis plummerae[b]
Osangularia plummerae
Osangularia spp.
Paralabamina lunata[a,b]
Sliteria varsoviensis[b]

Trochospiral flattened
Heronallenia lingulata

Milioline
Quinqueloculina sp.

Palmate
Frondicularia jarvisi
Neoflabellina delicatissima

EPIFAUNAL AGGLUTINATED

A: Tubular or branching

Table 2 (*Continued*).

Bathysiphon[e]
Hyperammina sp.[e]

B2: Coiled flattened and streptospiral
Ammodiscus cretaceus[e]
Ammodiscus latus
Ammodiscus macilentus
Ammodiscus spp.[e]
Glomospirella grzybowskii[e]
Glomospira sp.[c,d,e]
Repmanina charoides

INFAUNAL CALCAREOUS

Cylindrical tapered
Bulimina midwayensis
Bulimina trinitatensis[a,b]
Buliminella grata
Eouvigerina subsculptura[a]
Ellipsoidella spp.
Fursenkoina sp.
laevidentalinids
Pleurostomella spp.
Praebulimina reussi[b]
Praebulimina spp.
Pseudouvigerina plummerae[a,b]
Pyramidina rudita[a,b]
Sitella cushmani[b]
Stilostomella sp.[c]

Flattened tapered
Astacolus spp.
Aragonia velascoensis
Bolivinoides delicatulus[a,b]
Bolivinoides draco[a,b]
Coryphostoma decurrens
Coryphostoma incrassata[a]
Coryphostoma incrassata forma *gigantea*[b]
Coryphostoma plaitum
Loxostomum[a]
Vaginulina trilobata

Spherical/globose
Allomorphina polonica
Allomorphina velascoensis
Globulina spp.[a]
Guttulina sp.
Lagena spp.[a]
Quadrimorphina allomorphinoides?
Reussoolina spp.[a]

Rounded planispiral
Nonionella spp.[a]
Pullenia cretacea[a]
Pullenia coryelli[a]
Pullenia jarvisi[a]

Flattened ovoid
Buchnerina sp.
Paliolatella orbygniana

Table 2 (*Continued*).

Biconvex trochospiral
Gyroidinoides beisseli[f]
Oridorsalis umbonatus[g]

INFAUNAL AGGLUTINATED

B1: Globular unilocular
Saccammina placenta[e]
Saccammina sp.[e]

C1: Elongate multilocular
Arenobulimina truncata
Arenobulimina spp.[e]
Clavulinoides amorpha emend. Alegret and Thomas
Clavulinoides trilatera
Dorothia bulleta
Dorothia pupa
Gaudryina laevigata
Gaudryina pyramidata[e]
Marssonella indentata
Marssonella oxycona[e]
Spiroplectammina spp.[e]
Spiroplectammina dentata
Spiroplectammina aff. *S. israelski*
Spiroplectammina spectabilis
Reophax spp.[e,h]
Subreophax velascoensis
Subreophax spp.[e]
Vulvulina sp.

Flattened trochospiral
Haplophragmoides[h,i]

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[a] Widmark and Malmgren (1992a,b).
[b] Widmark and Speijer (1997a,b).
[c] Kaminski et al. (1996).
[d] Kuhnt and Kaminski (1990).
[e] Peryt et al. (1997).
[f] Alegret et al. (2001).
[g] Rathburn and Corliss (1994).
[h] Kaminski et al. (1995).
[i] Kuhnt et al. (1996), Gooday (1990) and Kaminski et al. (1999).

fractions is not sufficient to infer environmental changes with accuracy. A large part of the faunas may occur in the small-size fraction, especially in faunas disturbed by environmental changes, and this large part can thus easily be missed in studies of larger-size fractions. It is therefore difficult to compare our results to those by Pardo et al. (1996) > 105-μ fraction. This difficulty is aggravated because these authors did not document their taxonomy: they neither include a species description, nor a list of taxa with original authors and generic names. Because of this lack of documentation, we cannot compare our taxonomy directly with theirs, and surmise that some of our determinations of benthic foraminifera at the specific level may differ from the taxonomy used by these authors, as discussed below.

The comparison of fossil and recent communities of benthic foraminifera, in addition to morphotype analysis (e.g. Corliss, 1985; Corliss and Chen, 1988; Jones and Charnock, 1985), allows us to infer probable microhabitat preferences and environmental parameters such as the nutrient supply to the seafloor, its seasonality, and seawater oxygenation (e.g. Bernhard, 1986; Jorissen et al., 1995; Fontanier et al., 2002). One should be careful with the interpretation of these comparisons because the ecology of present foraminifera is complex and not fully understood (e.g. Murray, 2001), and we do not know to what extent the Cretaceous and Early Paleogene faunas were analogous to Recent faunas (e.g. Thomas et al., 2000; see also Alegret and Thomas, 2001; Alegret et al., 2001).

We allocated all foraminiferal taxa to morphogroups following Corliss (1985, 1991), Jones and Charnock (1985) and Corliss and Chen (1988) (Table 2). In general, benthic foraminifera with plano-convex, biconvex and rounded trochospiral tests, tubular and coiled flattened, as well as milioline and palmate tests, are inferred to have had an epifaunal mode of life, living at the sediment surface or in its upper few centimeters. Infaunal foraminifera, living in the deeper layers of the sediment (4–10 cm depth; deep infauna in Corliss, 1991), have cylindrical or flattened tapered, spherical, rounded planispiral, flattened ovoid, globular unilocular or elongate multilocular tests. Here also caution is necessary: for many taxa the close relationship between test morphology and microhabitat has not been observed, but it is extrapolated from data on other taxa (e.g. Jorissen, 1999); this is necessarily so for extinct taxa. In addition, many foraminifera move actively, vertically through the sediment (e.g. Bornmalm et al., 1997; Gooday and Rathburn, 1999; Jorissen, 1999; Gross, 2000; Fontanier et al., 2002). In one of the few studies evaluating the linkage between test morphology and microhabitat statistically, the authors argued that such as-

Table 3
Distribution of bathymetric indicator species

Depth-related species	Upper-depth limit	Common distribution
Anomalinoides acutus (Plummer)		Neritic–upper bathyal (5)
Bolivinoides delicatulus Cushman		Bathyal (1, p. 338); most common upper–middle bathyal, less common lower bathyal (7)
Bolivinoides draco (Marsson)		Outer neritic and bathyal (1, p. 378); most common upper–middle bathyal, less common lower bathyal (7)
Bulimina trinitatensis Cushman and Jarvis	500–700 m (1, 2)	Bathyal and abyssal (7); lower bathyal–abyssal (3); bathyal–abyssal (2)
Cibicidoides hyphalus (Fisher)	100 m (1c), 200–600 m (6)	Lower bathyal (1, 3); common at middle bathyal depths (7)
Cibicidoides velascoensis (Cushman)		Bathyal and abyssal (5); bathyal and abyssal (1, p. 372); common at middle bathyal depths (7)
Clavulinoides trilatera (Cushman)		Bathyal and abyssal (5); middle bathyal (6); lower bathyal–abyssal (1, 3, 8)
Coryphostoma incrassata (*Reuss*)		Outer neritic and bathyal (1, p. 384)
C. incrassata forma *gigantea* (Wicher)		Neritic–upper bathyal (7); most common upper–middle bathyal, less common lower bathyal (7)
Eouvigerina subsculptura MacNeil and Caldwell		Upper and middle bathyal (4, 7); most common upper–middle bathyal, less common lower bathyal (7)
Gaudryina pyramidata Cushman	200–300 m (1)	Bathyal–abyssal (5); lower bathyal and abyssal (3); upper–middle bathyal, less common lower bathyal (7)
Gyroidinoides globosus (Hagenow)	200–300 m (2)	Middle bathyal–abyssal (3); bathyal–abyssal (1c, 2)
Loxostomum eleyi (Cushman)		Outer shelf (9); 100–250 m (10, fig. 13)
Marssonella oxycona (Reuss)		Middle bathyal (500–1500 m; 10)
Nuttalides truempyi (Nuttall)	500–700 m (1, 2, 6)	Bathyal and abyssal (5); middle–lower bathyal and abyssal (1, 2, 3, 4)
Nuttalinella florealis (White)		Bathyal and abyssal (5); bathyal and abyssal (1c)
Oridorsalis plummerae (Cushman)		Most common upper–middle bathyal, less common lower bathyal (7); bathyal (10)
Osangularia plummerae Brotzen	50–100 m (1)	Neritic–upper bathyal (5)
Paralabamina lunata (Brotzen)		Bathyal to abyssal (7)
Praebulimina reussi (Morrow)		Bathyal to abyssal (7); middle bathyal (500–1500 m; 10)
Pseudouvigerina plummerae Cushman		Most common upper–middle bathyal, less common lower bathyal (7)
Pyramidina rudita (Cushman and Parker)		Common at middle bathyal depths (7)
Sitella cushmani (Sandidge)		Most common upper–middle bathyal, less common lower bathyal (7)
Spiroplectammina spectabilis (Grzybowski)	500–700 m (1)	Bathyal (11)
Stensioeina beccariiformis (White)	500–700 m (1, 3, 5)	Bathyal–abyssal (5); lower bathyal (3, 4); bathyal (2) and abyssal (2, 4); bathyal to abyssal (7)
S. beccariiformis forma *parvula* (ten Dam)	200–300 m (1)	
Stensioeina excolata (Cushman)		Outer neritic and bathyal (1, p. 382)

(1) Van Morkhoven et al. (1986), p. 8, fig. 5; (1c) Van Morkhoven et al. (1986), fold out; modified after Van Morkhoven et al., 1986; (2) Speijer (1994), p. 84, fig. 6; (3) Tjalsma and Lohmann (1983); (4) Widmark (2000), pp. 376–377; (5) Berggren and Aubert (1975); (6) R. Speijer, pers. commun., 2001; (7) Widmark and Speijer, 1997a; (8) Kaminski et al., 1988; (9) MacNeil and Caldwell, 1981; (10) Nyong and Olsson (1984); (11) Kaiho, 1992. Paleodepth estimates following Van Morkhoven et al. (1986).

signments for modern foraminifera may be accurate about 75% of the time (Buzas et al., 1993). We thus argue that only major changes in percentages of the morphogroups are likely to be significant.

The distribution of benthic foraminifera in the oceans is controlled by a series of depth-related parameters (e.g. Nyong and Olsson, 1984; Van Morkhoven et al., 1986), and benthic foraminifera can thus be used as paleobathymetric markers. In paleobathymetric assignments, however, there is much space for disagreement as well. Paleobathymetric inferences are usually based on the comparison between fossil and recent assemblages (thus relying on the inference that extinct species behave similarly to morphologically similar modern species), on the occurrence and abundance of such depth-related species, and on species' upper depth limits (e.g. Van Morkhoven et al., 1986; Berggren and Miller, 1989; Kaiho, 1992; Bolli et al., 1994). In addition, one can use comparisons to benthic foraminiferal assemblages at DSDP and ODP Sites where paleodepths can be derived independently by backtracking (e.g. Van Morkhoven et al., 1986; Nomura, 1991; Widmark and Malmgren, 1992a,b; Alegret and Thomas, 2001; Alegret et al., 2001; 2002). We used the bathymetric division as defined in Van Morkhoven et al. (1986) and Berggren and Miller (1989): neritic (0–200 m), upper bathyal (200–600 m), middle bathyal (600–1000 m), lower bathyal (1000– > 2000 m). We document our paleodepth assignments and the source of our assignments in Table 3.

3. Results

3.1. Paleobathymetry

Throughout the studied section at Agost, upper–middle bathyal taxa are consistently present, but their relative abundance varies (Figs. 3 and 4). Benthic foraminiferal assemblages from the *Abathomphalus mayaroensis* Biozone and the basal part of the *Plummerita hantkeninoides* Biozone contain abundant *Loxostomum eleyi*, as well as *Eouvigerina subsculptura* (upper–middle bathyal), laevidentalinids, *Sitella cushmani* (bathyal), *Spiroplectammina spectabilis* (upper bathyal), and *Stensioeina beccariiformis* forma *parvula* (outer shelf–upper bathyal); see Table 3 for paleodepth references. These faunas thus present a difficulty in paleodepth interpretation: the presence of abundant *L. eleyi* indicates outer shelf depths (MacNeil and Caldwell, 1981; Nyong and Olsson, 1984), which appears to be too shallow for the other species present (Table 3). We suggest that the paleodepths were in the uppermost bathyal zone (~ 200–500 m), with the depth of occurrence of *L. eleyi* possibly somewhat greater than at other locations because of a relatively high food supply, as indicated by the high relative abundance of infaunal taxa (see below).

In the lower *Plummerita hantkeninoides* Biozone (samples Agost −275 and Agost −240), the relative abundance of *Loxostomum eleyi* decreases significantly (Figs. 3 and 4), while that of deeper-dwelling species, such as *Praebulimina reussi*, increases. The latter species is most common at upper–middle bathyal depths (e.g. Widmark and Speijer, 1997a,b). Components of the bathyal and abyssal Velasco-type faunas (Berggren and Aubert, 1975; Tjalsma and Lohmann, 1983; Van Morkhoven et al., 1986) such as *Clavulinoides trilatera*, *Nuttallinella florealis*, *Cibicidoides velascoensis*, and *Cibicidoides hyphalus*, first appear or become more abundant where the relative abundance of *L. eleyi* declines. From the lower part of the *P. hantkeninoides* Biozone to the top of the section we recognized abundant species typical of middle bathyal environments in the Tethys area (e.g. Widmark and Speijer, 1997a), such as *Gaudryina pyramidata*, *Pseudouvigerina plummerae*, *Bolivinoides draco*, *Bolivinoides elicatulus*, *Eouvigerina subsculptura*, *Pyramidina rudita*, *Cibicidoides velascoensis*, *Cibicidoides hyphalus*, as well as species more common in deeper environments (*Paralabamina lunata*, *Praebulimina reussi*, *Bulimina trinitatensis*, *Stensioeina beccariiformis* s.s.; see Table 3). *Nuttallides truempyi*, a bathyal and abyssal species, is present throughout the section but never abundant.

These faunal changes indicate increasing water depths, as supported by changes in the morphology of *Stensioeina beccariiformis*. The shallow-water variant of this species, *Stensioeina beccariiformis* forma *parvula* (Van Morkhoven et al., 1986), occurs from the lowermost sample up to sample Agost −240 (Table 1). Stratigraphically higher (lower–middle part of the *Plummerita hantkeninoides* Biozone), only *Stensioeina beccariiformis* s.s., typical of bathyal through abyssal depths, was identified (Table 3; Fig. 4). We thus do not agree with Pardo et al. (1996), that *Stensioeina beccariiformis* forma *parvula* re-appears near the

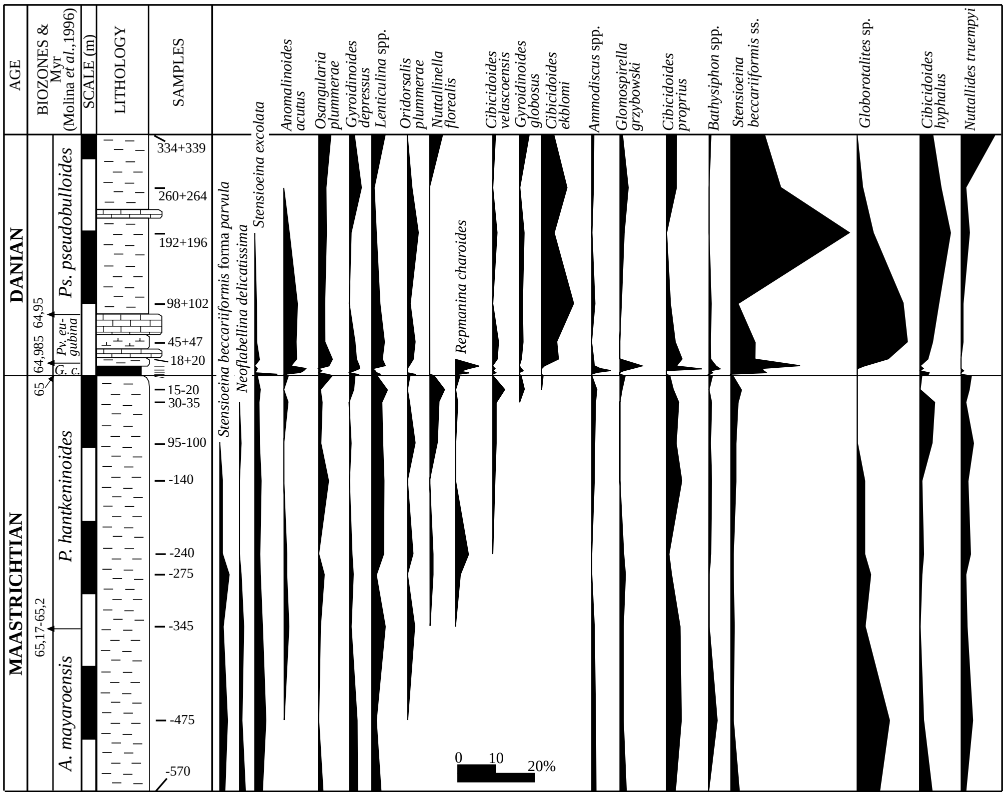

Fig. 4. Occurrence and relative abundance of the most characteristic epifaunal benthic foraminiferal species across the K/P transition at Agost. Abbreviation: *G. c.*, *Guembelitria cretacea* Biozone.

P0/P1 boundary, and suggest that they misidentified *Stensioeina beccariiformis* s.s. as this form.

The largest *Glomospirella* specimens are found in the lower part of the section (up to sample −140), with smaller ones throughout the rest of the section. According to Kuhnt and Kaminski (1990), the *Glomospira* and *Glomospirella* species are smaller at greater depths, where there is less organic matter input. The size distribution of *Glomospirella grzybowski* thus also suggests that the water depth increased in the early *Plummerita hantkeninoides* Biochron.

The clay layer deposited just after the K/P boundary (*Guembelitria cretacea* Biozone) contains sparse benthic faunas, containing species common at bathyal depths (e.g. *Spiroplectammina spectabilis*; Fig. 6), as well as species with a very large depth range (*Glomospirella grzybowski*, *Ammodiscus* spp.). These faunas cannot give precise paleodepth information, but they are not inconsistent with middle bathyal depths.

The remainder of the Danian part of the section (*Parvulorugoglobigerina eugubina* Biozone, *Parasubbotina pseudobulloides* Biozone) has common *Stensioeina beccariiformis* (s.s.), as well as *Globorotalites* spp., various species of *Cibicidoides* such as *Cibicidoides ekblomi* and *C. hyphalus*, *Gaudryina pyramidata*, and laevidentalinids. These are all typically middle bathyal taxa (Table 3).

3.2. Benthic foraminiferal turnover at the K/T boundary

The benthic foraminiferal assemblages at Agost are dominated by calcareous specimens (∼80%; Fig. 5) throughout the section, except for the lowermost 10 cm of the Danian, where they make up

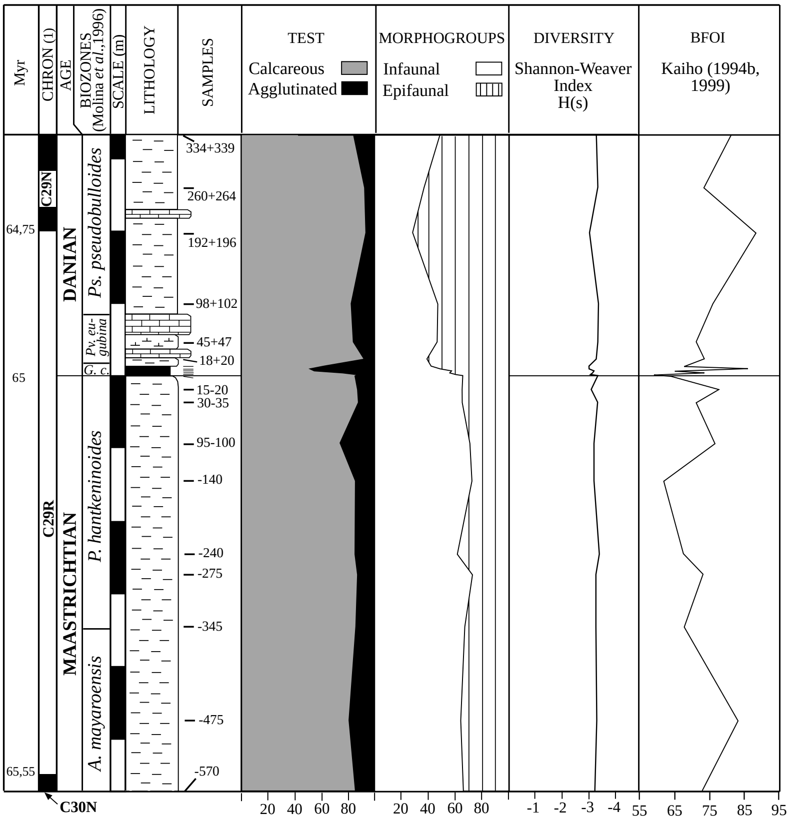

Fig. 5. Percentages of benthic foraminifera with calcareous and agglutinated tests; relative abundance of infaunal and epifaunal morphogroups; H (s) diversity index of benthic foraminiferal species, and the BFOI (Kaiho, 1994b, 1999) across the K/P transition at Agost. Key: (1) Magnetostratigraphy by Groot et al. (1989).

~30% of the assemblages. Due to the sampling resolution, no data are available from the upper 2 cm of the black clay.

Upper Maastrichtian assemblages are dominated by calcareous foraminifera with tapered tests (Figs. 3–5). The tapered taxon *Loxostomum eleyi*, various laevidentalinid taxa, and *Eouvigerina subsculptura* dominate in the *Abathomphalus mayaroensis* Biozone and the lower half of the *Plummerita hantkeninoides* Biozone. The upper half of the *Plummerita hantkeninoides* Biozone is dominated by different tapered, calcareous species such as *Praebulimina reussi*, *Spiroplectammina spectabilis* and laevidentalinids (Fig. 3). We thus interpret these faunas as being dominated by infaunal morphogroups (Fig. 5), suggesting a moderately eutrophic environment.

No significant changes in diversity occurred at the K/P boundary (Fig. 5), as far as can be ascertained with the low numbers of specimens present in the boundary clays (see below), where dissolution may have played a major role. A relatively minor number of species at Agost (5%) is represented by species that can be documented to have become extinct globally at the end of the Cretaceous, such as *Bolivinoides draco*. Many species are absent for a short interval (Lazarus taxa), and relative abundances changed drastically: the Danian assemblages are characterized by abundant trochospiral species, such as *Stensioeina beccariiformis*, *Globorotalites* spp., *Cibicidoides hyphalus*, *Cibicidoides ekblomi*, and *Gyroidinoides beisseli* (Figs. 3 and 4). Infaunal morphogroups (Table 2) make up 27–45% of fauna in the Danian, in contrast to 65–73% in the Upper Maastrichtian (Fig. 5). This dominance of the Danian benthic foraminiferal assemblages by epifaunal or mixed epifaunal–infaunal morphogroups suggests that the food supply to the benthos was less abundant than in the latest Cretaceous (e.g. following Jorissen et al., 1995; Van der Zwaan et al., 1999).

The data for the lowermost Danian black clay interval are not quantitatively reliable because benthic foraminifera are scarce (Table 1), but we shall speculate on their possible environmental meaning. Several peaks in relative abundance of *Ammodiscus* spp., *Glomospirella grzybowski*, *Pyramidina rudita*, *Repmanina charoides*, *Stilostomella* and especially *Haplophragmoides* sp. occur in the lower 10 cm of the Danian (Fig. 6). *Haplophragmoides* sp. may be considered as a shallow infaunal species (Kaminski et al., 1999) that can move through the sediment depending on food levels (Kuhnt et al., 1996), and which is tolerant to low-oxygen conditions as well as low-food conditions (Sliter, 1975; Ly and Kuhnt, 1994; Kuhnt et al., 1996). Several *Haplophragmoides* species show peaks in relative abundance in a low-oxygen interval with strong dissolution following the Paleocene–Eocene extinction of benthic foraminifera in Spanish bathyal sections (Ortiz, 1995; Orue-Etxebarria et al., 1996), and *Haplophragmoides* was reported from dysaerobic mid-Cretaceous shales by Koutsoukos et al. (1990). *Stensioeina beccariiformis* has a peak in relative abundance coeval with that of *Haplophragmoides*. Among calcareous foraminifera, the genera *Gavelinella* and *Pyramidina* were reported as characteristic of low-oxygen environments (Sliter, 1975), and they occur in shales with high organic matter levels (Holbourn et al., 2001).

Recent species of *Ammodiscus*, *Glomospira*, *Glomospirella*, and *Repmanina* are mobile epifaunal forms that feed on organic detritus (e.g. Ly and Kuhnt, 1994), and tolerate large environmental fluctuations, including variation in salinity and oxygenation (e.g. Kaminski et al., 1996). Therefore, we consider these taxa to be opportunistic species, which may bloom whenever other taxa cannot compete, e.g. in periods of environmental instability or low oxygenation (Kaminski et al., 1996).

Because in the present world high productivity and low oxygenation tend to be correlated, it is difficult to decide whether a specific fauna indicates a high organic carbon flux or lowered oxygen conditions (Jorissen et al., 1995; Van der Zwaan et al., 1999). Kaiho (1991, 1992, 1994a) suggested that an oxygenation index could be derived from the benthic foraminiferal faunal com-

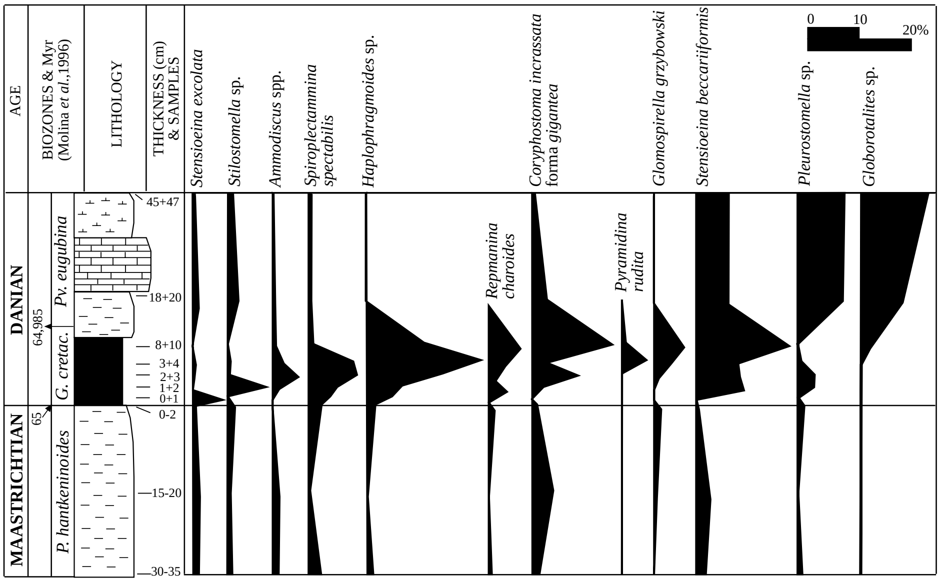

Fig. 6. Detailed occurrence and relative abundance of the benthic foraminiferal species at the K/P boundary.

Table 4
Classification of benthic foraminiferal species into Oxic (O), Suboxic (SA, SB, SC) and Dysoxic (D) groups according to Kaiho (1994b)

Benthic foraminiferal species	Group
Alabamina wilcoxensis	SA
Allomorphina polonica	D
Allomorphina velascoensis	D
Allomorphina sp.	D
Angulogavelinella avnimelechi	O
Angulogavelinella sp.	O
Anomalinoides acutus	O
Anomalinoides aegyptiacus	O
Anomalinoides affinis	O
Anomalinoides ammonoides	O
Anomalinoides rubiginosus	O
Anomalinoides cf. *susanaensis*	O
Anomalinoides spp.	O
Aragonia velascoensis	D
Astacolus spp.	SB
Bifarina sp.	SB
Bolivinoides draco	D
Bolivinoides delicatulus	D
Buchnerina sp.	SB
Bulimina midwayensis	SB
Bulimina trinitatensis	SB
Bulimina sp.	SB
Buliminella grata	SB
Buliminella sp.	SB
Cibicidoides aburdurbensis	O
Cibicidoides dayi	O
Cibicidoides ekblomi	O
Cibicidoides hyphalus	O
Cibicidoides pseudoacutus	O
Cibicidoides velascoensis	O
Cibicidoides howelli	O
Cibicidoides proprius	O
Cibicidoides sp.	O
Coryphostoma decurrens	D
Coryph. incrassata forma *gigantea*	D
Coryphostoma incrassata	D
Coryphostoma plaitum	D
Coryphostoma sp.	D
Ellipsodimorphina sp.	D
Ellipsoidella sp.	D
Eouvigerina subsculptura	SB
Frondicularia jarvisi	O
Frondicularia sp.	O
Fursenkoina sp.	D
Glandulina sp.	D
Globulina prisca	D
Globulina spp.	D
Globobulimina sp.	D
Guttulina sp.	D
Globorotalites michelinianus	O
Globorotalites sp.	O
Gyroidinoides beisseli	SB
Gyroidinoides depressus	SB
Gyroidinoides globosus	SB
Gyroidinoides goudkoffi	SB
Gyroidinoides girardanus	SB
Gyroidinoides subangulatus	SB
Gyroidinoides sp.	SB
Hemirobulina sp.	SB
Laevidentalina spp.	SB
Lagena spp.	SB
Lenticulina spp.	SB
Lingulina sp.	SB
Loxostomum eleyi	SB
Neoflabellina delicatissima	D
Neoflabellina sp.	D
Nodosarella sp.	SB
Nonionella sp.	SC
Nuttallides spp.	O
Nuttallides truempyi	O
Nuttallinella coronula	O
Nuttallinella florealis	O
Nuttallinella spp.	O
Oolina spp.	SB
Oridorsalis plummerae	SB
Oridorsalis umbonatus	SB
Oridorsalis sp.	SB
Osangularia plummerae	O
Osangularia spp.	O
Paliolatella sp.	SB
Paliolatella orbygniana	SB
Paralabamina hillebrandti	SB
Paralabamina lunata	SB
Pleurostomella sp.	D
Praebulimina reussi	SB
Praebulimina sp.	SB
Pseudopolimorphina sp.	D
Pseudouvigerina plummerae	SB
Pullenia coryelli	SB
Pullenia cretacea	SB
Pullenia jarvisi	SB
Pullenia sp.	SB
Pyramidina sp.	SB
Pyramidina rudita	SB
Pyrulina sp.	D
Pyrulinoides sp.	D
Quadrimorphina allomorphinoides	D
Quadrimorphina sp.	D
Quinqueloculina sp.	O
Ramulina spp.	O
Reusoolina sp.	SB
Saracenaria sp.	SB
Sitella cushmani	SB
Sliteria varsoviensis	O
Stensioeina beccariiformis	O
Stensioeina excolata	O
Stillostomella sp.	SB
Valvalabamina lenticula	SB
Vaginulina trilobata	SB

The BFOI has been calculated as: BFOI = [O/(O+D)]*100 (Kaiho, 1994b, 1999).

position of calcareous taxa, and later (Kaiho, 1994b, 1999) defined a Benthic Foraminiferal Oxygenation Index (BFOI) using data on living foraminifera. Recent research strongly suggests that such an index is not functional, possibly with the exception of environments with extremely low oxygenation levels (below 1.5 mg O_2/L; e.g. Morigi et al., 2001). We calculated the BFOI for our samples (Fig. 5; Table 4). Kaiho's (1991, 1994b) indexes are somewhat differently defined; we used his 1994b definition. The BFOI suggests a drop in oxygenation at the K/P boundary, followed by rapid fluctuations in the black clays, where geochemical and sedimentological evidence indicates anoxia/hypoxia (Martinez Ruiz et al., 1992, 1999). The rapid fluctuations might suggest an unstable environment (see below), but there are few specimens of foraminifera in the black clay samples, and consequently we are not confident of this interpretation. The index shows overall higher values in the Paleogene than in the Cretaceous, resulting of the higher percentages of infaunal taxa in the Cretaceous part of the studied section, as discussed above. In our opinion these differences do not suggest low-oxygen conditions in the Cretaceous, but lowered organic flux in the Paleogene, as discussed above.

4. Discussion

Benthic foraminiferal analysis of samples from the Agost section indicates an uppermost bathyal (200–500 m) depth of deposition for the lower 3 m of the studied section, corresponding to the upper part of *Abathomphalus mayaroensis* Biozone and the lower *Plummerita hantkeninoides* Biozone (Fig. 7). About two meters below the K/P boundary, i.e. 120–150 kyr before the K/P boundary according to the biostratigraphical calibration by Molina et al. (1996) and Arenillas et al. (2002), the basin deepened to middle bathyal (600–1000 m). Benthic foraminiferal faunal change occurred during the deepening of the basin (Figs. 3 and 4), when foraminifera typical of a neritic to uppermost bathyal environment (e.g. *Loxostomum eleyi*) significantly decreased in abundance. Benthic foraminifera indicate that the depth of deposition remained constant during the time that the rest of the section was deposited, without perceivable depth fluctuations at the K/P boundary (Fig. 7).

Our results agree with the paleobathymetry proposed by De Ruig et al. (1991), who used paleogeographical and sedimentary facies data to suggest that the K/P sediments were deposited on the middle slope, at about 600–700 m depth. They also agree with the depth estimates for the nearby Caravaca section by Coccioni and Galeotti (1994) and Widmark and Speijer (1997a,b). The latter authors studied samples from the upper 60 cm of the Maastrichtian only, and not from the lower part of the section at Caravaca, which we would suppose to correlate with the interval interpreted as uppermost bathyal at Agost.

Pardo et al. (1996) suggested an outer neritic–upper bathyal depth for the Upper Maastrichtian sediments, and a rise in relative sea level around 1.5 m below the K/P boundary to upper bathyal. They consider that such a sea-level rise is linked to an expansion of the oxygen minimum zone, associated with the increase in relative abundance of a low-oxygen tolerant, outer shelf species, *Praebulimina carseyae*. In contrast, our data indicate a deepening of the basin not at 1.5 but at 2.4 m below the K/P boundary. We consider that there is no evidence for low-oxygen conditions in the Maastrichtian part of the section (Fig. 5), and think that Pardo et al. (1996) misidentified *Praebulimina reussi* (with a triserial test and subterminal, comma-shaped aperture) as the species *Praebulimina carseyae*; we cannot be certain of this because of the lack of documentation of taxonomy by these authors.

According to Pardo et al. (1996), the sea-level rise led to sedimentation at bathyal depths for part of the section, but they did not specify which part of the slope, although they suggest upper bathyal in their table 4. Coccioni and Galeotti (1998) plot the Agost section at the boundary between shelf and upper slope at the time of the K/P boundary (their fig. 2), probably following Pardo et al. (1996).

Pardo et al. (1996) also proposed that there were two more changes in sea level at Agost during the Danian, including a drop just at the K/P boundary (Fig. 7). Our data do not support the occurrence of relative sea-level changes at the K/P boundary and in the Danian. This disagreement in depth assignment probably results from the fact that Pardo et al. (1996) assigned upper depth limits of taxa without consideration of the depths at which these taxa usually are observed, or are common. For example, Pardo et al. (1996) give in their table 4 an upper depth limit of 'Outer shelf' for *Nuttallinella florealis*, a species first described from the middle bathyal Velasco Formation (e.g. Berggren and Aubert, 1975; Van Morkhoven et al., 1986; Alegret and Thomas, 2001), and generally considered an indicator of middle bathyal through abyssal depths (Table 3).

Pardo et al. (1996) inferred a sea-level drop near the P0–P1 boundary (Fig. 7) based on the increase in relative abundance of *Stensioeina beccariiformis* forma *parvula*, and on the disappearance of common bathyal species. We disagree with the determination of *Stensioeina beccariiformis* forma *parvula* in the lower Danian; in our opinion the species at these levels is *Stensioeina beccariiformis* s.s. Changes in the abundance of the species may be interpreted not in terms of eustatic changes, but in terms of oxygenation and productivity fluctuations (e.g. Widmark and Speijer, 1997a,b).

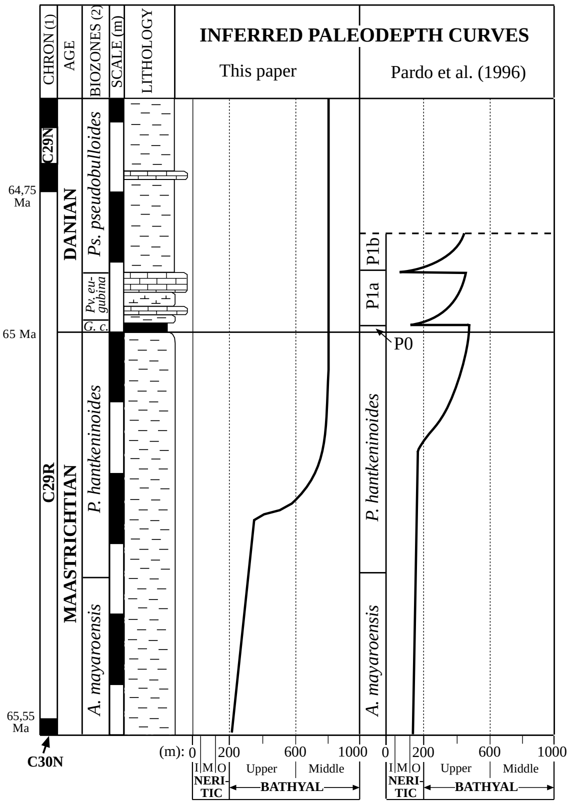

Fig. 7. Comparison between paleodepth curves inferred in this paper, and those interpreted by Pardo et al. (1996). Key: (1) Magnetostratigraphy by Groot et al. (1989); (2) Biostratigraphy by Molina et al. (1996); I, Inner neritic; M, Middle neritic; O, Outer neritic.

A temporary faunal turnover (for the duration of the *Guembelitria cretacea* Biochron, about 10 kyr; Mukhopadhyay et al., 2001) and not a mass extinction started at the K/P boundary, as marked by a 2-mm-thick red rusty clay layer where a catastrophic mass extinction of planktonic foraminifera occurred (Molina et al., 1996). A series of peaks in the relative abundance of *Ammodiscus* spp., *Glomospirella grzybowski*, *Pyramidina rudita*, *Repmanina charoides*, and *Haplophragmoides* sp. occurs in the lowermost 10 cm of the Danian (Fig. 6), where absolute abundances of benthic foraminifera are low, and dissolution may have affected the faunas, leading to relatively high abundances of agglutinated taxa. We interpret these peaks as reflecting an interval during which an overall decrease in productivity was combined with environmental instability. Nannoplankton communities in the nearby Caravaca section (Romein, 1977) indicate that the primary producer community in the region was unstable after the K/P extinction. Nannofloras show several alternating, major, short-term peaks in the relative abundance of such taxa as *Thoracosphaera*, *Braarudosphaera* and *Biscutum* sp., as has been observed in sections worldwide (e.g. Thierstein, 1981; Perch-Nielsen et al., 1982). *Thoracosphaera* spp. are calcareous cysts of dinoflagellates, and indicate that locally varying, large phytoplankton blooms occurred after the K/P extinction, even in the absence of $CaCO_3$-rich sediment contributed by nannoplankton. At times, large amounts of food may thus have reached the seafloor, especially during major blooms when a larger proportion of phytoplankton is transported to the bottom than during normal conditions (e.g. Ittekot, 1993; Verity et al., 1996; Shaw et al., 1998). Such blooms could have caused relatively rapid delivery of food to the seafloor even in the absence of pellet-producing zooplankton, which suffered mass extinction (d'Hondt et al., 1998).

We thus speculate that the strong variability in the fauna during the first 10–15 kyr of the Danian, as seen in the occurrence of various peaks of opportunistic benthic taxa as well as the low diversity and abundance of benthic foraminifera, reflects not just a collapse of the food supply (e.g. Zachos and Arthur, 1986), but also a major change in the composition of the food supply as a result of the mass extinction of phytoplankton, as well as a rapidly changing, boom-bust food supply driven by blooms. After evolutionary recovery of the phytoplankton (at the end of the *Guembelitria cretacea* Biochron) and stabilization of the ecosystems in surface waters, productivity did not quite recover to pre-extinction levels at Agost in the studied interval (∼200 kyr after the K/P boundary), as seen in the increase in relative abundance of epifaunal species (Fig. 5). A similar drop in productivity and lack of recovery to pre-extinction levels during several hundred thousand years have been reported from the South Atlantic (Widmark and Malmgren, 1992b), Mexico (Alegret and Thomas, 2001; Alegret et al., 2001; 2002), Austria (Peryt et al., 1997), and Tunisia (Peryt et al., 2002).

Geographic variability in the composition and extent of the phytoplankton blooms might be a cause of the different patterns of post-K/P benthic foraminifera faunal composition at different sites after the extinction (e.g. Coccioni et al., 1993; Culver, 2002). These authors interpret a very short period of high-food, low-oxygen benthic foraminifera in the Caravaca section that we do not see at Agost, and suggest that low-oxygen conditions developed on the seafloor due to the enhanced organic flux triggered by the mass mortality. We may have missed such a peak (in <1 cm of sediment) at Agost, but it may also be that at Agost the low-oxygen conditions were more severe than at Caravaca, as suggested by the geochemical data (Martinez Ruiz et al., 1999), so that the buliminid taxa could not thrive.

Kuhnt (1990) and Kuhnt and Kaminski (1993) found an increase in shallow infaunal (over deep infaunal) morphogroups after the K/P boundary in Italian and northern Spanish sections, and interpret this as a response to the collapse of the food web as a consequence of the reduced primary productivity. Peryt et al. (1997), however, remark that the 'shallow-infaunal' morphogroup distinguished by these authors cannot easily be classified as low-food indicators. We suggest that the instability in the food supply on geographical and temporal scales may be a major cause of the variability in benthic foraminiferal pattern seen at various localities (e.g. Coccioni and Galeotti, 1998; Culver, 2002).

The question remains whether the geographically and temporally limited phytoplankton blooms just after the K/P boundary could have supplied so much organic matter to the seafloor that conditions at Agost could become hypoxic to anoxic for 10–15 kyr (Martinez Ruiz et al., 1992, 1999). Low-oxygen conditions just after the K/P boundary were reported at many sites at intermediate water depths worldwide (e.g. Coccioni et al., 1993; Kaiho et al., 1999; Culver, 2002). Therefore, Coccioni et al. (1993) and Coccioni and Galeotti (1998) suggested that low-oxygen conditions resulted from rotting of biomass representing organisms that died in the mass extinction. The latter appears quantitatively highly improbable. Oceanic biomass in the present world is only a very small fraction of the world's biomass (aquatic biosphere pool 1–2 Gt; Falkowski et al., 2000), and oxidation of the complete oceanic biomass would not use up enough oxygen to keep the oceans anoxic for thousands of years, even at the higher ocean temperatures of the end-Cretaceous and Early Danian (Wilf et al., 2003). Note that the black clays represent most of the duration of the *Guembelitria cretacea* Biozone, estimated at about 15 kyr (e.g. Smit, 1990) to about 10 kyr (Mukhopadhyay et al., 2001).

Speculatively, the widespread anoxia/hypoxia could be explained by causes other than local high productivity or decaying biomass after a mass extinction. In K/P sections worldwide (including Caravaca; Romein and Smit, 1981) $\delta^{13}C$ values in bulk sediment (mainly calcareous nannofossils) and in tests of planktonic foraminifera (e.g. Zachos and Arthur, 1986; Kaiho et al., 1999) are very low just after the K/P extinction. These carbon isotope excursions have been interpreted as resulting from a drop in oceanic productivity (e.g. Zachos and Arthur, 1986), but quantitative evaluation of the isotope records shows that a drop in productivity by itself can not explain the observed planktonic–benthic patterns (e.g. Ivany and Salawitch, 1993). In order to explain both surface and deep water patterns, one has to assume the addition of isotopically light carbon to the surface waters. Ivany and Salawitch (1993) assumed that this isotopically light carbon was supplied by the burning of large amounts of continental biomass. An alternative explanation of the carbon isotope record, however, could be found in the dissociation of gas hydrates present along continental margins (Max et al., 1999). Such hydrate dissociation would have been caused by the large slumps and massive failures of sediment that occurred along the western North Atlantic margin due to a meteorite impact at Chicxulub, Yucatan Peninsula, Mexico (e.g. Norris et al., 1999, 2001; Soria et al., 2001). The dissociation would liberate large amounts of isotopically anomalously light methane gas into the atmosphere; subsequently the methane would be oxidized to CO_2 within about 10 years. Some oxidation of methane could have occurred within the oceans, leading to low-oxygen conditions, as well as to a locally enhanced bacterial food supply to the benthos (e.g. De Angelis et al., 1993). The methane hydrate dissociation could well have been the cause of the recently reconstructed very high atmospheric pCO_2 levels (Beerling et al., 2002), although exact levels of pCO_2 and the timing of their fluctuations are still under debate (Nordt et al., 2002).

5. Conclusions

- Benthic foraminifera indicate an uppermost bathyal depth of deposition at Agost (southeastern Spain) during the *Abathomphalus mayaroensis* and the lower part of the *Plummerita hantkeninoides* Biochrons. Depths increased to middle bathyal about 2.4 m (about 120–150 kyr) below the K/P boundary. Paleodepths remained unchanged (within the resolution of benthic foraminiferal depth zonation) through the rest of the section (through the *Parasubbotina pseudobulloides* Biochron, ∼200 kyr after the K/P boundary).
- The net, overall benthic foraminiferal turnover across the K/P boundary within the studied section, which was interrupted by a period (10–15 kyr) of environmental instability, is characterized by a decrease in relative abundance of infaunal morphogroups, probably reflecting a decrease in food supply to the benthos as the result of a decrease in primary productivity and/or of food delivery to the sea bottom.
- Directly after the K/P boundary black clays were deposited during about 10–15 kyr, for which geochemical indicators suggest low-oxygen conditions. Benthic foraminifera were rare, and faunas show a series of short-term peaks of low-oxygen tolerant, opportunistic taxa. Possibly, local plankton blooms and/or input of food from bacterially oxidized methane occurred during this period of environmental instability.
- It is not clear whether the plankton blooms could supply sufficient organic matter to sustain low-oxygen conditions. We speculate that the collapse of the continental margin along the North Atlantic caused by the impact in the Yucatan Peninsula (Mexico) might have led to dissociation and oxidation of methane hydrates, accounting for the local as well as more widespread low-oxygen conditions.
- The faunal changes thus are compatible with the effects of a bolide impact at the K/P boundary, which deeply destabilized the oceanic, phytoplankton-based food web, as well as indirect results of the impact.

Acknowledgements

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Appendix 1. Taxonomic list and original references of the benthic foraminiferal species identified in the Upper Cretaceous and lower Paleogene at Agost

157 taxa were identified at the specific or generic level in the Upper Cretaceous and Lower Paleogene sediments from the Agost section. For the determinations at the generic level, we largely followed the taxonomy established by Loeblich and Tappan (1988); in most cases, species concepts are those employed by Alegret and Thomas (2001). Taxa are listed below alphabetically.

Alabamina wilcoxensis Toulmin 1941, p. 603, pl. 81, figs. 10–14; textfig. 4A–C.

Allomorphina polonica Gawor-Biedowa 1992, p. 147, pl. 31, figs. 5–7.

Allomorphina velascoensis Cushman 1926a, p. 604, pl. 20, fig. 20a–c.

Ammodiscus cretaceus (Reuss) = *Operculina cretacea* Reuss 1845, p. 35, pl. 13, figs. 64 and 65.

Ammodiscus latus Grzybowski 1898, p. 282, pl. 10, figs. 27 and 28.

Ammodiscus macilentus (Myatlyuk) = *Grzybowskiella macilenta* Myatlyuk 1970, p. 72, pl. 13, figs. 2 and 3.

Angulogavelinella avnimelechi (Reiss) = *Pseudovalvulineria avnimelechi* Reiss 1952, p. 269, fig. 2a–c.

Anomalinoides acutus (Plummer) = *Anomalina ammonoides* (Reuss) var. *acuta* Plummer 1926, p. 149, pl. 10, fig. 2a–c.

Anomalinoides aegyptiacus (LeRoy) = *Anomalina aegyptiaca* LeRoy 1953, p. 17, pl. 7, figs. 21–23.

Anomalinoides affinis (Hantken) = *Pulvinulina affinis* Hantken 1875, p. 78, pl. 10, fig. 6a,b.

Anomalinoides ammonoides (Reuss) = *Rotalina ammonoides* Reuss 1844, p. 214.

Anomalinoides rubiginosus (Cushman) = *Anomalina rubiginosa* Cushman 1926a, p. 607, pl. 21, fig. 6a–c.

Anomalinoides susanaensis (Browning) = *Cibicides susanaensis* Browning 1959. See Mallory (1959, p. 271, pl. 32, figs. 11 and 12).

Aragonia velascoensis (Cushman) = *Textularia velascoensis* Cushman 1925, p. 18, pl. 3, fig. 1a–c.

Arenobulimina truncata (Reuss) = *Bulimina truncata* Reuss 1845, p. 37, pl. 8, fig. 73.

Bathysiphon sp. A Alegret and Thomas = *Bathysiphon* sp. A Alegret and Thomas 2001, p. 278.

Bathysiphon sp. B Alegret and Thomas = *Bathysiphon* sp. B Alegret and Thomas 2001, p. 279, pl. 2, fig. 9.

Bathysiphon sp. C Alegret and Thomas = *Bathysiphon* sp. C Alegret and Thomas 2001, p. 279, pl. 2, fig. 10.

Bolivinoides delicatulus Cushman = *Bolivinoides decorata* (Jones) var. *delicatula* Cushman 1927a, p. 90, pl. 12, fig. 8.

Bolivinoides draco (Marsson) = *Bolivina draco* Marsson 1878, p. 157, pl. 3, fig. 25.

Bulimina midwayensis Cushman and Parker = *Bulimina arkadelphiana* Cushman and Parker var. *midwayensis* Cushman and Parker 1936, p. 42, pl. 7, figs. 9 and 10.

Bulimina trinitatensis Cushman and Jarvis 1928 *Bulimina trinitatensis*, p. 102, pl. 14, fig. 12.

Buliminella grata Parker and Bermudez 1937, p. 515, pl. 59, fig. 6a–c.

Cibicidoides abudurbensis (Nakkady) = *Cibicides abudurbensis* Nakkady 1950, p. 691, pl. 90, figs. 35–38.

Cibicidoides dayi (White) = *Planulina dayi* White 1928b, p. 300, pl. 41, fig. 3a–c.

Cibicidoides ekblomi Brotzen 1948, p. 82, pl. 13, fig. 2.

Cibicidoides howelli (Toulmin) = *Cibicides howelli* Toulmin 1941, p. 609, pl. 82, figs. 16–18.

Cibicidoides hyphalus (Fisher) = *Anomalinoides hyphalus* Fisher 1969, p. 198, fig. 3a–c.

Cibicidoides proprius Brotzen 1948, p. 78, pl. 12, figs. 3 and 4.

Cibicidoides pseudoacutus (Nakkady) = *Anomalina pseudoacuta* Nakkady 1950, p. 691, pl. 90, figs. 29–32.

Cibicidoides velascoensis (Cushman) = *Anomalina velascoensis* Cushman 1925, p. 21, pl. 3, fig. 3a–c.

Clavulinoides amorpha (Cushman) emend. Alegret and Thomas = *Clavulina amorpha* Cushman 1926a, p. 589, pl. 17, fig. 5.

Clavulina amorpha (Cushman) emend. Alegret and Thomas 2001, p. 282, pl. 5, figs. 1–3.

Clavulinoides trilatera (Cushman) = *Clavulina trilatera* Cushman 1926a, p. 588, pl. 17, fig. 2.

Coryphostoma decurrens Ehrenberg = *Grammostomum*? *decurrens* Ehrenberg 1854, p. 22, pl. 30, fig. 17 (*fide* Ellis and Messina, Cat. Foram.)

Coryphostoma incrassata (Reuss) = *Bolivina incrassata* Reuss 1851, p. 45, pl. 4, fig. 13.

Coryphostoma incrassata forma *gigantea* (Wicher) = *Bolivina incrassata* Reuss, forma *gigantea* Wicher 1949, p. 57, pl. 5, figs. 2 and 3.

Coryphostoma plaitum (Carsey) = *Bolivina plaitum* Carsey 1926, p. 26, pl. 4, fig. 2.

Dorothia bulleta (Carsey) = *Gaudryina bulleta* Carsey 1926, p. 28, pl. 4, fig. 4.

Dorothia pupa (Reuss) = *Textularia pupa* Reuss 1860, p. 232, pl. 13, fig. 4a,b.

Eouvigerina subsculptura MacNeil and Caldwell = *Eouvigerina subsculptura* (*nomen novum*) MacNeil and Caldwell 1981, p. 21, pl. 18, figs. 20 and 21.

Frondicularia jarvisi Cushman 1939, p. 91, pl. 16, fig. 6 (in Bolli et al., 1994).

Gaudryina laevigata Franke 1914, p. 431, pl. 27, figs. 1 and 2.

Gaudryina pyramidata Cushman = *Gaudryina laevigata* Franke var. *pyramidata* Cushman 1926a, p. 587, pl. 16, fig. 8a,b.

Globorotalites michelinianus (d'Orbigny) = *Rotalina micheliniana* d'Orbigny 1840, p. 31, pl. 3, figs. 1–3.

Globulina prisca Reuss 1862, p. 79, pl. 9, fig. 8.

Glomospirella grzybowski Jurkiewicz 1960, p. 342, pl. 38, figs. 7, 10, 11.

Gyroidinoides beisseli (White) emend. Alegret and Thomas = *Gyroidina beisseli* White 1928b, pp. 291–292, pl. 39, fig. 7a–c.

Gyroidinoides beisseli (White) emend. Alegret and Thomas 2001, p. 286, pl. 7, figs. 1–10.

Gyroidinoides depressus (Alth) = *Rotalina depressa* Alth 1850, p. 266, pl. 13, fig. 21.

Gyroidinoides girardanus (Reuss) = *Rotalina girardana* Reuss 1851, p. 73, pl. 5, fig. 34.

Gyroidinoides globosus (Hagenow) emend. Alegret and Thomas = *Nonionina globosa* Hagenow 1842, p. 574.

Gyroidinoides globosus (Hagenow) emend. Alegret and Thomas 2001, p. 288, pl. 8, figs. 1–5.

Gyroidinoides goudkoffi (Trujillo) = *Eponides goudkoffi* Trujillo 1960, p. 333, pl. 48, fig. 6.

Gyroidinoides subangulatus (Plummer) = *Rotalia soldanii* (d'Orbigny) var. *subangulata* Plummer 1926, p. 154, pl. 12, fig. 1a–c.

Loxostomum eleyi (Cushman) = *Bolivinita eleyi* Cushman 1927a, p. 91, pl. 12, fig. 11.

Marssonella indentata (Cushman and Jarvis) = *Gaudryina indentata* Cushman and Jarvis 1928, p. 92, pl. 13, fig. 7.

Marssonella oxycona (Reuss) = *Gaudryina oxycona* Reuss 1860, p. 229, pl. 12, fig. 3a–c.

Neoflabellina delicatissima (Plummer) = *Frondicularia delicatissima* Plummer 1926, p. 120, pl. 5, fig. 4.

Nuttallides truempyi (Nuttall) = *Eponides truempyi* Nuttall 1930, p. 287, pl. 24, figs. 9, 13, 14.

Nuttallinella coronula (Belford) = *Nuttallina coronula* Belford 1958, p. 97, pl. 19, figs. 1–14; textfig. 4.

Nuttallinella florealis (White) = *Gyroidina florealis* White 1928b, p. 293, pl. 40, fig. 3a–c.

Oridorsalis plummerae (Cushman) = *Eponides plummerae* Cushman 1948, p. 44, pl. 8, fig. 9.

Oridorsalis umbonatus (Reuss) = *Rotalina umbonata* Reuss 1851, p. 75, pl. 5, fig. 35.

Osangularia plummerae Brotzen 1940, p. 30, textfig. 8.

Palliolatella orbignyana (Seguenza) = *Fissurina orbignyana* Seguenza 1862, p. 66, pl. 2, figs. 25 and 26.

Paralabamina hillebrandti (Fisher) = *Neoeponides hillebrandti nomen novum* Fisher 1969, p. 196.

Paralabamina lunata (Brotzen) = *Eponides lunata* Brotzen 1948, p. 77, pl. 10, figs. 17 and 18.

Praebulimina reussi (Morrow) = *Bulimina reussi* Morrow 1934, p. 195, pl. 29, fig. 12.

Pseudouvigerina plummerae Cushman 1927, p. 115, pl. 23, fig. 8.

Pullenia coryelli White 1929, p. 56, pl. 5, fig. 22a,b.

Pullenia cretacea Cushman 1936, p. 75, pl. 13, fig. 8a,b.

Pullenia jarvisi Cushman 1936, p. 77, pl. 13, fig. 6a,b.

Pyramidina rudita (Cushman and Parker) = *Bulimina rudita* Cushman and Parker 1936, p. 45 (*fide* Ellis and Messina, Cat. Foram.).

Quadrimorphina allomorphinoides (Reuss) = *Valvulina allomorphinoides* Reuss 1860, p. 223, pl. 11, fig. 6.

Reophax globosus Sliter 1968, p. 43, pl. 1, fig. 12.

Repmanina charoides (Jones and Parker) = *Trochammina squamata* Jones and Parker var. *charoides* Jones and Parker 1860, p. 304.

Saccammina placenta (Grzybowski) = *Reophax placenta* Grzybowski 1898, p. 276, pl. 10, figs. 9 and 10.

Sitella cushmani (Sandidge) = *Buliminella cushmani* Sandidge 1932, p. 280, pl. 42, figs. 18 and 19.

Sliteria varsoviensis Gawor-Biedowa 1992, p. 156, pl. 33, figs. 9–13.

Spiroplectammina dentata (Alth) = *Textularia dentata* Alth 1850, p. 262, pl. 13, fig. 13.

Spiroplectammina israelsky Hillebrandt 1962, p. 30, pl. 1, figs. 5–7.

Spiroplectammina spectabilis (Grzybowski) = *Spiroplecta spectabilis* Grzybowski 1898, p. 293, pl. 12, fig. 12.

Stensioeina beccariiformis (White) = *Rotalia beccariiformis* White 1928b, p. 287, pl. 39, figs. 2a–4c.

Stensioeina excolata (Cushman) = *Truncatulina excolata* Cushman 1926b, p. 22, pl. 3, fig. 2.

Subreophax velascoensis (Cushman) = *Nodosinella velascoensis* Cushman 1926a, p. 583, pl. 20, fig. 9a,b.

Vaginulina trilobata (d'Orbigny) = *Marginulina trilobata* d'Orbigny 1840, p. 16, pl. 1, figs. 16 and 17.

Valvalabamina lenticula (Reuss) = *Rotalina lenticula* Reuss 1845, p. 35, pl. 12, fig. 17.

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