

## Mass extinction in planktic foraminifera at the Cretaceous/Tertiary boundary in subtropical and temperate latitudes

by EUSTOQUIO MOLINA\*, IGNACIO ARENILLAS\* and JOSÉ A. ARZ\*\*

*Key-words.* – Extinction, Foraminifera, Cretaceous, Tertiary, Spain, Tunisia.

*Abstract.* – The high resolution sampling across the Cretaceous/Tertiary (K/T) boundary of the most expanded and continuous sections located in Spain and Tunisia allows us to test and elucidate the extinction model of Cretaceous planktic foraminifera in subtropical and temperate latitudes. The planktic foraminiferal extinction occurred over a short period, with 5% of the species disappearing in the late Maastrichtian, 70% of the species became extinct at the K/T boundary and about 25% of the species are ranging into the early Danian. The species that became extinct at the K/T boundary were large, complex tropical and subtropical forms that dwelled in deep and intermediate water depths. Their disappearance constitutes the largest and most sudden extinction event in the history of planktic foraminifera. Nevertheless, the small cosmopolitan surface dwellers with simple morphologies appear to have survived and the last of them gradually disappeared in the early Danian. The planktic foraminiferal extinction model can be interpreted as a catastrophic mass extinction that was centred at the K/T boundary, and was superimposed on a less evident and controversial gradual mass extinction which apparently began in the late Maastrichtian and continued into the early Danian. The catastrophic pattern of extinction of 70% of the species at the K/T boundary is very compatible with the effect of a large asteroid impact.

### Extinction en masse des foraminifères planctoniques à la limite Crétacé/Tertiaire en latitudes tropicales et tempérées

*Mots-clés.* – Extinction, Foraminifères, Crétacé, Tertiaire, Espagne, Tunisie.

*Résumé.* – L'échantillonnage de haute résolution à travers la limite Crétacé/Tertiaire (K/T) des coupes les plus étendues et continues situées en Espagne et en Tunisie nous permet de réviser et d'élucider le modèle d'extinction des foraminifères planctoniques du Crétacé en latitudes tropicales et tempérées. L'extinction en masse s'est produite durant une courte période; 5% des espèces apparemment disparaissent au Maastrichtien supérieur, 70% se sont éteintes précisément à la limite K/T et à peu près 25% semblent avoir disparu au Danien inférieur. Les espèces ayant disparues à la limite K/T sont grandes et complexes, comparables aux formes vivant en milieux océaniques relativement profonds tropicaux et subtropicaux. Leur disparition représente l'événement d'extinction le plus important et soudain de l'histoire des foraminifères planctoniques. Toutefois, les petites formes cosmopolites ayant une morphologie simple et vivant dans les eaux superficielles semblent avoir survécu et la plupart ont disparu progressivement au cours du Danien inférieur. Le modèle d'extinction des foraminifères planctoniques peut être considéré comme une extinction en masse catastrophique concentrée à la limite K/T et superposée à une extinction en masse graduelle moins évidente et polémique qui apparemment aurait commencé au Maastrichtien supérieur et aurait continué jusqu'au Danien inférieur. Le patron d'extinction catastrophique de 70% des espèces à la limite K/T est bien compatible avec les effets de l'impact d'un grand astéroïde.

#### VERSION FRANÇAISE ABRÉGÉE

Actuellement il y a un consensus très généralisé parmi les spécialistes sur le modèle d'extinction des foraminifères planctoniques à travers la limite Crétacé/Tertiaire (K/T) qui est considéré comme un modèle d'extinction en masse. Cependant, il existe une forte controverse sur la nature de l'extinction en masse, plus catastrophique pour les uns [Smit, 1977, 1979, 1982, 1990; Smit et Hertogen, 1980; Brinkhuis et Zachariasse, 1988; Haslett, 1994] ou plus graduelle pour les autres [Keller, 1988, 1989a et b, 1993, 1994, 1996; Keller *et al.*, 1995; Canudo *et al.* 1991; MacLeod et Keller, 1994] et par conséquent sur les causes qui l'aurait provoquée.

L'échantillonnage de haute résolution à travers la limite K/T de plusieurs coupes situées en Espagne, en Tunisie et en Italie nous permet de réviser et d'élucider le modèle d'extinction de foraminifères planctoniques du Crétacé en latitudes tropicales et tempérées. Les coupes étudiées qui sont les plus étendues et continues, connues jusqu'à présent sont les suivantes : Agost et Caravaca (Cordillères Bétiques, Sud de l'Espagne), Zumaya (Pyrénées, Nord de l'Espagne) et Ain Settara (Atlas, Tunisie centrale).

L'extinction en masse des foraminifères planctoniques à travers la limite Crétacé/Tertiaire en latitudes tropicales et tempérées s'est produite durant une courte période; 5% des espèces apparemment disparaissent au Maastrichtien supérieur, 70% se sont éteintes précisément à la limite K/T et à peu près 25% semblent avoir disparu au Danien inférieur. Les espèces ayant disparues à la limite K/T sont grandes et complexes, des formes vivant en milieux océaniques profonds tropicaux et subtropicaux [Keller, 1993, 1994, 1996]. Ces formes ne constituent qu'environ 20% des spécimens de la population de taille supérieure à 63 microns et 30% de la population supérieure à 100 microns. Cependant, leur disparition représente l'événement d'extinction le plus important et soudain de l'histoire des foraminifères planctoniques [Luterbacher et Premoli Silva, 1964; Molina, 1994, 1995; Molina *et al.*, 1996; Arenillas, 1996; Arz, 1996].

Toutefois, les petites formes cosmopolites ayant une morphologie simple et vivant dans les eaux superficielles semblent avoir survécu et la plupart ont disparu progressivement au cours du Danien inférieur. Quelques-unes d'entre elles sont probablement remaniées et des études isotopiques seraient nécessaires pour confirmer cette hypothèse. Les formes cosmopolites vivant en eaux superficielles furent moins affectées [Keller, 1994; Pardo, 1996], la raison étant très probablement qu'elles étaient protégées en hautes latitudes, recolonisant les basses latitudes après l'événement K/T.

Le modèle d'extinction des foraminifères planctoniques peut être considéré comme une extinction en masse catastrophique concentrée à la limite K/T et superposée à une extinction moins évidente et polémique en masse graduelle qui aurait commencé au Maastrichtien supérieur et aurait continué jusqu'au Danien inférieur [Molina, 1994, 1995; Molina *et al.*,

\* Departamento de Ciencias de la Tierra, Universidad de Zaragoza, E-50009 Zaragoza, Spain.

\*\* Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, MEX-67700 Linares, México.  
Manuscrit déposé le 20 février 1997; accepté après révision le 26 novembre 1997.

1996]. Le patron d'extinction catastrophique de 70 % des espèces à la limite K/T est bien compatible avec les effets de l'impact d'un grand astéroïde [Alvarez *et al.*, 1980; Smit et Hertogen, 1980; D'Hondt, 1994], tandis que l'incertain patron d'extinction graduelle de 30 % des espèces au cours de la transition Maastrichtien-Danien le serait avec des changements de température ou probablement du niveau de la mer [Keller et Barrera, 1990] qui pourraient être en rapport avec un volcanisme massif [Courtillet *et al.*, 1986].

En conclusion, les foraminifères planctoniques étaient très abondants et diversifiés durant le Crétacé terminal dans toutes les coupes étudiées. Les assemblages étaient composés d'espèces adaptées à différentes niches écologiques. Les grandes morphologies ornées étaient des espèces de stratégie K qui colonisèrent les milieux relativement profonds. Ces assemblages tropicaux et tempérés qui constituaient environ 70 % des espèces se sont éteints soudainement et simultanément à la limite K/T précisément, en coincidence avec le niveau contenant les évidences d'impact météoritique. Ce patron d'extinction en masse catastrophique constitue l'événement d'extinction le plus important et soudain de l'histoire des foraminifères planctoniques. Cet événement est très compatible avec les effets catastrophiques causés par l'impact d'un grand astéroïde. Cet important patron est superposé à un patron moins évident d'extinction apparemment graduelle d'environ 30 % des espèces. Celles-ci étaient les espèces les plus cosmopolites et opportunistes de stratégie r qui vivaient dans les eaux superficielles. Ce patron d'extinction graduelle pourrait être aussi le résultat à long terme de l'impact d'un grand astéroïde ou de la concurrence avec les nouvelles espèces, mais le polémique petit déclin de 5 % des espèces durant le Crétacé terminal, s'il ne s'agit pas simplement de l'extinction du fond ou de l'effet Signor-Lipps, serait plus compatible avec l'effet graduel causé par un volcanisme massif.

## INTRODUCTION

The model of extinction in planktic foraminifera at the K/T boundary was attributed to a global catastrophic mass extinction by Alvarez *et al.* [1980] when they proposed the famous hypothesis of the extraterrestrial cause for the K/T extinction. Based on the Gubbio section, which is a very condensed section [Luterbacher and Premoli-Silva, 1964; Premoli-Silva, 1977], it was assumed by many geologists that almost all the Cretaceous planktic foraminifera became extinct just at the boundary. Alvarez *et al.* [1980] stated that planktic foraminifera were nearly exterminated. This hypothesis was developed by Smit [1977, 1979; 1982; 1990] and Smit et Hertogen [1980], who studied the planktic foraminifera at Caravaca and Agost (Spain) and concluded that all but one Cretaceous species suddenly became extinct at the K/T boundary. Brinkhuis and Zachariasse [1988] also stated that *Guembelitra cretacea* was the sole planktic foraminifer which survived the K/T extinction event at El Kef (Tunisia). Similarly, Haslett [1994] concluded that with the exception of *G. cretacea* and *Rugoglobigerina hexacamerata* all Cretaceous planktic foraminifera became extinct at the K/T boundary at Bidart (SW France). On the contrary, Keller [1988; 1989a, b; 1993; 1994; 1996] and Keller *et al.* [1995], studying the same sections as Smit, concluded that species extinctions were gradual and selective rather than random and abrupt. Furthermore, Canudo *et al.* [1991] concluded that species extinctions occurred over an extended time period, with about 39-45 % of the species becoming extinct at the K/T boundary and 1/3 of the species surviving into the Tertiary.

These opposed conclusions generated a strong controversy between specialists who favour either a more catastrophic or a more gradual mass extinction model. In order to resolve this controversy the El Kef section in Tunisia was resampled, and unlabeled samples were studied by four specialists (Canudo, Master, Olsson and Orue-Etxebarria). The results of this test were presented at the Snowbird III Conference and both Smit [1994] and Keller *et al.* [1995] claimed that the outcome supported their interpretations. Furthermore, to solve this controversy Molina *et al.* [1996] restudied the Agost section, concluding that the planktic foraminifera extinction model in subtropical latitudes can be interpreted as a catastrophic mass extinction of 47 species that centred at the K/T boundary, and was superimposed on a gradual mass extinction of 23 species, which began in the late Maastrichtian and continued into the early Danian.

Nevertheless, the controversy still continues because the research in this particular field has to take into account the fact that the model of extinction in planktic foraminifera at the K/T boundary can be different across latitudes and depths [Keller 1993; 1994; 1996]. Furthermore, a great part of the controversy about the K/T boundary event is caused by different interpretations of the data and on the methodology used to obtain these data [Molina, 1994; 1995]. The high resolution sampling at a well expanded section is a basic requirement to establish the model of extinction. In addition, to rigorously interpret the data, the Signor and Lipps [1982] effect and the possibility of reworking have to be considered very carefully. Evidently the section has to be continuous [MacLeod and Keller, 1991a, b; D'Hondt and Herbert, 1992; MacLeod, 1996].

In order to elucidate the planktic foraminifera extinction model and the probable causes of extinction at the K/T boundary in subtropical and temperate latitudes we have studied several sections across these latitudes. The most expanded and continuous sections studied are Agost, Caravaca and Zumaya in Spain and Aïn Settara in Tunisia. These belong to the most expanded marine sections known to date. Other sections have also been studied in Italy (Gubbio) and Spain (Alamedilla, Músquiz, Osinaga, etc), but these sections are very condensed or not continuous [Canudo and Molina, 1992; Arenillas *et al.*, 1996]. Although the latter sections are not so relevant to be analyzed in this synthesis, their data have also been taken into account.

## MATERIALS AND METHODS

The Agost and Caravaca sections are located in the Betic Cordillera of southeastern Spain [see the detailed map in Canudo *et al.*, 1991], the section of Zumaya (also known as Zumaia in the Basque language) is located in the western Pyrenees of northern Spain [see the detailed map in Lamolda *et al.*, 1988] and the Aïn Settara section is located in the Atlas of central Tunisia [see the detailed map in Dupuis *et al.*, 1998]. The paleolatitudinal and paleogeographical location of the main K/T boundary sections studied is indicated in figure 1.

A high resolution sampling across the K/T boundary clay was accomplished in every section. Distance between samples is indicated on the figures 2 to 7. Samples were collected at centimetre or decimetre intervals, sampling more in detail across the critical K/T boundary interval.

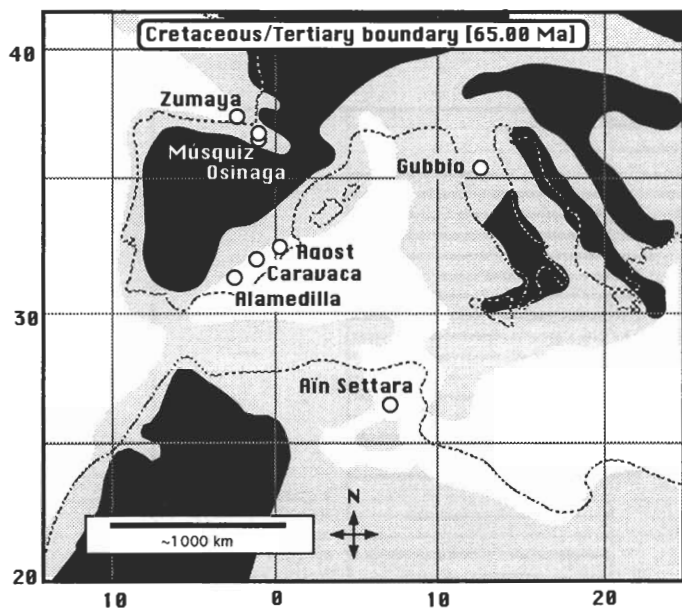


FIG. 1. – Paleolatitudinal and paleogeographic location of the main sections studied [modified from Denham and Scotese, 1987].

FIG. 1. – Localisation paléolatitudinale et paléogéographique des principales coupes étudiées [modifié de Denham et Scotese, 1987].

Samples were disaggregated in tap water and diluted H<sub>2</sub>O<sub>2</sub>, then washed through a 63 micron sieve and dried at 50 °C. The quantitative planktic foraminiferal analysis was based on representative splits, using a modified Otto microsplitter, of 300 or more specimens in the size fraction larger than 63 microns. All the representative specimens were picked, identified and mounted on microslides for a permanent record. Finally, the remaining sample was scanned for rare species.

In figures 2 to 5 the range of abundant species found in the representative splits are indicated by thick lines, whereas the range of the rare species found by scanning of the remaining sample are indicated by thin lines.

## THE K/T BOUNDARY MASS EXTINCTION

At present, there is a general agreement among specialists that the extinction model in planktic foraminifera at the K/T boundary is a mass extinction model, and the controversy deals with the more catastrophic or the more gradual nature of the mass extinction. To solve this controversy is important since, at present, there is also a general agreement that a large asteroid impacted at the K/T boundary, and in the case of the coincidence of the impact with a sudden catastrophic mass extinction the cause-effect relation could be established.

What was the extinction pattern in planktic foraminifera during the late Cretaceous? Was there a decline prior to the K/T boundary? Lamolda *et al.* [1983], Orue-Etxebarria *et al.* [1984], Lamolda [1990], Canudo *et al.* [1991] in Spain, and Longoria and Gamper [1995] in Mexico, observed that faunal changes started before the physical features attributed to the K/T impact. Molina *et al.* [1996] indicated that in the Agost section 7 species disappeared (*Gansserina wiedenmayeri*, *Gansserina gansseri*, *Contusotruncana plicata*, *Rugoglobigerina milamensis*, *Archaeoglobigerina cretacea*, *Rugoglobigerina pennyi* and *Gublerina acuta*) but only one evolved (*Plummerita*

*hantkeninoides*) during the uppermost 13 metres of the Maastrichtian. Nevertheless, the extinctions of *G. wiedenmayeri*, *G. gansseri* and *C. plicata* which are previous to the K/T event can be considered as the result of background extinction. These data are confirmed in the Agost section. In the Caravaca section the same pattern has been recognized in the terminal Maastrichtian, revealing the disappearance of the last three species (*A. cretacea*, *R. pennyi* and *G. acuta*) because our study only includes the uppermost metre of the Maastrichtian (fig. 2 and fig. 3).

In the Zumaya section, three species (*A. cretacea*, *Archaeoglobigerina blowi* and *Contusotruncana walfischensis*) disappear in the uppermost 2.30 metres of the Maastrichtian and only one species (*Abathomphalus mayaroensis*) reappears. Lamolda [1983] recognized the *A. mayaroensis* biozone and indicated the absence of the index species in the uppermost Maastrichtian. Our more intensive search has allowed us to find *A. mayaroensis* in the uppermost Maastrichtian sample. This reappearance of *A. mayaroensis* in the topmost Maastrichtian is also found in the Ain Settara section. The reappearance of *A. mayaroensis* in the last sample just below the boundary both in Zumaya and Ain Settara may have been due to a sea level rise prior to the K/T boundary. This probably was the same sea level rise that Schmitz *et al.* [1992] observed to begin 40 cm below the iridium-rich K/T boundary clay at Stevns Klint (Denmark).

The differences among the Zumaya and the other sections are due to latitudinal reasons, and these differences are more evident in the quantitative analysis [Arz *et al.*, 1992; Arz, 1996]. For instance, *Heterohelix glabrans* and *Heterohelix planata* are more abundant at Zumaya (Pyrenees) than at Ain Settara (Atlas), Agost and Caravaca (Betics). Apart from that, *A. blowi* and *C. walfischensis* seem to have disappeared earlier in Zumaya than in the Atlas and in the Betic sections, and *R. milamensis* among others is absent in the Zumaya section. Consequently, only *A. cretacea* became extinct at Zumaya section prior to the K/T boundary.

Due to latitudinal differences, it was necessary to use two different biozones for the same interval of the uppermost Maastrichtian, *Pseudoguembelina hariaensis* biozone at Zumaya [Arz, 1996; Arenillas *et al.*, 1996] and *Plummerita hantkeninoides* biozone at Agost, Caravaca and Ain Settara [Pardo *et al.*, 1996; Molina *et al.*, 1996]. These biozones correspond to the upper part of the *A. mayaroensis* biozone of the classical biozonations of Bolli [1966] and Blow [1979] (fig. 4 and fig. 5).

Consequently, we can conclude that there is a very small decline during the terminal Cretaceous, since only one species appears and about 7 disappear in the late Maastrichtian, but only 4 of these extinctions are related to the K/T event. This decline seems to be more intensive than the constant background extinction and could constitute the beginning of a gradual mass extinction pattern across the K/T boundary.

How many species became extinct precisely at the K/T boundary? The answer to this question strongly depends on the methodology used, since some rare species could appear to become extinct before their real moment of extinction. This is the Signor-Lipps effect, which we attempted to avoid by scanning intensively the residue of the uppermost Maastrichtian samples [Molina, 1994, 1995; Arz and Arenillas, 1996]. Using such methodology it can be established that in coincidence with the yellow-red layer that marks the K/T boundary 47 species disappear at Agost, 46 species at Caravaca, 44 species at Ain Settara and 44 species at Zumaya. These species were large, complex subtropical forms that dwelled in deep and intermediate water

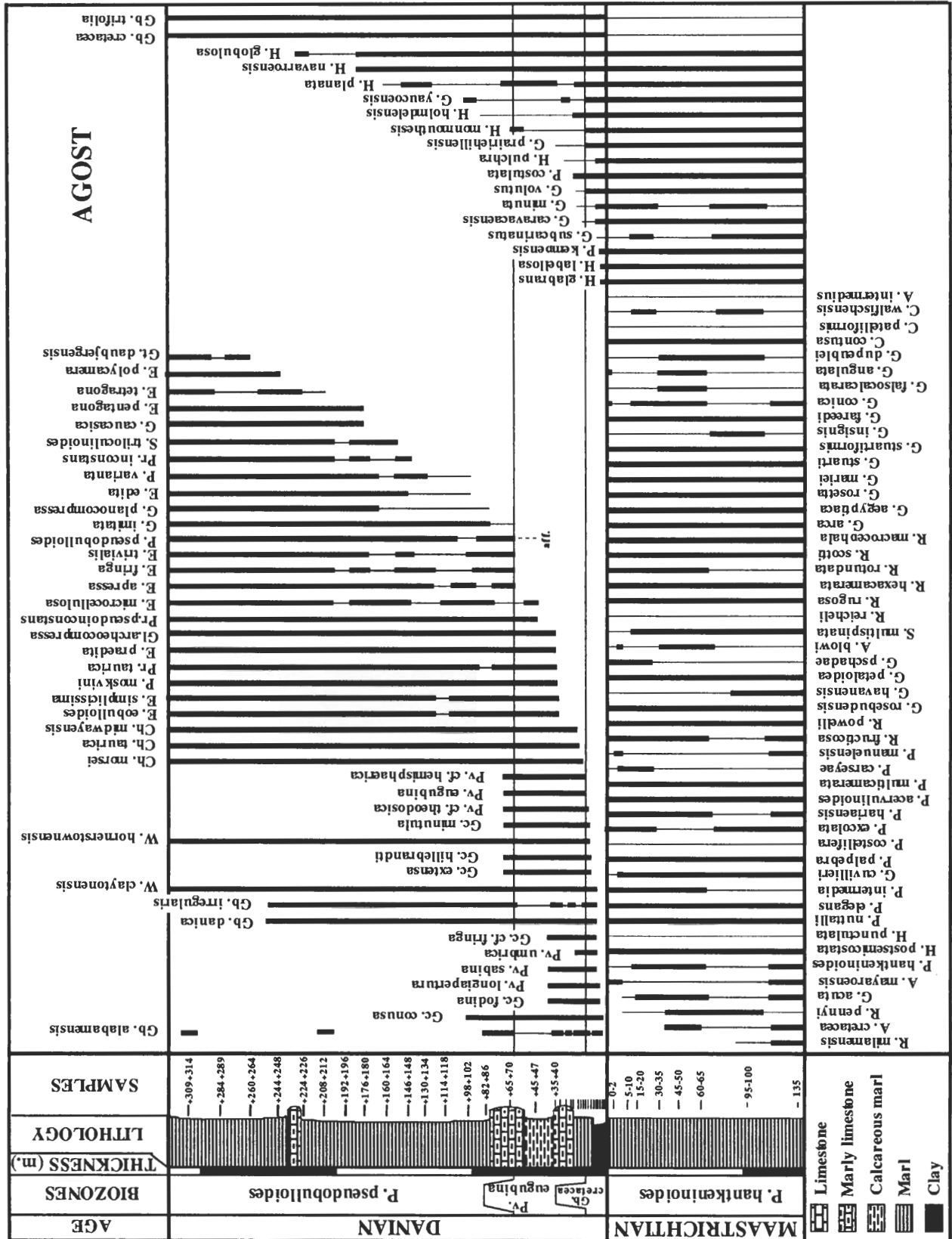


Fig. 2. - Species ranges of planktic foraminifera in the Agost section.  
 Fig. 2. - Distribution stratigraphique des foraminifères planctoniques dans la coupe d'Agost.

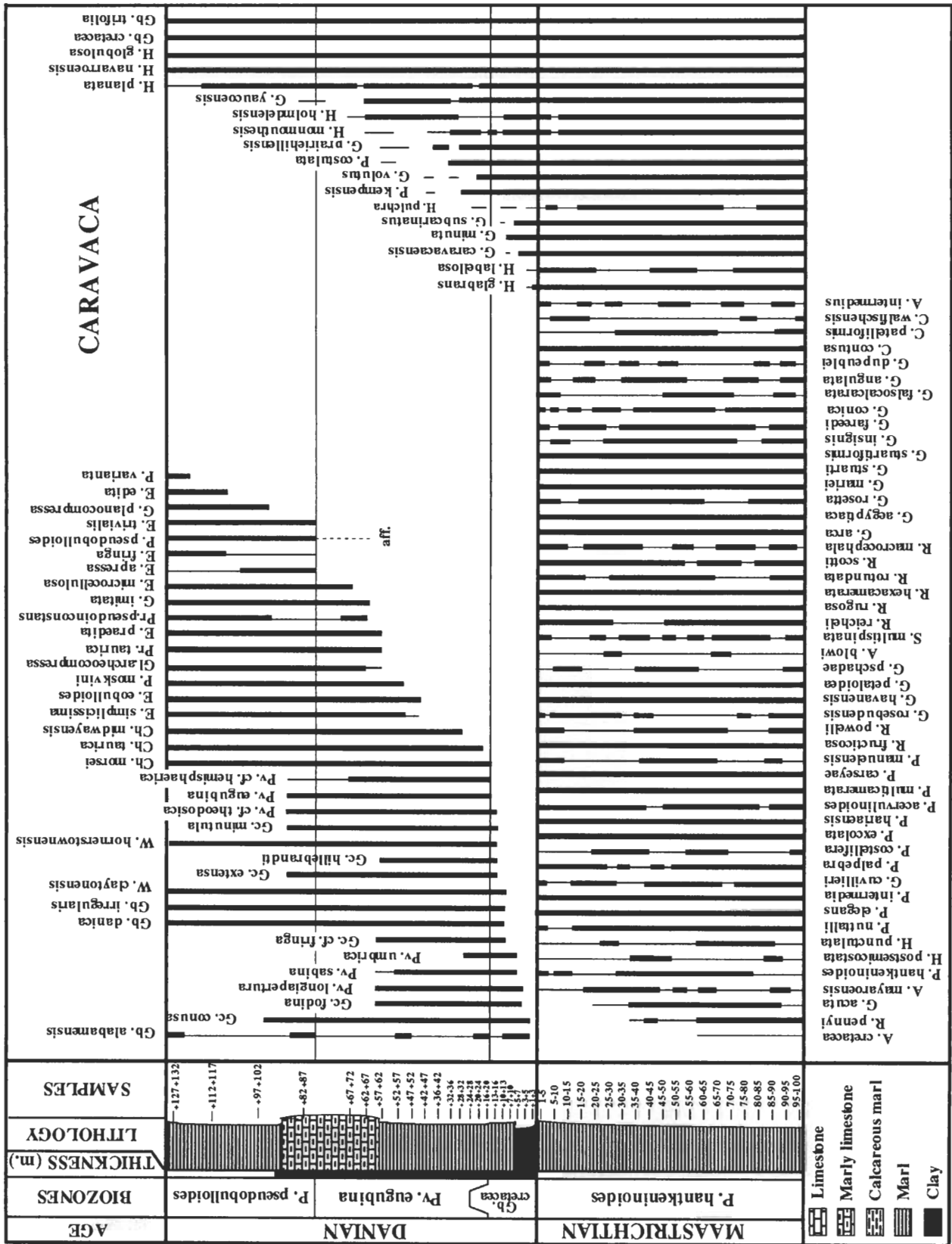


FIG. 3. — Distribution stratigraphique des foraminifères planctoniques dans la coupe de Caravaca.

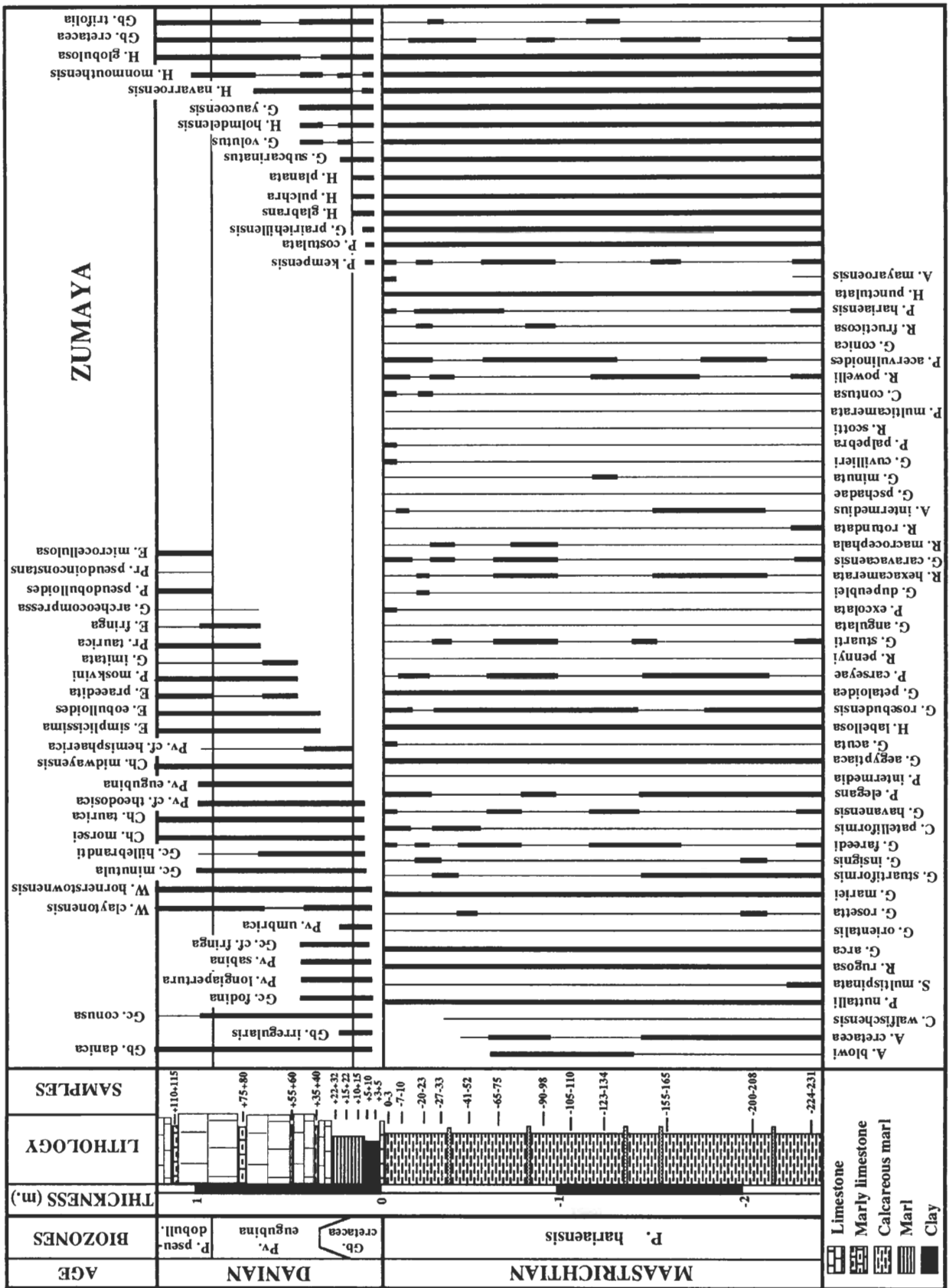


FIG. 4. - Species ranges of planktic foraminifera in the Zumaya section.  
 FIG. 4. - Distribution stratigraphique des foraminifères planctoniques dans la coupe de Zumaya.

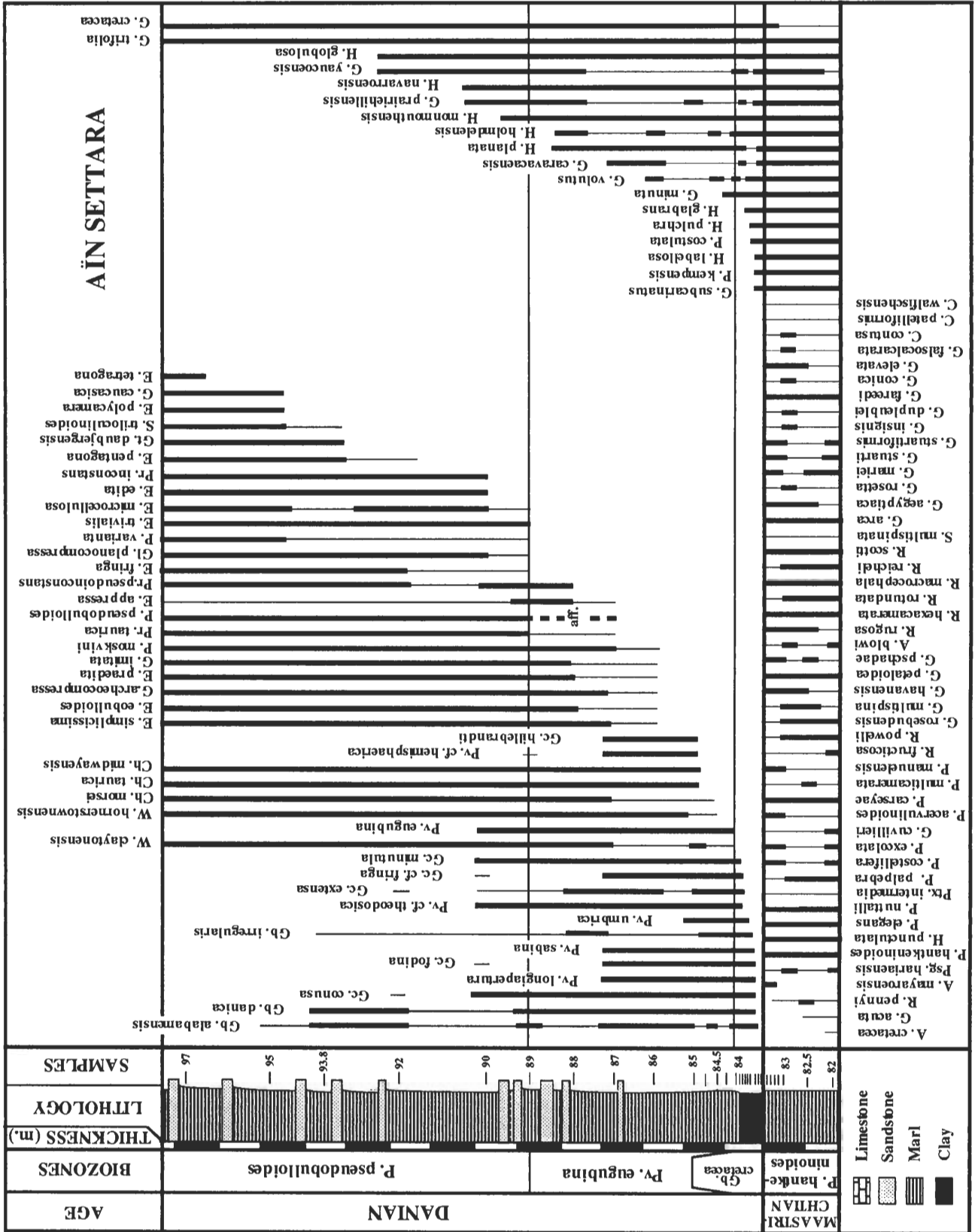


FIG. 5. - Species ranges of planktic foraminifera in the Ain Settara section.  
 FIG. 5. - Distribution stratigraphique des foraminifères planctoniques dans la coupe d'Ain Settara.

depths [Keller, 1993; 1994; 1996]. The differences among the four sections are primarily due to their different paleogeographical location, which explains why in Zumaya only one subtropical species (*A. cretacea*) lived and disappeared during the late Maastrichtian. Furthermore, fewer species seem to have become extinct in Ain Settara than in Agost. The reason may be that some of the deep dwellers species were not present at Ain Settara which is a more shallow section. The sudden extinction affected a total of about 70% of the species, but this represented in all sections about 20% of the specimens in the population larger than 63 microns, 30% in the population larger than 100 microns and 70% in the population larger than 150 microns. Obviously in the 150-micron sieve only the larger species are found, but in the 63-micron sieve the juvenile specimens could produce some redundancy. This simultaneous disappearance constitutes the greatest and most sudden extinction event in the history of planktic foraminifera and can be considered as a catastrophic mass extinction (fig. 6 and fig. 7).

The possibility of reworking has to be carefully considered. The rigorous methodology is important, since sampling with a high resolution technic, the number of reworked specimens should be greater between two closely spaced samples. Our data indicate that 18 Cretaceous species are present in the basal Tertiary at Agost, Caravaca and Ain Settara, whereas 15 are present in Zumaya. This difference can be explained as a result of the higher latitude position of Zumaya section. Some of these species are very probably reworked. Historically, many micropaleontologists assumed that all the Cretaceous specimens present in basal Tertiary samples were reworked and consequently did not survive to the K/T boundary main extinction event [Smit 1982, 1990; Huber, 1991]. Nevertheless, using stable isotope evidence Barrera and Keller [1990] stated that *Heterohelix globulosa*, which is commonly present in Maastrichtian and Danian sediments, exhibits significantly lower  $^{18}\text{O}/^{16}\text{O}$  and  $^{13}\text{C}/^{12}\text{C}$  ratios in Tertiary sediments relative to specimens from Maastrichtian sediments, demonstrating the survival of this important Cretaceous taxon after the K/T boundary event. Hence, some of these specimens were not reworked and about 1/3 of the species survived the K/T event [Keller, 1988, 1989a,b, 1993, 1994; Canudo *et al.*, 1991]. This conclusion is also based in the fact that most of the species present in the basal Danian have a constant presence in several samples from different sections. These species became extinct in the early Danian and the last of them gradually disappeared in the *Parasubbotina pseudobulloides* biozone.

Consequently, apart from the sudden catastrophic pattern of mass extinction coinciding precisely with the K/T boundary, a more gradual pattern of mass extinction can be recognized across the K/T boundary. This gradual pattern is less evident and extended from the late Maastrichtian to the earliest Danian (*P. pseudobulloides* biozone). During this relatively short interval of time about 22 Maastrichtian species became extinct, which represents about 30% of the species and between 70% and 80% of the specimens in the population.

Some concepts of the mass extinction theory [Kauffman and Harries, 1996 and Harries *et al.*, 1996] applied to early Danian planktic foraminifera at Poty quarry in Brazil (Koutsoukos, 1996) can be applied more in detail to our quantitative data. The species that became extinct at the K/T boundary were the deep dwellers of K-strategy, whereas the survivors were the surface dwellers of r-strategy. The species found in the basal Danian are small opportunistic cosmopolitan surface dwellers with simple morphologies which were less affected by the K/T event. The very probable reason is that they also lived in high latitudes, being short-term

refugia species which recolonized the low latitudes immediately after the impact event. In contrast to the benthic foraminifera, in which there are many good examples of Lazarus taxa, the planktic foraminiferal recolonization of the low latitudes would have been very fast and the Lazarus effect would not be evident, due to the different nature of the habitat. Some of the opportunistic species such as *G. cretacea* and *Guembelitra trifolia* were disaster species that bloomed immediately after the K/T boundary in the *G. cretacea* biozone. Others, such as *Hedbergella monmouthensis* and *Hedbergella holmdelensis* were opportunistic pre-adapted survivors that bloomed at the same time (fig. 6 and fig. 7).

Both disaster species and opportunistic species are specifically adapted to stressed environments. When the environment began to recover there was a first radiation of new species from progenitor taxa [Arenillas and Arz, 1996; Arenillas 1996]. These new species were also opportunistic and some of them proliferated (*Parvularugoglobigerina longiapertura*, *Parvularugoglobigerina umbrica*, *Parvularugoglobigerina sabina*, *Globoconusa conusa*, and *Globoconusa fodina*). Most of them can be considered failed crisis progenitors since soon they became extinct in the *P. eugubina* biozone. The survival interval comprises the *G. cretacea* biozone. After the survival interval the ecosystem recovered and new species evolved. These new species have a normal size from the base of *P. pseudobulloides* biozone, where the last failed crisis progenitors (*P. eugubina*, *Parvularugoglobigerina cf. theodosica*, *Globoconusa minutula*, *Globoconusa extensa* and *Globoconusa cf. fringa*) became extinct.

## CAUSES OF THE EXTINCTIONS

Multidisciplinary studies are necessary in order to rigorously conclude the causes of the extinctions across the K/T boundary. This is today the best studied extinction event and it is very evident that a mass extinction took place affecting many groups of organisms. There is strong evidence that a large extraterrestrial body impacted precisely at the K/T boundary and that intensive volcanism and other geological phenomena, such as temperature and sea level changes, took place across the K/T boundary. Nevertheless, many questions concerning the mechanisms and the causes of the extinctions still exist [Molina, 1994; Canudo, 1994; MacLeod, 1996]. Our planktic foraminifera data from the most continuous sections known to date can help to solve these questions.

Were the extinctions caused by the catastrophic effect of a large extraterrestrial bolide impact? This is the most popular question and the answer is not so simple as it seems based on the coincidence of the impact and the extinctions. Applying a rigorous methodology, the cause-effect relation can not be established solely on the basis of the coincidence of the extinction of only a group of microfossils with the impact event. Consequently we will discuss the compatibility of the patterns of extinction with the main possible causes. At present, the extinction of some groups such as the calcareous nannoplankton is generally interpreted as abrupt at the K/T boundary, whereas the extinction of others such as the rudists was more gradual and occurred before the boundary. Other groups are not very well known and their pattern of extinction still is very controversial. For example, the dinosaur extinction model is very controversial due to the discontinuous nature of their fossil record.

On the contrary, the planktic foraminiferal fossil record is one of the most continuous and best studied. Nevertheless, certain discontinuous sections such as Alamedilla [Li-

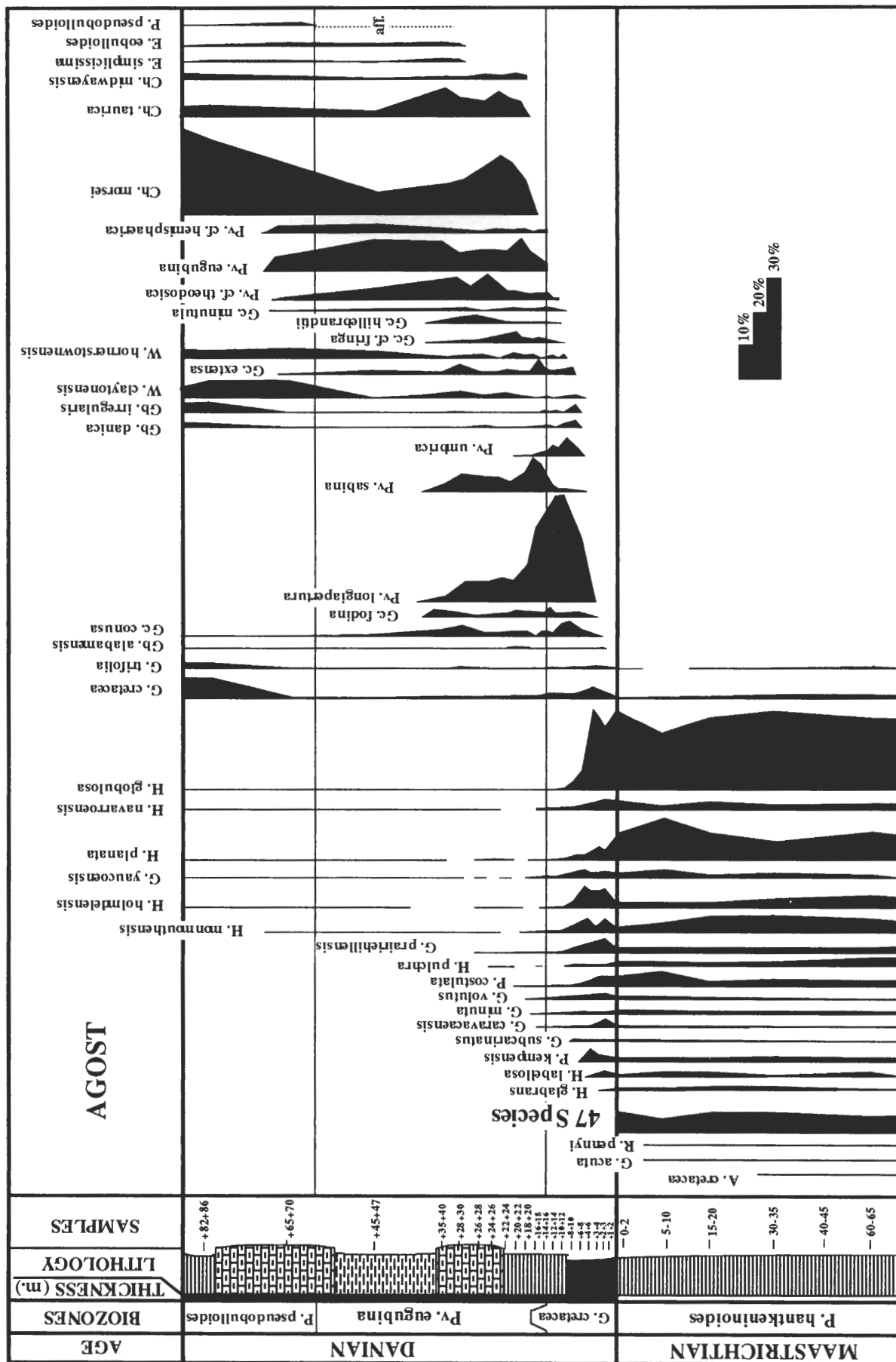


FIG. 6. — Relative abundance of planktic foraminifera species in the Agost section. FIG. 6. — Abondance relative des espèces de foraminifères planctoniques dans la coupe d'Agost.

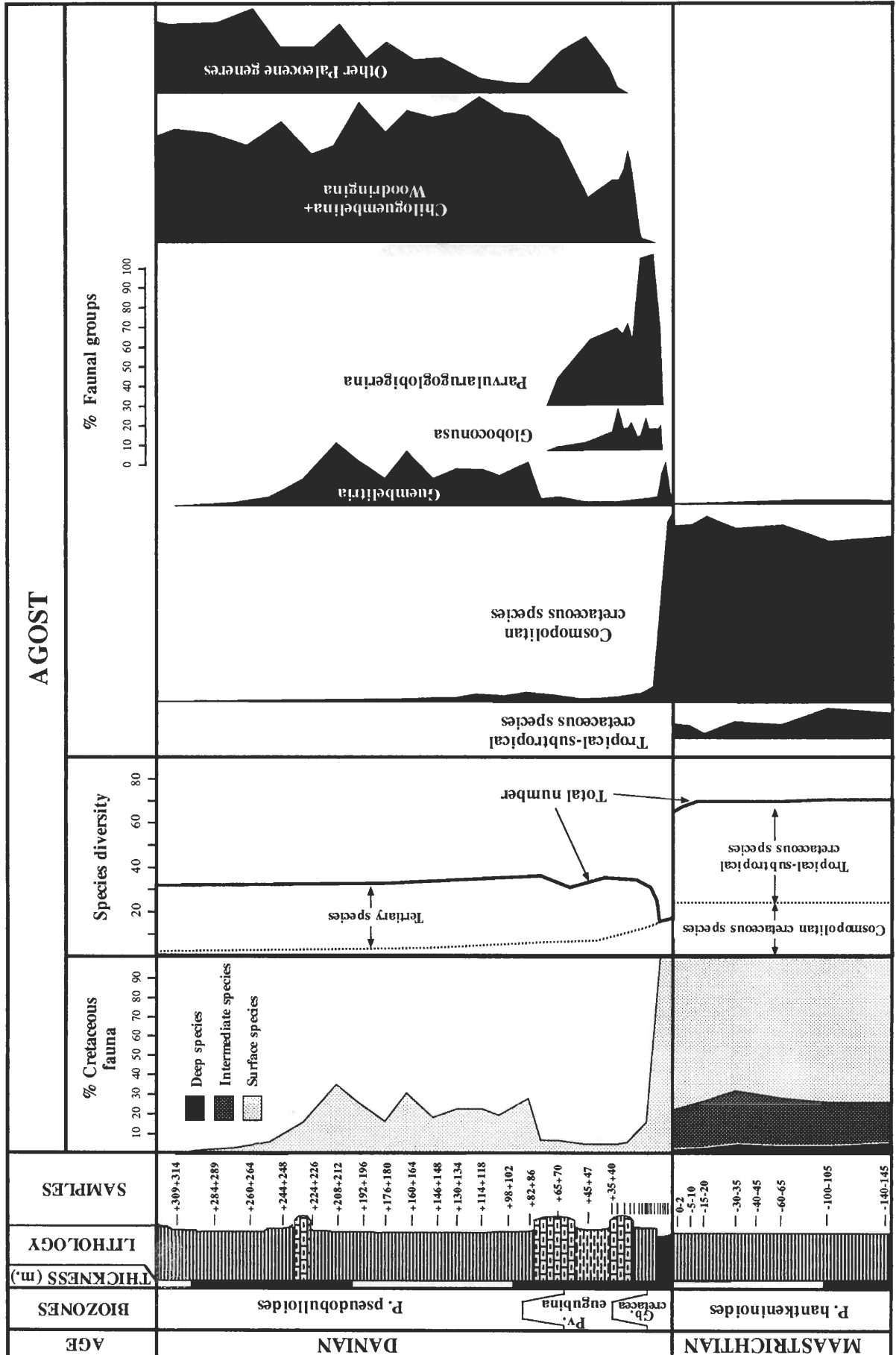


Fig. 7. - Quantitative distribution of planktic foraminifera in the Agost section.  
 Fig. 7. - Distribution quantitative des foraminifères planctoniques dans la coupe d'Agost.

nares and Martínez-Gallego, 1971; Arz, 1996], Músquiz and Osinaga [Arenillas *et al.*, 1996] and Monte Urko [Orue-Etxebarria *et al.*, 1991] are not suitable to study the model of extinction, since it will appear to have been very catastrophic due to hiatuses. Our data from several continuous sections located in subtropical and temperate latitudes provide evidence that favours certain causes of the extinction. The model of extinction based on the continuous sections of Agost, Caravaca, Aïn Settara and Zumaya shows a major catastrophic mass extinction that was centred at the K/T boundary and was superimposed on a less evident gradual mass extinction, which began in the youngest Maastrichtian and ended in the early Danian.

The catastrophic pattern of mass extinction in planktic foraminifera coincides precisely with the level containing the iridium anomaly and other extraterrestrial impact evidence in all the sections studied [Schmitz, 1994; Molina, 1994; 1995]. This coincidence was also reported by Peryt *et al.* [1993] in the Gosau (eastern Alps, Austria). This pattern is very compatible with the catastrophic effects of a large extraterrestrial bolide impact and the cause-effect relation between impact and extinction has been already established by some authors [Smit, 1979, 1982, 1990, 1994; D'Hondt, 1994a,b; D'Hondt *et al.*, 1996]. This catastrophic mass extinction affected the large tropical and subtropical species, which were also well represented in temperate latitudes. This pattern of extinction is not evident in higher latitudes since in their cooler waters lived different assemblages that were not affected by mass extinctions at the K/T boundary [Keller, 1993; Keller *et al.*, 1993; MacLeod and Keller, 1994; Pardo, 1996]. The high-latitude assemblages were composed by small cosmopolitan cold water species. The cosmopolitan species also lived in the temperate and subtropical latitudes and probably were also affected by the impact event in low latitudes, but they were recolonized immediately after the impact event by "refugia" specimens that had been protected in high latitudes.

The gradual pattern of mass extinction in planktic foraminifera is less evident and its causes are more difficult to establish. It occurred over an extended period of time, with about 4 species disappearing in the topmost Maastrichtian and about 18 species in the early Danian, and the possible cause had a gradual effect. The species that became extinct in the early Danian could have also been the long term result of the extraterrestrial impact or the competition with the new evolving species, but this does not explain the small decline in the topmost Maastrichtian before the impact event. The gradual pattern of extinction is more compatible with the effect of intensive volcanism [Courtilot *et al.*, 1986] such as the Deccan volcanism that pre-dated the K/T boundary, since the basal flows overlies infra-trappian beds bearing *A. mayaroensis* [Prasad and Khajuria, 1995]. The volcanism would have generated changes in temperature which have been detected by some authors such as Barrera [1994] and could have been the direct cause of the gradual extinctions. The volcanism and the subsequent changes in temperature could also have produced sea level

changes documented from Texas to Brazil by Keller *et al.* [1994] and Keller and Stinnesbeck [1996] and in Tunisia by Dupuis *et al.* [1998]. The most evident sea level rise took place in the topmost Maastrichtian and pre-dated the K/T boundary. Furthermore, a sea level drop was demonstrated in the earliest Danian (*P. pseudobulloides* biozone) by Mancini *et al.* [1989]. The effect of the level rise produced quantitative changes in the populations and the re-appearance of the deep dweller *A. mayaroensis* in shallow sections such as Aïn Settara. The sea level change could have contributed to the gradual extinctions [Keller and Barrera, 1990] but could not have been an important cause of them, since more intensive sea level changes have been documented throughout the geological history and no mass extinction is clearly associated with them.

## CONCLUSIONS

The planktic foraminifera were very abundant and diversified during the late Cretaceous in all the sections studied. The assemblages were composed of species adapted to different ecological niches. Some large and ornamented morphologies were K-strategy organisms and colonized the deeper environments. Late Maastrichtian planktic foraminifera were very diversified and some species reached very large size. These subtropical assemblages that constituted about 70% of the species suddenly became extinct simultaneously at the K/T boundary in coincidence with the level containing the extraterrestrial bolide impact evidence. This pattern of catastrophic mass extinction constitutes the largest and most sudden extinction event in the history of planktic foraminifera. This extinction event is very compatible with the catastrophic effects caused by the impact of a large extraterrestrial body.

This catastrophic mass extinction at the K/T boundary was superimposed on a less evident gradual mass extinction of about 30% of the species which began during the youngest Maastrichtian and continued during the early Danian. These were the most cosmopolitan and opportunistic r-strategy species that dwelled in shallower water depths, and were survived in higher latitudes during the K/T boundary event. The gradual extinction pattern could also have been the long term result of a large bolide impact or the competition with the new evolving species, but the small decline of 5% of the species in the topmost Maastrichtian could be compatible with a gradual effect caused by massive volcanism.

*Acknowledgements.* – We thank Steven D'Hondt for his helpful comments and English corrections. Comments from the referees Hans Peter Luterbacher and Birger Schmitz improved the manuscript. This research was funded by DGICYT project PB94-0566 and by Gobierno de Navarra project OF/478/92. Ignacio Arenillas is grateful to the Spanish Ministerio de Educacion y Cultura for the postdoctoral grant EX96-0016020964 at Tübingen (Germany).

## References

- ALVAREZ L.W., ALVAREZ W., ASARO F. & MICHEL H.V. (1980). – Extraterrestrial cause for the Cretaceous-Tertiary extinction. – *Science*, **208**, 1095-1108.
- ARENILLAS I. (1996). – Los foraminíferos planctónicos del Paleoceno-Eoceno inferior: sistemática, bioestratigrafía y paleoceanografía. – Doct. Thesis, Univ. Zaragoza. 513 p. (unpublished).
- ARENILLAS I. & ARZ J.A. (1996). – Origen y filogenia de las primeras especies de foraminíferos planctónicos del Paleoceno basal, tras el límite Cretácico/Terciario. – *XII Bienal Real Sociedad Española de Historia Natural*, 267-272.
- ARENILLAS I., ARZ J.A. & MOLINA E. (1996). – El límite Cretácico/Terciario con foraminíferos planctónicos en Osinaga y Músquiz (Navarra, Pirineos). – *Geogaceta*, **21**, 25-28.
- ARZ J.A. (1996). – Los foraminíferos planctónicos del Campaniense y Maastrichtiense: bioestratigrafía, cronoestratigrafía y eventos paleoecológicos. – Doct. Thesis, Univ. Zaragoza, 419 p. (unpublished).
- ARZ J.A. & ARENILLAS I. (1996). – Discusión de los modelos de extinción para los foraminíferos planctónicos del límite Cretácico/Terciario en el corte de Agost (Cordilleras Béticas). – *XII Bienal RSEHN*, 281-286.
- ARZ J.A., CANUDO J.I. & MOLINA E. (1992). – Estudio comparativo del Maastrichtiense de Zumaya (Pirineos) y Agost (Béticas) basado en el análisis cuantitativo de los foraminíferos planctónicos. – *Actas III Cong. Geol. Esp.*, Salamanca, **1**, 487-491.
- BARRERA E. (1994). – Global environmental changes preceding the Cretaceous-Tertiary boundary: early-late Maastrichtian transition. – *Geology*, **22**, 877-880.
- BARRERA E. & KELLER G. (1990). – Stable isotope evidence for gradual environmental changes and species survivorship across the Cretaceous/Tertiary boundary. – *Paleoceanography*, **5**, 6, 867-890.
- BLOW W.H. (1979). – The Cretaceous Globigerinida. – E.J. Brill, Leiden, 1413.
- BOLLI H.M. (1966). – Zonation of Cretaceous to Pliocene marine sediments based on Planktonic foraminifera. – *Asoc. Venez. Geol. Miner. Petrol.*, **9**, 1, 3-32.
- BRINKHUIS H. & ZACHARIASSE W.J. (1988). – Dinoflagellate cysts, sea level changes and planktonic foraminifera across the Cretaceous-Tertiary boundary at El Haria, Northwest Tunisia. – *Mar. Micropaleontol.*, **13**, 153-191.
- CANUDO J.I. (1994). – Bioestratigrafía y evolución de los foraminíferos planctónicos en el tránsito Cretácico-Terciario en España. In: MOLINA E., Ed., Extinción y registro fósil. Extinction and the fossil record. – *Cuad. Interdiscipl.*, **5**, 140-164.
- CANUDO J.I. & MOLINA E. (1992). – Bioestratigrafía y evolución de los foraminíferos planctónicos del límite Cretácico/Terciario en Osinaga (Pirineo de Navarra). – *III Cong. Geol. Esp.*, **2**, 54-62.
- CANUDO J.I., KELLER G. & MOLINA E. (1991). – Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, S.E. Spain. – *Mar. Micropaleontol.*, **17**, 319-341.
- COURTILLOT V.E., BESSE J., VANDAMME D., MONTIGNY R., JAEGER J.J. & CAPPETTA H., (1986). – Deccan flood basalts at the Cretaceous/Tertiary boundary. – *Earth Planet. Sci. Lett.*, **80**, 361-374.
- DENHAM C.R. & SCOTSE C.R. (1987). – Terra Mobilis: A plate tectonic program for the Macintosh, version 1.1 – Geoimages, Austin, 26.
- D'HONDT S. (1994a). – The evidence for a meteorite impact at the Cretaceous/Tertiary boundary. In: E. MOLINA, Ed., Extinción y registro fósil. Extinction and the fossil record. – *Cuad. Interdiscipl.*, **5**, 75-95.
- D'HONDT S. (1994b). – The impact of the Cretaceous-Tertiary boundary. – *Palaios*, **9**, 221-223.
- D'HONDT S. & HERBERT T.D. (1992). – Comment on "Hiatus distributions and mass extinctions at the Cretaceous/Tertiary boundary". – *Geology*, **20**, 380-382.
- D'HONDT S., HERBERT T.D., KING J. & GIBSON C. (1996). – Planktic foraminifera, asteroids, and marine production: Death and recovery at the Cretaceous-Tertiary boundary. – *Geol. Soc. Amer. Spec. Paper*, **307**, 303-317.
- DUPUIS C., STEURBAUT E., MOLINA E., RAUSCHER R., SCHULER M., TRIBO-VILLARD N.P., ARENILLAS I., ARZ J.A., ROBASZYNSKI F., CARON M. & LARQUE P. (1998). – Biotic evolution and events across the Cretaceous-Tertiary (K/T) boundary in the newly discovered Ain Settara section (Kalaat-Senan area, Central Tunisia). – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* (in press).
- HARRIES P.J., KAUFFMAN E.G. & HANSEN T.A. (1996). – Models for biotic survival following mass extinction. In: M.B. HART, Ed., Biotic Recovery from mass extinction events. – *Geol. Soc. Sp. Publ.*, **102**, 41-60.
- HASLETT S.K. (1994). – Planktonic foraminiferal biostratigraphy and paleoceanography of the Cretaceous-Tertiary boundary section at Bidart, south-west France. – *Cretaceous Res.*, **15**, 179-192.
- HUBER B.T. (1991). – Maastrichtian planktonic foraminifer biostratigraphy and the Cretaceous/Tertiary boundary at hole 738C (Kerguelen plateau, Southern Indian Ocean). – *Proc. ODP. Scient. Results*, **119**, 451-465.
- KAUFFMAN E.G. & HARRIES P.J. (1996). – The importance of crisis progenitors in recovery from mass extinction. In: M.B. HART, Ed., Biotic recovery from mass extinction events. – *Geol. Soc. Sp. Publ.*, **102**, 15-39.
- KELLER G. (1988). – Extinction, survivorship and evolution of planktic foraminifera across the Cretaceous/Tertiary boundary at El Kef, Tunisia. – *Mar. Micropaleontol.*, **13**, 239-263.
- KELLER G. (1989a). – Extended period of extinctions across the Cretaceous/Tertiary boundary in planktonic foraminifera of continental shelf sections: Implications for impact and volcanism theories. – *Geol. Soc. Amer. Bull.*, **101**, 1408-1419.
- KELLER G. (1989b). – Extended Cretaceous / Tertiary boundary extinctions and delayed population change in planktonic foraminiferal faunas from Brazos River, Texas. – *Paleoceanography*, **4**, 287-332.
- KELLER G. (1993). – The Cretaceous/Tertiary boundary transitions in the Antarctic Ocean and its global implications. – *Mar. Micropaleontol.*, **21**, 1-45.
- KELLER G. (1994). – Mass extinction and evolution patterns across the Cretaceous-Tertiary boundary. In: E. MOLINA, Ed., Extinción y registro fósil. Extinction and the fossil record. – *Cuadernos Interdiscipl.*, **5**, 165-199.
- KELLER G. (1996). – The Cretaceous-Tertiary mass extinction in planktonic foraminifera: biotic constraints for catastrophe theories. In: N. MACLEOD & G. KELLER, Ed., Cretaceous-Tertiary mass extinctions: biotic and environmental changes. – Norton & Company, New York, 49-84.
- KELLER G. & BARRERA E. (1990). – The Cretaceous/Tertiary boundary impact hypothesis and the paleontological record. – *Geol. Soc. Amer. Spec. Pap.*, **247**, 563-575.
- KELLER G., BARRERA E., SCHMITZ B. & MATTSON E. (1993). – Gradual mass extinction, species survivorship, and long-term environmental changes across the Cretaceous/Tertiary boundary in high latitudes. – *Geol. Soc. Amer. Bull.*, **105**, 979-997.
- KELLER G., LI L. & MACLEOD N. (1995). – The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia: how catastrophic was the mass extinction? – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **119**, 221-254.
- KELLER G. & STINNESBECK W. (1996). – Near-K/T age of clastic deposits from Texas to Brazil: impact, volcanism and/or sea-level lowstand? – *Terra Nova*, **8**, 277-285.
- KELLER G., STINNESBECK W. & LOPEZ-OLIVA J.G. (1994). – Age, deposition and biotic effects of the Cretaceous/Tertiary boundary event at Mimbral, NE Mexico. – *Palaios*, **9**, 144-157.
- KOUTSOUKOS E.A.M. (1996). – Phenotypic experiments into new pelagic niches in early Danian planktonic foraminifera: aftermath of the K/T boundary event. In: M.B. HART, Ed., Biotic recovery from mass extinction events. – *Geol. Soc. Sp. Publ.*, **102**, 319-335.
- LAMOLDA M.A. (1983). – Biostratigraphie du Maastrichtien basco-cantabrique; ses foraminifères planctoniques. – *Géol. Méditerran.*, **X**, 3-4, 121-126.
- LAMOLDA M.A. (1990). – The Cretaceous-Tertiary boundary crisis at Zumaya (Northern Spain). Micropaleontological data. In: E.G. KAUFFMAN & O.H. WALLISER, Ed. Extinction events in Earth History. – *Lecture Notes in Earth Sciences*, **30**, 393-399.

- LAMOLDA M.A., MATHEY B. & WIEDMANN J. (1988). – Field-Guide Excursion to the Cretaceous-Tertiary boundary section at Zumaya (northern Spain). – *Rev. Española Paleontol.*, n° extra, 141-155.
- LAMOLDA M.A., ORUE-ETXEBARRIA X. & PROTO-DECIMA F. (1983). – The Cretaceous-Tertiary boundary in Sopelana (Biscay, Basque Country). – *Zitteliana*, **10**, 663-670.
- LONGORIA J.F. & GAMPER M.A. (1995). – Planktonic foraminiferal faunas across the Cretaceous-Tertiary succession of Mexico : implications for the Cretaceous-Tertiary boundary problem. – *Geology*, **23**, 4, 329-332.
- LINARES D. & MARTINEZ-GALLEGO J., (1971). – Observaciones sobre el tránsito Cretáceo-Paleógeno en el sector de Alamedilla (provincia de Granada). – *Cuad. Geol.*, **2**, 137-146.
- LUTERBACHER H.P. & PREMOLI-SILVA I. (1964). – Biostratigrafia del limite Cretaceo-Terziario nell'Appennino Centrale. – *Riv. Ital. Paleont. Strat.*, **70**, 1, 67-128.
- MACLEOD N. (1996). – The nature of the Cretaceous-Tertiary planktonic foraminiferal record : stratigraphic confidence intervals, Signor-Lipps effect, and patterns of survivorship. In : N. MACLEOD & G. KELLER, Ed., Cretaceous-Tertiary mass extinctions : biotic and environmental changes. – Norton & Company, New York, 85-138.
- MACLEOD N. & KELLER G. (1991a). – Hiatus distribution and mass extinctions at the Cretaceous/Tertiary boundary. – *Geology*, **19**, 497-501.
- MACLEOD N. & KELLER G. (1991b). – How complete are the K/T boundary sections ? – *Geol. Soc. Amer. Bull.*, **103**, 1439-1457.
- MACLEOD N. & KELLER G. (1994). – Comparative biogeographic analysis of planktic foraminiferal survivorship across the Cretaceous/Tertiary (K/T) boundary. – *Paleobiology*, **20**, 2, 143-177.
- MANCINI E.A., TEW B.H., SMITH C.C. (1989). – Cretaceous-Tertiary contact, Mississippi and Alabama. – *J. Foram. Res.*, **19**, 93-104.
- MOLINA E. (1994). – Aspectos epistemológicos y causas de la extinción. In : E. MOLINA, Ed., Extinción y registro fósil. Extinction and the fossil record. – *Cuad. Interdiscipl.*, **5**, 11-30.
- MOLINA E. (1995). – Modelos y causas de extinción masiva. – *Interciencia*, **20**, 2, 83-89.
- MOLINA E., ARENILLAS I. & ARZ J.A. (1996). – The Cretaceous/Tertiary boundary mass extinction in planktic foraminifera at Agost, Spain. – *Revue Micropaleontol.*, **39**, 225-243.
- ORUE-ETXEBARRIA X., LAMOLDA M.A. & APELLANIZ E. (1984). – Los foraminíferos planctónicos del Paleoceno vizcaino y su biostratigrafía. – *Rev. Esp. Micropaleontol.*, **16**, 59-74.
- ORUE-ETXEBARRIA X., ROCCHIA R., PUJALTE V. APELLANIZ E. & BACETA J.I., (1991). – Estudio preliminar del tránsito Cretácico/Terciario en la sección del Monte Urko (Eibar, País Vasco). – *I Congr. Esp. Terc.*, Vic., 240-243.
- PARDO A. (1996). – Latitudinal variation in the K/T event : inferences from planktic foraminifera. – *Geogaceta*, **20**, 1, 66-69.
- PARDO A., ORTIZ N. & KELLER G. (1996). – Latest Maastrichtian and K/T boundary foraminiferal turnover and environmental changes at Agost, Spain. In : N. MACLEOD & G. KELLER, Ed., Cretaceous-Tertiary mass extinctions : biotic and environmental changes. – Norton & Company, New York, 139-171.
- PERYT D., LAHODYNSKY R., ROCCHIA R. & BOCKET D. (1993). – The Cretaceous/Paleogene boundary and planktonic foraminifera in the Flyschogosau (Eastern Alps, Austria). – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **104**, 239-252.
- PRASAD G.V.R. & KHAJURIA C.K. (1995). – Implications of the infra- and inter-trappean biota from the Deccan, India, for the role of volcanism in Cretaceous-Tertiary boundary extinctions. – *J. Geol. Soc. London*, **152**, 289-296.
- PREMOLI-SILVA I. (1977). – The earliest Tertiary *Globigerina eugubina* Zone : paleontological significance and geographical distribution. – *Mem. Seg. Cong. Latin. Geol.*, **3**, 1541-1555.
- SCHMITZ B. (1994). – Geochemical high-resolution stratigraphy of Cretaceous/Tertiary boundary in Denmark, Spain and New Zealand. In : E. MOLINA, Ed., Extinción y registro fósil. Extinction and the fossil record. – *SIUZ Cuad. Interdiscipl.*, **5**, 121-140.
- SCHMITZ B., KELLER G. & STENVALL O. (1992). – Stable isotope and foraminiferal changes across the Cretaceous-Tertiary boundary at Stevns Klint, Denmark : Arguments for long-term oceanic instability before and after bolide-impact event. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **96**, 233-260.
- SIGNOR P.W. & LIPPS J.H. (1982). – Sampling bias, gradual extinction patterns and catastrophes in the fossil record. – *Geol. Soc. Amer. Spec. Pap.*, **190**, 291-296.
- SMIT J. (1977). – Discovery of a planktonic foraminiferal association between the *Abathomphalus mayaroensis* Zone and the "*Globigerina*" *eugubina* Zone at the Cretaceous/Tertiary boundary in the Barranco del Gredero (Caravaca, SE Spain) : A preliminary report. – *Proc. Kon. Ned. Acad. Wet.*, **80**, 4, 280-301.
- SMIT J. (1979). – The Cretaceous/Tertiary transition in the Barranco del Gredero, Spain. In : W.K. CHRISTENSEN and T. BIRKELUND, Ed. – *Proc. C-T bound. events Symp.*, **II**, 156-163.
- SMIT J. (1982). – Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. – *Geol. Soc. Amer. Spec. Paper*, **190**, 329-352.
- SMIT J. (1990). – Meteorite impact, extinctions and the Cretaceous-Tertiary Boundary. – *Geol. Mijnb.*, **69**, 187-204.
- SMIT J. (1994). – Blind tests and muddy waters. – *Nature*, **368**, 809-810.
- SMIT J. & HERTOGEN J. (1980). – An extraterrestrial event at the Cretaceous-Tertiary boundary. – *Nature*, **285**, 198-200.