

Foraminiferal event-stratigraphy across the Cretaceous/Paleogene boundary

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With 10 figures

ALEGRET, L., ARENILLAS, I., ARZ, J. A. & MOLINA, E. (2004): Foraminiferal event-stratigraphy across the Cretaceous/Paleogene boundary. – N. Jb. Geol. Paläont., Abh., **234**: 25–50 Stuttgart.

Abstract: A detailed micropaleontological study of low and middle latitude sections from the Tethyan area and the Gulf of Mexico found three planktic foraminiferal acme stages, which coincide with significant benthic foraminiferal and calcareous nannofossil assemblage turnovers. The sudden change from a typical polytaxic oceanic episode in the late Maastrichtian to an oligotaxic oceanic episode in the earliest Paleogene suggests an important disruption in the stratification of the water column and in the food-web coinciding with the mass extinction at the K/Pg boundary. The stepped recovery pattern of the assemblages reflects the gradual recovery of the environmental conditions after the K/Pg boundary impact event.

Zusammenfassung: Detaillierte mikropaläontologische Untersuchungen von Profilen in niedrigen und mittleren Breiten der Tethys und des Golfes von Mexico weisen bei den planktonischen Foraminiferen drei Acme-Stadien auf, die mit bedeutenden Erneuerungen der Vergesellschaftungen der benthonischen Foraminiferen und des kalkigen Nannoplanktons übereinstimmen. Der abrupte Wechsel von typisch polytaxischen ozeanischen Verhältnissen im jüngeren Maastricht zu oligotaxischen Verhältnissen im frühen Paleogen weist auf die Umwälzung der Schichtung der Wassersäule und den Zusammenbruch der Nahrungskette hin, die mit dem K/Pg-Massenaussterben übereinstimmen. Die schrittweise Erholung der Vergesellschaftungen planktonischer Foraminiferen während des frühen Paläozäns entspricht der allmählichen Wiederherstellung normaler Umweltsbedingungen nach dem Impakt-Ereignis an der K/Pg-Grenze.

Introduction

The coincidence of the sudden catastrophic planktic foraminiferal mass extinction with the Cretaceous/Paleogene (K/Pg) boundary is very compa-

tible with the effects of a large extraterrestrial bolide impact (ALVAREZ et al. 1980, SMIT & HERTOGEN 1980, SMIT 1982). The K/Pg catastrophic mass extinction coincides exactly with the layer containing the Ir anomaly and other extraterrestrial impact evidence such as shocked quartz and altered microtektites in most sections around the world (e. g., SMIT 1990, MOLINA et al. 1998). According to the impact theory, the rapid extinction of the Cretaceous planktic foraminifera and phytoplankton mass mortality is the result of a sudden atmospheric darkening caused by the impact-generated dust in the atmosphere (MILNE & MCKAY 1982). The blackout of sunlight caused a global climatic cooling or "impact winter" which ceased all photosynthesis and caused a severe disruption of the food chain (HSÜ & MCKENZIE 1989). The global negative excursion of the $\delta^{13}\text{C}$ values (SMIT 1982) and a significant decrease in the abundance of phosphorus (KAIHO et al. 1999) at the K/Pg boundary suggest a sudden reduction in primary productivity and abrupt mass mortality. Whereas several marine groups such as planktic foraminifera or calcareous nannofossils show a catastrophic mass extinction pattern across the K/Pg boundary, benthic foraminifera were not as strongly affected and they exhibit a temporary reorganization of their communities after the K/Pg boundary (e. g., THOMAS 1990, ALEGRET et al. 2001, PERYT et al. 2002).

After the K/Pg mass extinction, small and new planktic foraminiferal species appeared following a model of "explosive" adaptive radiation (LUTERBACHER & PREMOLI SILVA 1964, SMIT 1982, D'HONDT 1991, MACLEOD 1993, ARENILLAS et al. 1998). The rapid evolution and diversification of the early Danian planktic foraminifera may be correlated to the recovery of the benthic foraminifera and the calcareous nannofossils after the K/Pg boundary (ARENILLAS et al. 1998, GARDIN & MONECHI 1998, ALEGRET et al. 2003). These faunal changes were paralleled by the long-term environmental turnover after the catastrophic K/Pg boundary event. The detailed quantitative analysis of benthic and planktic foraminiferal assemblages in low and middle latitude sections from the Tethys area (the Spanish Agost and Caravaca sections and the Tunisian Ain Settara and El Kef sections) and from the Gulf of Mexico area (Coxquihui, La Lajilla and El Mulato sections) allowed us to establish several stages in the succession of planktic foraminiferal populations larger than 63 μm . The planktic foraminiferal acme stages were initially observed in several sections in northern Spain by ARENILLAS et al. (1998) and ARZ et al. (1999a) and in other Tethyan and Gulf Coast sections by ARENILLAS et al. (2000a, b).

This foraminiferal event-stratigraphy may help to test phylogenetic and adaptational hypotheses in the foraminiferal record and may be useful for correlation and the detection of hiati in the K/Pg boundary interval. Since benthic foraminifers are strongly dependent on environmental parameters such as the nutrient supply to the seafloor and the oxygenation of the sea

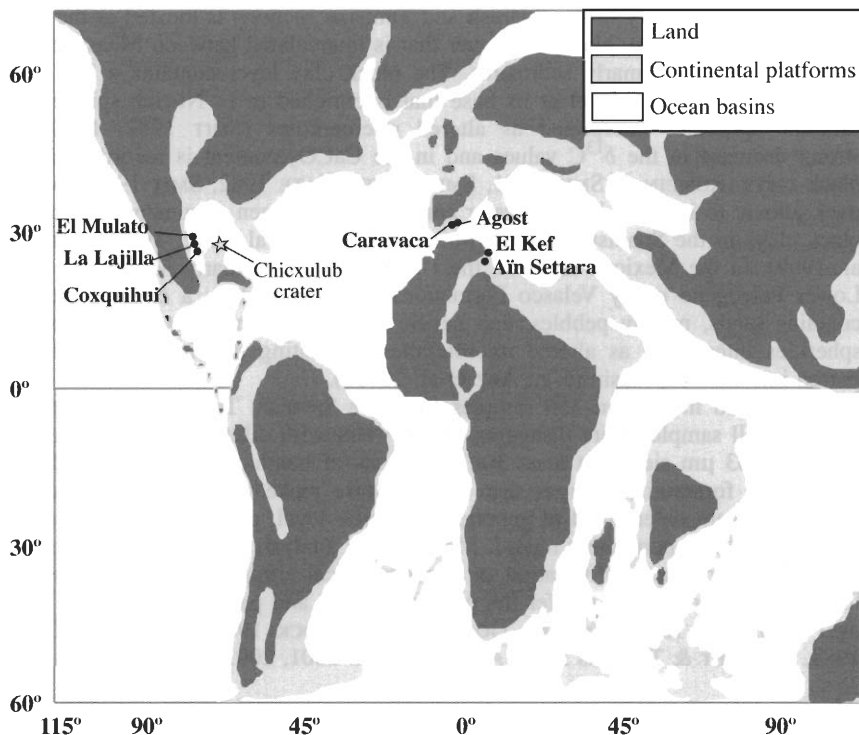


Fig. 1. Location of the seven studied K/Pg boundary sections. Paleogeographical distribution according to DENHAM & SCOTSE (1987).

water (e. g. BERNHARD 1986, JORISSEN et al. 1995) changes in their composition reflect the paleoenvironmental evolution during the same interval.

Material and methods

We performed a quantitative study of the latest Maastrichtian and earliest Danian benthic and planktic foraminiferal assemblages from seven sections located in the Tethys and Gulf of Mexico areas (Fig. 1). We selected some of the most expanded K-Pg boundary sections from both areas (Spain: Agost and Caravaca sections, Tunisia: Ain Settara and El Kef sections, Gulf of Mexico area: Coxquihui, La Lajilla and El Mulato sections). These sections represent a wide paleobathymetric range: El Kef and Ain Settara – outer shelf to upper bathyal (PERYT et al. 2002), Agost and Caravaca - upper to middle bathyal (ALEGRET et al. 2003), La Lajilla and El Mulato – upper part of lower bathyal, Coxquihui – lower part of lower bathyal (ALEGRET et al. 2001, 2002 a, b).

The K/Pg boundary in the Spanish and Tunisian sections is located at the base of a 10 to 60-cm thick black clay layer that is intercalated between Maastrichtian and Danian pelagic marly sediments. The black clay layer contains a 2-3 mm-thick, red, ferruginous level at its base that is enriched in Ir, Ni-rich spinels and sanidine spherules interpreted as altered microtektites (SMIT 1982; 1990). A strong decrease in the $\delta^{13}\text{C}$ values and in the CaCO_3 content is recorded in the black clays (ROMEIN & SMIT 1981, SMIT & TEN KATE 1982, SMIT 1990). Moreover, anoxic to hypoxic bottom water conditions have been documented from the black clays in the Spanish sections (MARTINEZ-RUIZ et al. 1992, 1999, KAIHO et al. 1999). In the Mexican sections, the Upper Cretaceous marly Méndez and the Lower Paleogene marly Velasco Formations are separated by a clastic unit that contains sands, muddy pebbles, and neritic (shallow) faunas mixed with microspherules interpreted as altered microtektites, indicating that it has been transported into the deep basin (e.g., ARZ et al. 2001b).

We studied more than 350 samples from the Spanish, Tunisian and Mexican sections. All samples were disaggregated in water with diluted H_2O_2 and washed through a 63 μm sieve. At least 300 specimens of benthic foraminifera and 300 of planktic foraminifera larger than 63 μm were picked from each sample; all specimens were determined at generic or specific level, counted and mounted in microslides for a permanent record. Morphotypic analysis of benthic foraminifera as well as additional information on morphological similarity to recent benthic foraminifera allowed us to infer the paleoecological and paleoenvironmental turnover across the K/Pg boundary (JONES & CHARNOCK 1985, CORLISS & CHEN 1988, ALEGRET & THOMAS 2001, ALEGRET et al. 2001, 2003).

Planktic foraminiferal biostratigraphy

We used the planktic foraminiferal zonations proposed by ARZ & MOLINA (2002) and ARENILLAS et al. (2004), who distinguished several subzones within the biozones proposed by MOLINA et al. (1996). We identified the later Maastrichtian *Abathomphalus mayaroensis* Zone, and mainly studied the *Plummerita hantkeninoides* Subzone. The *Plummerita hantkeninoides*


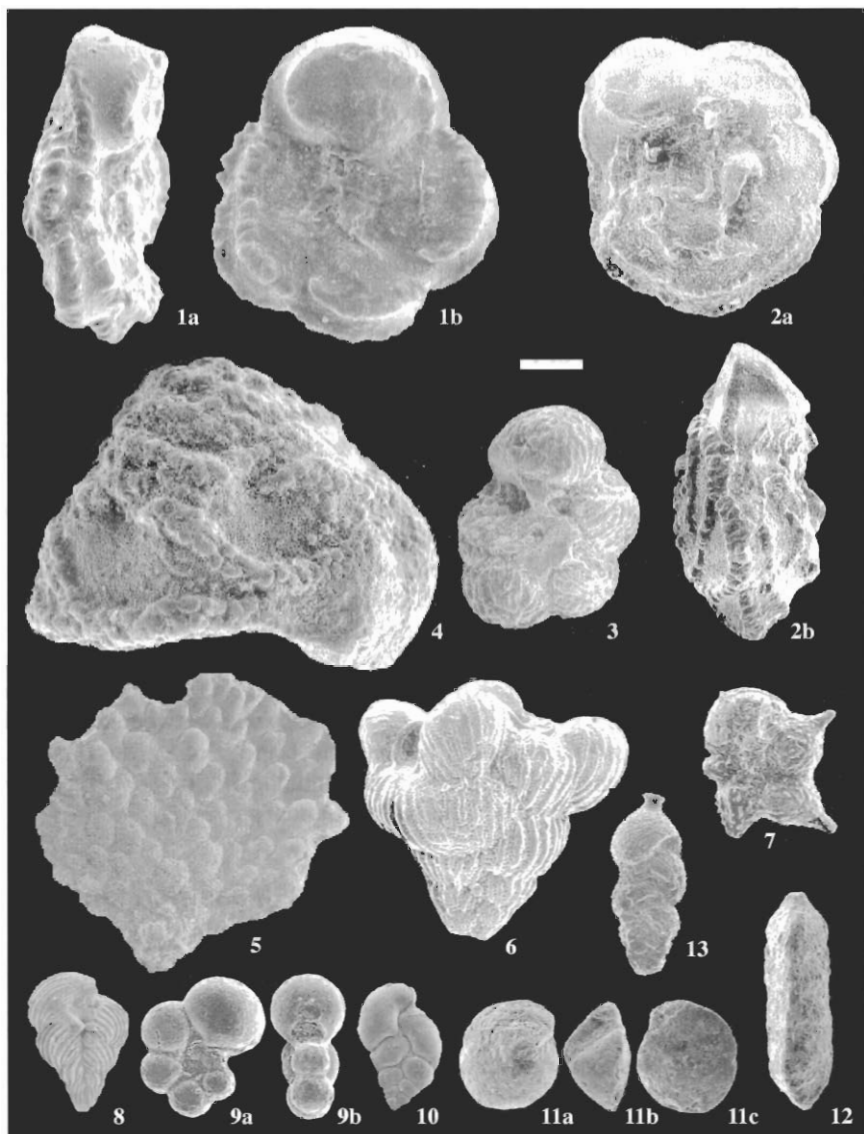


Fig. 2. Most significant species of the *P. hantkeninoides* Zone: 1a,b: *Abathomphalus mayaroensis*, from Aïn Settara, Tunisia; 2a,b: *Globotruncana arca*, from Aïn Settara, Tunisia; 3: *Rugoglobigerina hexacamerata*, from Agost, Spain; 4: *Contusotruncana contusa*, from Caravaca, Spain; 5: *Planoglobulina manuelensis*, from Aïn Settara, Tunisia; 6: *Racemiguembelina powelli*, from Aïn Settara, Tunisia; 7: *Plummerita hantkeninoides*, from Caravaca, Spain; 8: *Pseudoguembellina costulata*, from Aïn Settara, Tunisia; 9: *Heterohelix pulchra*, from Aïn Settara, Tunisia; 10a,b: *Globigerinelloides volutus*, from El Kef, Tunisia; 11a,c: *Gyroidinoides beisseli*, from La Lajilla, Mexico; 12: *Eouvigerina subsculptura*, from Aïn Settara, Tunisia; 13: *Clavulinoides trilatera*, from La Lajilla, Mexico (Scale bar corresponds to 100 μm).



Subzone is defined by the total range of the nominate species. The youngest occurrences of *Plummerita hantkeninoides* and *Abathomphalus mayaroensis* are precisely at the K/Pg boundary (MOLINA et al. 1996), dated at 65 Ma by BERGGREN et al. (1995) and at 65.5 Ma by RÖHL et al. (2001).

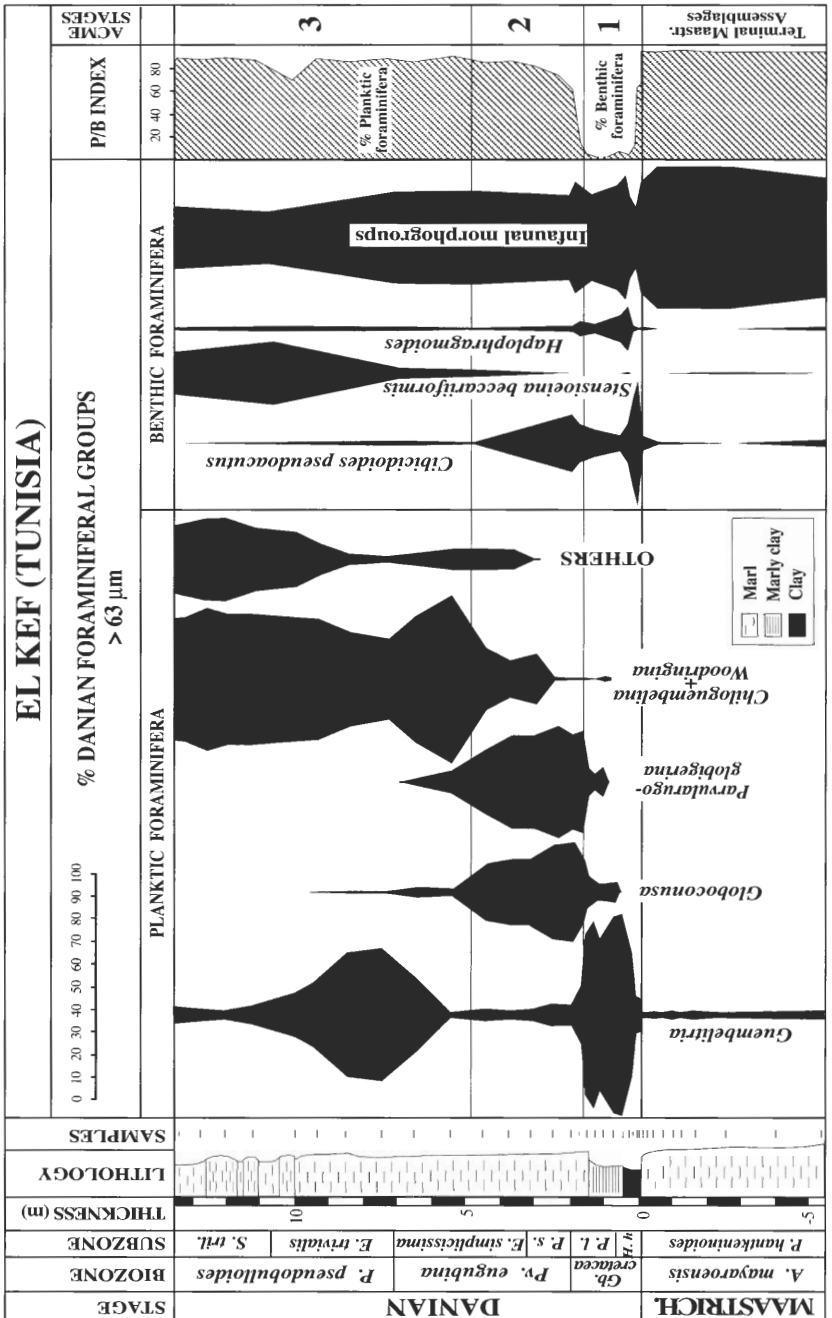
In the lower Danian, we identified the *Guembelitra cretacea* Zone, subdivided into the *Hedbergella holmdelensis* and *Parvularugoglobigerina longiapertura* subzones, the *Parvularugoglobigerina eugubina* Zone, with the *Parvularugoglobigerina sabina* and *Eoglobigerina simplicissima* subzones, and the *Parasubbotina pseudobulloides* Zone, with the *Eoglobigerina trivialis* and the *Subbotina triloculinoides* subzones. For the definition of the Danian biozones and subzones, ARENILLAS et al. (2004) used the lowest stratigraphic occurrences of *Pv. longiapertura*, *Pv. eugubina*, *E. simplicissima*, *P. pseudobulloides*, *S. triloculinoides* and *G. compressa*. The earliest stratigraphic occurrence of *Pv. longiapertura* (base of the biozone of the same name) approximately corresponds to the earliest record of Paleogene species. Therefore, the *H. holmdelensis* Subzone is equivalent to the *Guembelitra cretacea* Zone of CANUDO et al. (1991) and APELLÁNIZ et al. (1997) and the Zone P0 of BERGGREN et al. (1995) and KELLER et al. (1995).

The biomagnetostratigraphic correlation and calibration established at Agost, Caravaca and Zumaya allowed us to estimate the age for the first appearances (FA) of the Danian index species (ARENILLAS et al. 2004). The estimated ages are the following: the FA of *Pv. longiapertura* occurred between 5.7 and 6.7 ky after K/Pg boundary, the FA of *Pv. eugubina* between 18.4 and 21.5 ky, the FA of *E. simplicissima* between 33.4 and 39.1 ky, the FA of *P. pseudobulloides* between 54.1 and 63.4 ky, the FA of *S. triloculinoides* between 225.7 and 264.5 ky, and the FA of *G. compressa* between 454.6 and 536.8 ky after the K/Pg boundary event.

Stable oceanic conditions during the late Maastrichtian

Typical planktic foraminiferal assemblages (> 63 µm) of youngest Maastrichtian age are mainly dominated by *Heterohelix globulosa* as well as by the biserial genus *Heterohelix*, *Pseudotextularia* and *Pseudoguembelina*. Other cosmopolitan taxa are frequent, such as *Globigerinelloides* and *Hedbergella*. Nevertheless, most assemblages are rich in large, complex, tropical-subtropical species of globotruncanids (*Globotruncana*, *Globotruncanita*, *Abathomphalus*, *Contusotruncana*) and complex heterohelicids (*Racemi-guembelina*, *Planoglobulina* and *Gublerina*) (Fig. 2). Quantitative studies by

Fig. 3. Relative abundance of foraminiferal groups, acme stages and P/B ratio in the El Kef section (Tunisia).



ARZ et al. (1999a, b, 2000, 2001a, b) find little variation among the relative abundance of the different species within the latest Maastrichtian (*P. hantkeninoides* Subzone) of the Tethyan and Gulf Coast sections. The Cretaceous oceanic assemblages and quantitative studies suggest a typical polytaxic oceanic episode (ARENILLAS et al. 2002). More than 70% of the species became extinct at the K/Pg boundary, coinciding with the base of the layer with the impact evidence (SMIT 1982, MOLINA et al. 1998). If we discount the Cretaceous planktic species whose post-K/Pg survival is doubtful or unproven, the K/Pg extinction affected more than 95% of the planktic species.

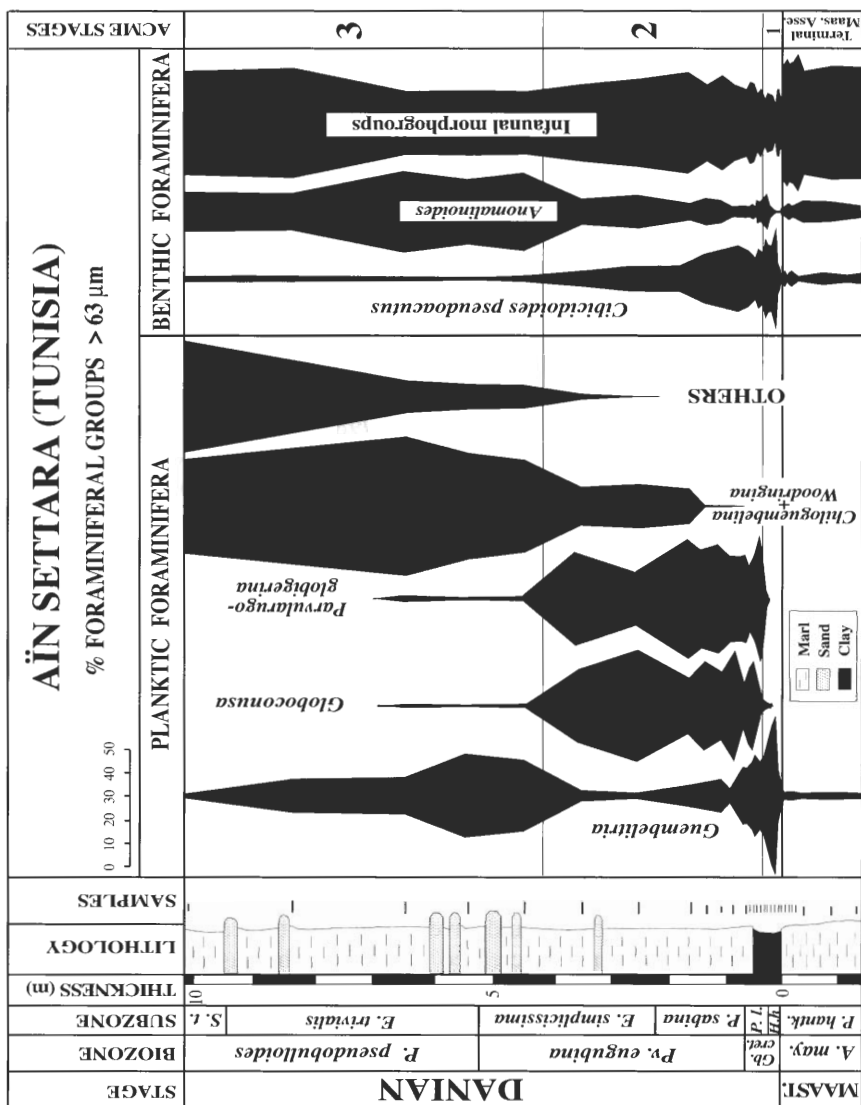
Benthic foraminiferal assemblages during the youngest Cretaceous are also polytaxic, with a complex trophic structure and are composed of mixed infaunal and epifaunal morphogroups, indicating mesotrophic conditions at the sea floor and environmental stability toward the end of the Cretaceous (ALEGRET et al. 2001, 2002a, b, 2003, ARZ et al. 2001a). An increase in shallow infaunal species such as *Clavulinoides trilatera*, *Eouvigerina subsculptura* and *Gyroidinoides beisseli* (LUTZE & COULBOURN 1983, MACKENSEN et al. 1995) is found in bathyal Mexican sections towards the uppermost Maastrichtian, and indicates high organic fluxes and high productivity probably related to local changes in oceanic circulation (ALEGRET et al. 2001). According to GARDIN & MONECHI (1998), the youngest Maastrichtian calcareous nannoplankton assemblages are also abundant and diverse in middle-low latitudes, suggesting mesotrophic and relatively stable oceanic conditions.

Early Danian event-stratigraphy

After the global cooling during the K/Pg impact winter, only some of the smaller, cosmopolitan, Cretaceous planktic foraminiferal taxa such as guembeltriids, hedbergellids, heterohelicids and globigerinellids species, could survive (KELLER 1993, KELLER et al. 1993, 1995, APELLANIZ et al. 1997). Nevertheless, the possible survivorship of some of these Cretaceous species in the early Danian is still controversial (see ARZ et al. 2000). Assuming that several Maastrichtian taxa survived, their supposed gradual extinction in the lower Danian could be related to the long-term effects of the impact-greenhouse effect, disruption in the water column stratification, etc. and/or to biological causes such as competition or endemism (MOLINA et al. 1998).

O'KEEFE & AHRENS (1989) and WOLFE (1990) suggested a high release of CO₂ into the atmosphere after the K/Pg impact winter, due to impact-

Fig. 4. Relative abundance of foraminiferal groups and acme stages in the Ain Settara section (Tunisia).



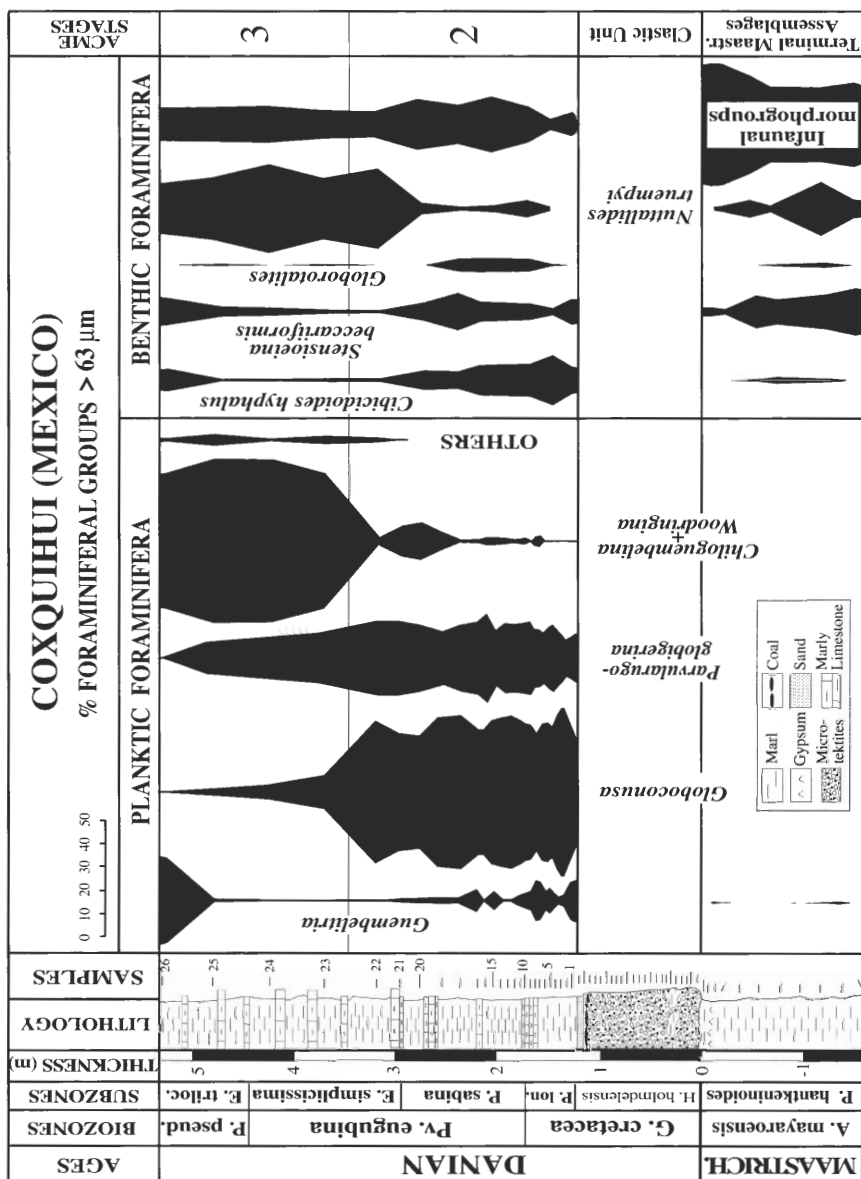
induced CO₂ volatilized from the carbonates of the target area and the short-term cessation of photosynthesis. Alternatively, other authors suggest that the impact-triggered methane hydrate dissociation at the continental margins was the main cause of high pCO₂ levels in the atmosphere (BEERLING et al. 2002; see ALEGRET et al. 2003). The atmospheric accumulation of CO₂ would enhance greenhouse warming, leading to a global increase in temperature for a period of 10,000 years, which is approximately the duration of the boundary clay deposition (see Stage 1). Nevertheless, the exact levels of pCO₂ and the timing of their fluctuations are still under debate (NORDT et al. 2002). The progressive recuperation of 'normal' conditions at the surface of the oceans could have favoured the rapid planktic foraminiferal evolutionary radiation after the K/Pg boundary event (SMIT 1982, D'HONDT 1991, MACLEOD 1993, ARENILLAS et al. 2000 a, b).

The appearance of the earliest Danian planktic foraminiferal species is gradual and several evolutionary events can be recognized (SMIT 1982). We identified three acme stages in the evolution of the post-K/Pg boundary planktic foraminifera (ARENILLAS et al. 1998), which were easily recognized at the El Kef-stratotype section (Fig. 3) as well as in the other sections from both the Tethyan and Gulf Coast areas (Figs. 4-6). The planktic foraminiferal acme stages can be correlated with significant turnovers within the benthic foraminiferal and calcareous nannofossil assemblages (Fig. 7), suggesting an environmental control in the evolution and diversification of the early Danian planktic foraminifers. The three stages are included in the general oligotaxic oceanic episode after the K/Pg boundary event.

Stage 1 - predominance of *Guembelitra*

This stage mainly spans the *H. holmdelensis* Subzone and the lower part of the *Pv. longiapertura* Subzone (\approx 12-13 ky) and is dominated by *Guembelitra cretacea* and *Guembelitra trifolia* (Fig. 8). The planktic/benthic foraminiferal ratio, the percentage of CaCO₃ and the $\delta^{13}\text{C}$ values suddenly dropped after the K/Pg boundary, suggesting a drastic decrease in oceanic productivity. The abundance and diversity of the typical large Cretaceous planktic species suddenly decreased (Fig. 3), whereas the opportunistic 'disaster species' of guembelitriids bloomed immediately after the K/Pg boundary event. In all studied sections, planktic foraminifera of the earliest Danian samples are smaller than 150 μm , except for some Cretaceous specimens that are probably reworked. Some Cretaceous species belonging to

Fig. 5. Relative abundance of foraminiferal groups and acme stages in the Agost section (Spain).



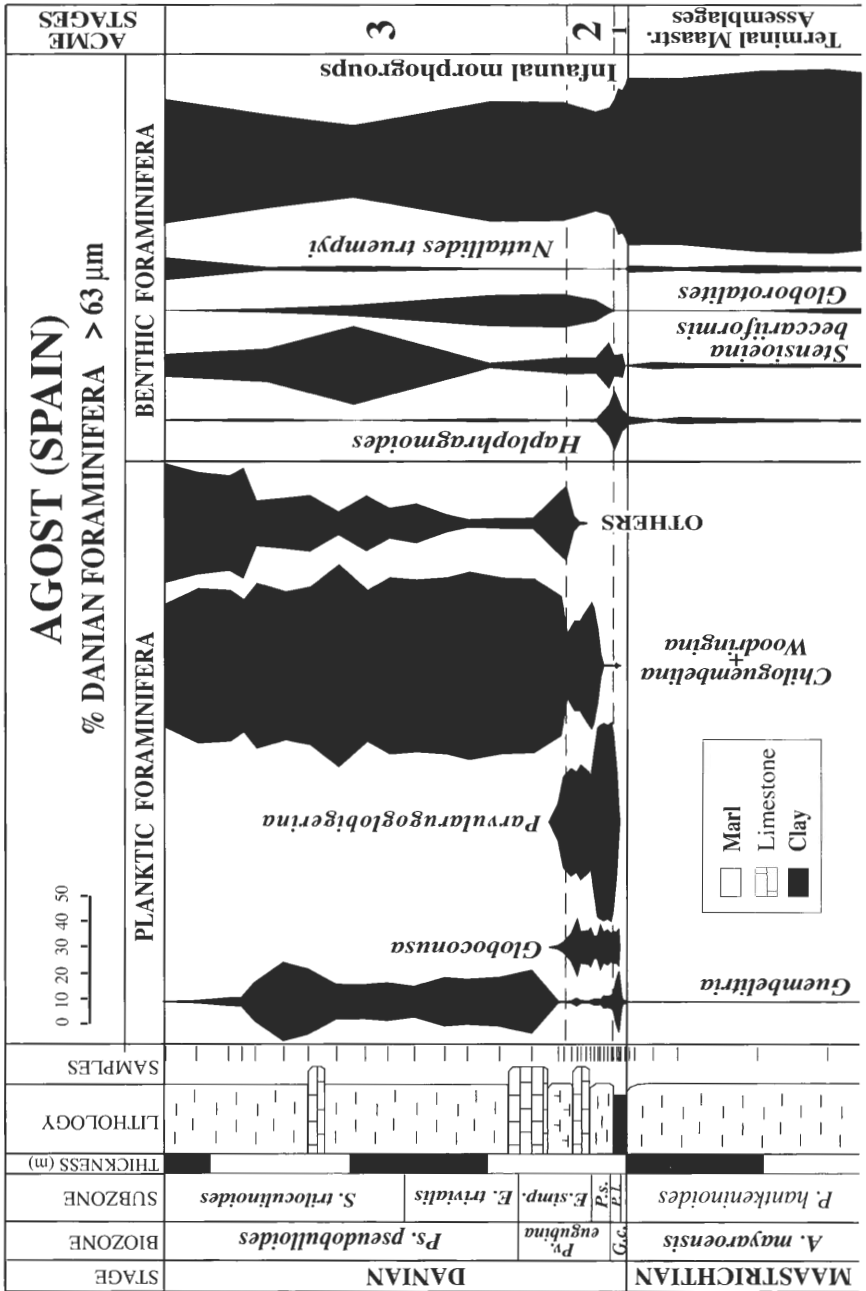
Guembelitra, *Hedbergella* and *Heterohelix* could be considered as possible Cretaceous survivors.

The abundance of infaunal benthic foraminifera drastically decreased at the K/Pg boundary, but only a few extinctions are recorded (e.g., THOMAS 1990, PERYT et al. 1997, 2002, ALEGRET et al. 2001, 2003, CULVER 2003). Most infaunal groups temporarily disappeared and returned during the early Paleogene (Stages 2 and 3) as 'Lazarus taxa'. The percentage of epifaunal morphogroups rapidly increased just after the K/Pg boundary, coinciding with the *Guembelitra* bloom. Thus, *Cibicidoides pseudoacutus* bloomed in shallow, outer-platform to upper bathyal sections such as El Kef or Aïn Settara (Figs. 3, 4), whereas deeper, bathyal sections in both the Tethys area (Agost, Caravaca) and the Gulf of Mexico (Coxquihui, La Lajilla, El Mulato sections) contain abundant *Stensioeina beccariiiformis* and/or *Cibicidoides hyphalus*, among others (Figs. 5, 6). The latter species has been related to oligotrophic environments, typically in deep, bathyal sections (SPEIJER & VAN DER ZWAAN 1996, VAN MORKHOVEN et al. 1986).

The dominance of epifaunal morphogroups strongly supports a decrease in the food supply to the sea-floor due to the collapse of surface-water productivity at the K/Pg boundary (e.g., ZACHOS & ARTHUR 1986, D'HONDT et al. 1998). The bloom of *Guembelitra* and *Cibicidoides/Stensioeina*, as well as the appearance of several quantitative peaks in the abundance of opportunistic benthic foraminiferal genera such as *Haplophragmoides*, *Ammodiscus*, *Glomospirella* or *Repmanina* and others (ALEGRET et al. 2003) is paralleled by an increase in the relative abundance of the calcareous dinocyst *Thoracosphaera* (PERCH-NIELSEN et al. 1982, GARDIN & MONECHI 1998). According to ESHET et al. (1992), the bloom of *Thoracosphaera* indicates a productivity minimum during Stage 1 and a drastic disruption in the stratification of the water column. ALEGRET et al. (2003) recently suggested that the short quantitative peaks in opportunistic benthic foraminiferal species in this stage may reflect environmental instability, with benthos receiving food from local blooms of primary producers, such as *Thoracosphaera*, *Braarudosphaera* and *Biscutum*, which have been documented worldwide (e.g., THIERSTEIN 1981, PERCH-NIELSEN et al. 1982). They conclude that the benthic foraminiferal turnover in the earliest Danian (Stage 1) reflects not just a collapse of the food supply, but also a major change in its composition as a result of the mass extinction of phytoplankton.

Furthermore, a probable initial decrease in oxygenation of the sea-floor just after the K/Pg boundary has also been documented worldwide at many

Fig. 6. Relative abundance of foraminiferal groups and acme stages in the Coxquihui section (Mexico).



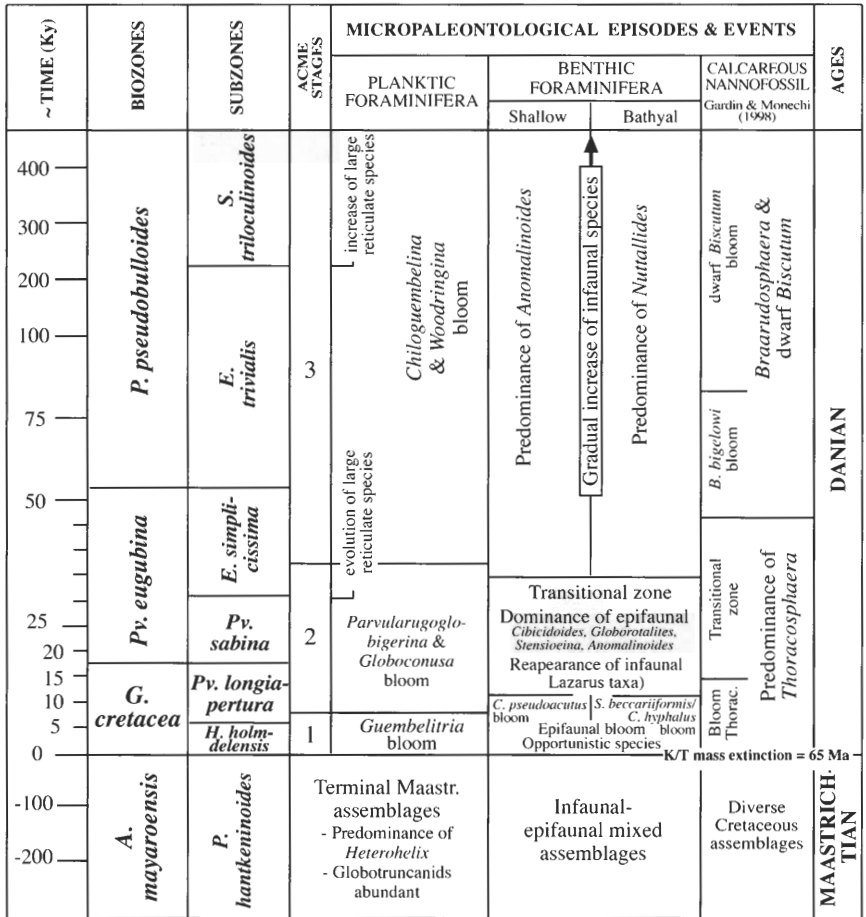
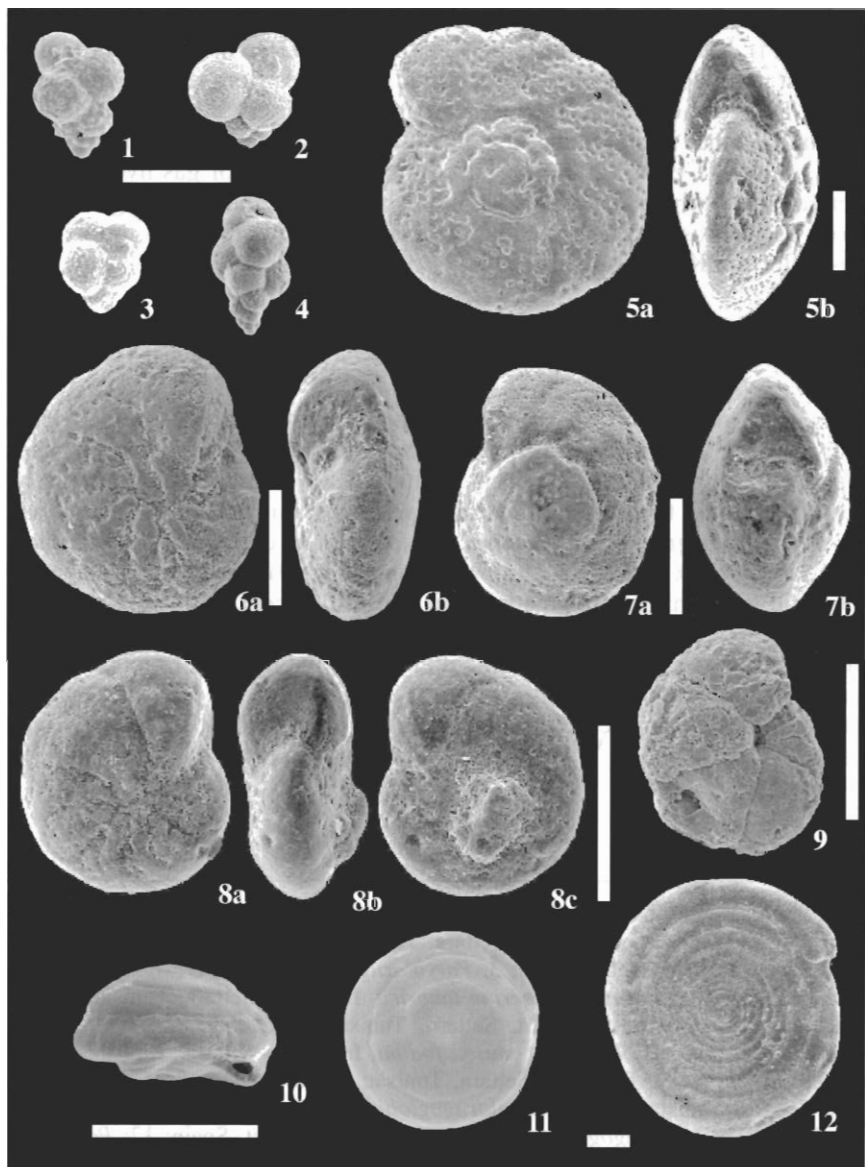


Fig. 7. Correlation of biozones and foraminiferal and nannofossil calcareous acme stages.

Fig. 8. Some species of the *G. cretacea* Zone: 1: *Guembelitra cretacea*, from Ain Settara, Tunisia; 2: *Guembelitra trifolia*, from Ain Settara, Tunisia; 3: *Guembelitra? alabamensis*, from Ain Settara, Tunisia; 4: *Guembelitra irregularis*, from Ain Settara, Tunisia; 5a,b: *Cibicidoides pseudoacutus*, from Ain Settara, Tunisia; 6a,b: *Stensioeina beccariiiformis*, from Agost, Spain; 7a,b: *Cibicidoides hyphalus*, from La Lajilla, Mexico; 8a,b,c: *Stensioeina beccariiiformis*, from La Lajilla, Mexico; 9: *Haplophragmoides*, from Agost, Spain; 10, 11: *Repmanina charoides*, from Agost, Spain; 12: *Ammodiscus cretaceus*, from Ain Settara, Tunisia (Scale bar corresponds to 100 μ m).



sites at intermediate water depths (e. g., COCCIONI et al. 1993, COCCIONI & GALEOTTI 1998, KAIHO et al. 1999, CULVER 2003). These authors mainly suggest that a low oxygen event occurred on the sea floor immediately after the K/Pg event, due to an enhanced organic flux triggered by the K/Pg mass mortality. Since this hypothesis is likely to be quantitatively highly improbable, ALEGRET et al. (2003) proposed the dissociation of gas hydrates present along continental margins as the main cause of the low-oxygen conditions as well as the locally enhanced bacterial food supply to the benthos just after the K/Pg boundary.

Stage 2 - predominance of *Parvularugoglobigerina* and *Globoconusa*

This stage mainly corresponds to the youngest part of the *Pv. longiapertura* Subzone, the *Pv. sabina* Subzone and the older part of the *E. simplicissima* Subzone (approximately between 12 and 40 ky after the K/Pg boundary-event). Planktic foraminiferal assemblages are dominated by *Pv. longiapertura*, *Pv. perexigua*, *Gc. alticonusa*, *Gc. fodina*, *Gc. cf. fringa*, *Gc. minutula*, and later by *Pv. eugubina* and *Pv. sabina* (Fig. 9). Within this stage, all planktic foraminifera are smaller than 150 μm , except in its youngest part. Stage 2 includes the first radiation of new opportunistic species of guembeltriids, woodringinids, chiloguembelinids, and mainly small globoconusids and parvularugoglobigerinids (D'HONDT 1991, MACLEOD 1993, ARENILLAS et al. 1998). A progressive increase in the planktic/benthic foraminiferal ratio, %CaCO₃ and $\delta^{13}\text{C}$ is recorded during this stage.


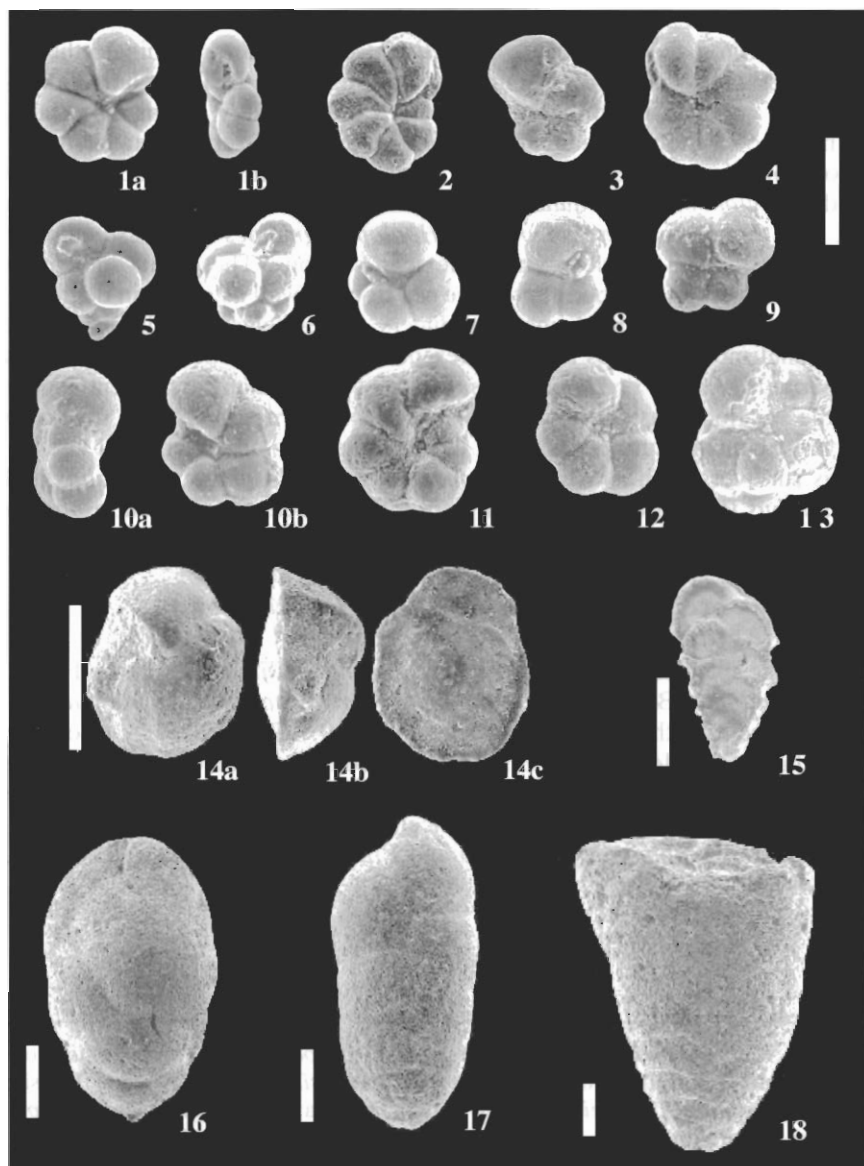


Fig. 9. Most significant species of the *Pv. eugubina* Zone: 1a,b: *Parvularugoglobigerina longiapertura*, from Aïn Settara, Tunisia; 2: *Parvularugoglobigerina longiapertura*, from El Kef, Tunisia; 3: *Parvularugoglobigerina perexigua*, from Agost, Spain; 4: *Parvularugoglobigerina umbrica*, from Aïn Settara, Tunisia; 5: *Globoconusa? alticonusa*, from Aïn Settara, Tunisia; 6: *Globoconusa? alticonusa*, from El Kef, Tunisia; 7: *Globoconusa? fodina*, from Aïn Settara, Tunisia; 8: *Globoconusa? minutula*, from Aïn Settara, Tunisia; 9: *Globoconusa? cf. fringa*, from Aïn Settara, Tunisia; 10a,b: *Parvularugoglobigerina eugubina*, from Aïn Settara, Tunisia; 11: *Parvularugoglobigerina eugubina*, from Agost, Spain; 12: *Parvularugoglobigerina sabina*, from Agost, Spain; 13: *Parvularugoglobigerina cf. hemisphaerica*, from Aïn Settara, Tunisia; 14a,b,c: *Globorotalites*, from El Mulato, Mexico; 15: *Tappanina selmensis*, from Aïn Settara, Tunisia; 16: *Praeglobobulimina quadrata*, from Aïn Settara, Tunisia; 17: *Dorothia bulleta*, from La Lajilla, Mexico; 18: *Marssonella oxycona*, from Aïn Settara, Tunisia (Scale bar corresponds to 100 μm).



During Stage 2, epifaunal benthic foraminiferal taxa such as *Cibicidoides*, *Globorotalites*, *Stensioeina* or *Anomalinoidea* and others, dominate the assemblages, and their diversity increases during Stage 2. The relative abundance of infaunal morphogroups increases only slightly during this stage, either due to the reappearance of some infaunal 'Lazarus' taxa or to the evolution of new ones. Among the infaunal foraminifera, *Globobulimina* and *Praeglobobulimina quadrata* are common in shallow sections such as the Tunisian ones, whereas *Dorothia*, *Haplophragmoides* or *Marssonella* are most common in the deep-water Mexican sections. These data indicate a slight recovery in the food flux to the sea floor as well as a certain degree of stabilization among the primary producers. Nevertheless, the dominance of epifaunal morphogroups and the presence of opportunistic species such as *Haplophragmoides* or *Tappanina selmensis* suggest that the nutrient supply to the sea floor was still low. The nannofossil *Thoracosphaera* (a dinocyst) is very abundant during this stage, but there are also other acmes of Cretaceous survivors such as *Braarudosphaera*, *Cyclagelosphaera*, *Markalius* and *Octolithus* (GARDIN & MONECHI 1998). The increase of *Braarudosphaera* indicates a progressive recuperation of oceanic surface productivity.

Stage 3 - predominance of *Chiloguembelina* and *Woodringina*

This stage spans the younger part of the *E. simplicissima* Subzone and the *P. pseudobulloides* Biozone. *Woodringina hornerstownensis* and *Chiloguembelina morsei* are the dominant species (Fig. 10); *G. cretacea* is also very abundant in the older part of this stage. A second radiation of new Paleogene species is initiated in Stage 3 (ARENILLAS et al. 1998), as indicated by the appearance of taxa with perforate cancellate walled-texture, such as *Eoglobigerina*, *Parasubbotina*, *Subbotina* and *Praemurica* (LIU & OLSSON 1992, OLSSON et al. 1992).


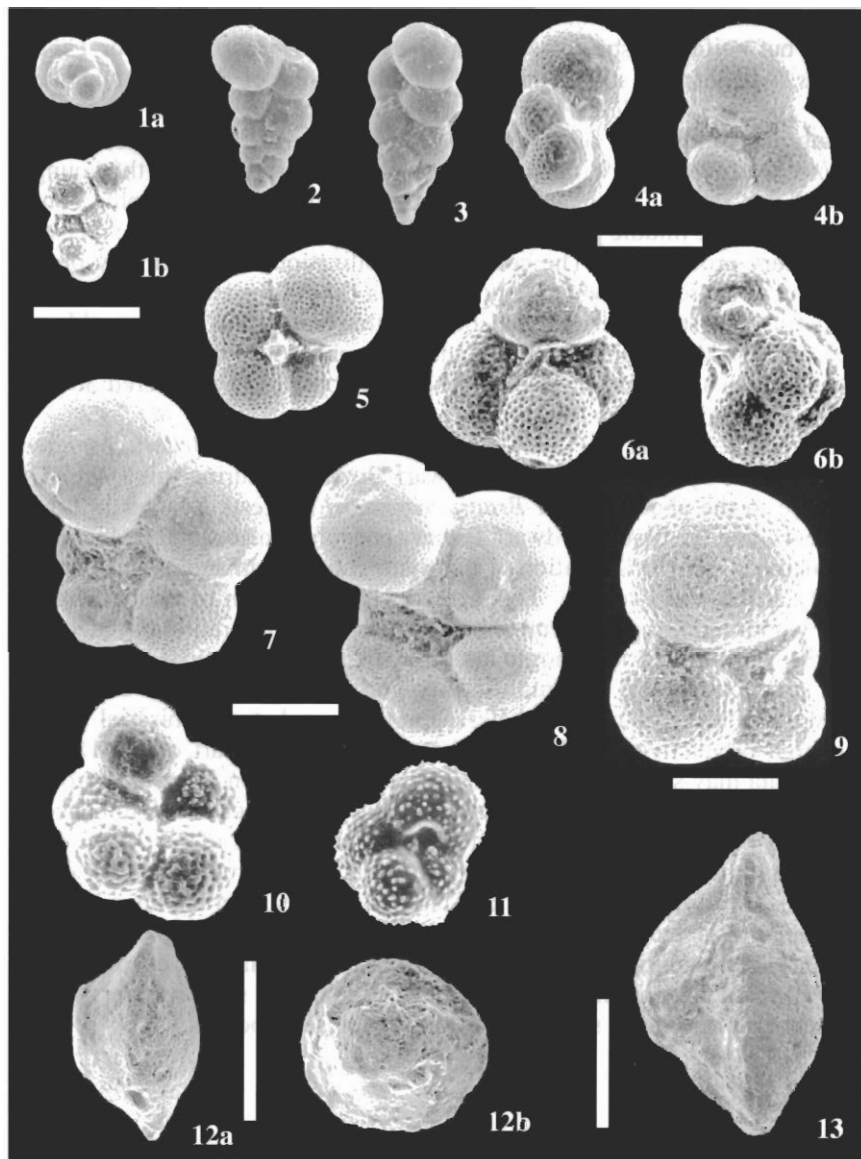


Fig. 10. Most significant species of Stage 3: 1a,b: *Woodringina claytonensis*, from Aïn Settara, Tunisia; 2: *Woodringina hornerstownensis*, from Aïn Settara, Tunisia; 3: *Chiloguembelina morsei*, from Aïn Settara, Tunisia; 4a,b: *Eoglobigerina simplicissima*, from Aïn Settara, Tunisia; 5: *Parasubbotina moskvini*, from Aïn Settara, Tunisia; 6a,b: *Eoglobigerina trivialis* from Caravaca, Spain; 7: *Parasubbotina pseudobulloides*, from Aïn Settara, Tunisia; 8: *Praemurica inconstans*, from Aïn Settara, Tunisia; 9: *Subbotina trilocolinoides*, from Aïn Settara, Tunisia; 10: *Eoglobigerina edita* from Agost, Spain; 11: *Globoconusa daubjergensis*, from Sidi Naseur, Tunisia; 12a,b: *Nuttallides truempyi*, from La Lajilla, Mexico; 13: *Nuttallides truempyi*, from Aïn Settara, Tunisia (Scale bar corresponds to 100 μm).



The abundance of infaunal morphogroups keeps increasing during this stage, but epifaunal species such as *Stensioeina beccariiiformis* or *Cibicides hyphalus* are still dominant. The abundance of the epifaunal 'low-food' species *Nuttallides truempyi* (Fig. 6) increased in bathyal settings during the middle part of Stage 3 (VAN MORKHOVEN et al. 1986, SPEIJER & VAN DER ZWAAN 1996) and progressively decreased towards the younger part of this stage. This quantitative peak may indicate oligotrophic conditions during the middle part of Stage 3, followed by the progressive recovery of primary productivity. The continued stabilization of the primary producers and an increased food supply to the sea floor allowed the development of more diverse and heterogeneous benthic foraminiferal assemblages. Nevertheless, the dominance of epifaunal morphogroups by the end of Stage 3 suggests that primary productivity had not completely recovered 300 kyr after the K/Pg boundary.

GARDIN & MONECHI (1998) report several blooms of *Braarudosphaera bigelowi* and new Tertiary species (dwarf *Biscutum*) during this stage. The increase in the abundance of *Braarudosphaera* suggests a larger influx of nutrients, and the bloom of dwarf Tertiary coccoliths also suggests increased productivity, poor stratification of the water column and anomalous nutrient supply at the water surface. This agrees with the bloom of chiloguembelids, woodringinids and guembelitriids, since the proliferation of Paleogene biserial and triserial morphogroups (and small globigerinids) is related to high productivity and an amplified oxygen minimum zone (BOERSMA & PREMOLI SILVA 1989). Nevertheless, this relation between biserial groups and high productivity could be different in the early part of the Danian. These data may simply imply a progressive recuperation of surface productivity and a slow return to more stable conditions. In fact, the dominance of epifaunal benthic foraminifera and the high percentage of *N. truempyi* indicate that the nutrient flux had not completely recovered in bathyal environments. Toward the upper part of Stage 3, a decrease in the abundance of *N. truempyi* is recorded in deeper environments, and the percentage of infaunal communities significantly increased in shallow environments. Overall, benthic foraminiferal assemblages indicate a slow recovery of the nutrient flux and more stable conditions at the sea floor.

Conclusions

Three planktic foraminiferal acme stages may be recognised in sections from the Tethyan and Gulf of Mexico areas during the early Danian immediately following the mass extinction at the K/Pg boundary. These acme stages correlate with significant benthic foraminiferal and calcareous nanofossil assemblage turnovers, suggesting an environmental control in the evolution and diversification of the early Danian planktic foraminifers.

Stage 1 is represented by the *Guembelitra* bloom, which coincides with blooms of the epifaunal benthic foraminiferal *Cibicidoides/Stensioeina* associations and of the dinocyst *Thoracosphaera*, suggesting a sudden drop in primary productivity just after the K/Pg boundary mass extinction event. Stage 2 is represented by blooms of *Parvularugoglobigerina* and *Globocornusa* and contains transitional assemblages of benthic foraminifera and calcareous nannofossils. Stage 3 corresponds to the blooms of *Woodringina* and *Chiloguembelina*, which are coeval to blooms of the calcareous nannofossils *Braarudosphaera* and dwarfed *Biscutum* and the dominance of epifaunal benthic foraminiferal assemblages with *Nuttallides*, *Cibicidoides* and *Stensioeina*. Stages 2 and 3 indicate a progressive recuperation of surface productivity and a slow return to more stable conditions.

Acknowledgements

This research was funded by DGES project BTE2001-1809, DGA group and project P131/2001 of the Departamento de Educación y Ciencia, and Universidad de Zaragoza project UZ2001-CIEN-01. L. ALEGRET's research was funded by a post-doctoral fellowship (n° ref. EX2003-0007) of the Spanish Ministerio de Educación, Cultura y Deporte.

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Eingegangen am 20. Oktober 2003, angenommen am 3. Januar 2003

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