



Evidence and causes of the main extinction events in the Paleogene based on extinction and survival patterns of foraminifera



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ABSTRACT

We review the four main extinction events in the Paleogene, from the Cretaceous/Paleogene boundary to the Eocene/Oligocene boundary, integrating the results obtained from a study of foraminiferal assemblages with other paleontological and geological data. Different survival strategies followed by the species are described and the duration of the phases of extinction, survival, and recovery is estimated. The models and patterns of extinction of the foraminifera are highlighted. We present a range of evidence and paleo-environmental factors and analyze the possible causes of extinction. A new terminology for mass extinction events is proposed: sudden mass extinction would have happened virtually instantaneously and the process would have taken a few years or decades (Cretaceous/Paleogene boundary). Rapid mass extinction is defined as that which occurred in relatively short events, around 100 kyr (Paleocene/Eocene and Eocene/Oligocene boundaries). Slow mass extinctions are suggested to have lasted around 1 Myr (Bartonian/Priabonian transition) and may even have lasted for several million years.

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1. Introduction

The first general insights into the extinction events of organisms were those of some naturalists in the 18th and early 19th centuries, such as Georges Louis Leclerc (Buffon) and Georges Cuvier, who drew attention to the extinction of species in the fossil record, which gave rise to the catastrophist paradigm (Rudwick, 2008). In the 19th century, the French naturalist Alcide d'Orbigny, founder of the field of Micropaleontology, proposed the existence of 27 total extinctions followed by as many successive periods of creation (Moreau and Dory, 2005).

The catastrophist paradigm was soon replaced by the uniformitarian paradigm, which also accepted the concept of extinction. Darwin (1859) suggested the successive gradual extinction of species, one after another, and claimed that natural selection could adequately explain it. He attributed massive extinction events to imperfections in the fossil record. From the 19th century until relatively recently, there have been several authors who dealt with the subject such as the German Schindewolf (1963), but the question of extinction events had not aroused great interest until Alvarez et al. (1980) proposed the impact theory. This theory has revolutionized the field of Earth Sciences, contributing to the replacement of the gradual evolutionary paradigm by the neo-catastrophist evolutionary paradigm. In the past three decades, a large amount of data has been gathered on the various extinction events and theoretical concepts have been developed for

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the phenomenon of extinction (Berggren and Van Couvering, 1984; Chaloner and Hallam, 1989; Donovan, 1989; Kauffman and Walliser, 1990; Raup, 1991; Glen, 1994; Molina, 1994; Hart, 1996; Hallam and Wignall, 1997; Palmer, 2003; Molina, 2004; Taylor, 2004; Twitchett, 2006, among others).

In addition to the background extinction process, which makes species disappear slowly and continually due mainly to biological causes (e.g. competition, endemism), there were periods of time in which the rate of extinction accelerated, giving rise to mass extinction events. There are basically two models: gradual mass extinction and catastrophic mass extinction, the latter of which should be more correctly termed 'sudden' as opposed to 'gradual' (Molina, 1995, 2006, 2007). Gradual mass extinctions can be subdivided according to their duration. Mass extinction events are mainly triggered by geological or extra-terrestrial causes (Alvarez et al., 1980; Kaiho, 1994; Thomas, 2007; Schulte et al., 2010; McGowan, 2012, among others). Biological causes, such as the predominance of a single species, do not appear to have been the origin of mass extinctions, during the greater part of the Phanerozoic. However, recent data suggest that an event of this type is currently on-going: the most obvious cause of the mass extinction event is the extraordinary proliferation of the human species and its industrial activities (Leakey and Lewin, 1995).

Paleontologists have demonstrated that mass extinctions are selective and have affected some species more than others. During a mass extinction event, three phases or intervals can be identified: extinction, survival, and recovery (Kauffman and Erwin, 1995; Kauffman and Harries, 1996). In the course of these phases the different taxa react in a variety of ways, becoming extinct at the moment of the event (extinct taxa) or shortly thereafter (delayed extinction taxa), taking advantage opportunistically of the altered conditions (disaster taxa), fleeing from the altered conditions by migrating to refuges from which they return when conditions return to normal (Lazarus taxa), generating new more or less ephemeral forms that represent the beginning of new lineages (progenitor taxa), or resisting the altered environmental conditions (survivor taxa). Apart from the background extinctions, that result from normal competition and natural selection, it is generally accepted that throughout the Phanerozoic there have been five major mass extinction events, which occurred at the end of the Ordovician, the Frasnian (Late Devonian), the Permian, the Triassic, and the Cretaceous (Hallam and Wignall, 1997). Furthermore, there were many other significant mass extinction events, although of smaller amplitude than the five major extinctions, and several of them were in the Paleogene.

After the mass extinction at the Cretaceous/Paleogene boundary, organisms started new evolutionary trends as a greenhouse world evolved into an icehouse world, including rapid global warming and cooling events during the Paleogene. Foraminiferal extinctions are mainly related to meteorite impacts, hyperthermal events, glaciation events and other geologic phenomena. The chronology of the Paleogene Period has recently been updated (Wade et al., 2011; Vandenberghe et al., 2012), allowing a more accurate evaluation of the patterns and duration of the Paleogene extinction events. The aim of this review paper is to analyze the extinction events of the Cretaceous/Paleogene, Paleocene/Eocene, Middle–Late Eocene and Eocene/Oligocene, evaluating the magnitude of each event, its causes, extinction patterns, and survival strategies of planktic and smaller benthic foraminifera. In addition, we propose a new terminology for mass extinction events and we estimate the duration of the principal extinction events of the Paleogene.

2. Materials and methods

Not all groups of fossilized organisms allow us to ascertain with the same degree of precision their extinction patterns and survival strategies, since they require highly detailed biostratigraphic studies which for many groups are just not possible. A good number of groups were

highly restricted to particular environments or were very rarely fossilized, making it difficult to establish their models and causes of extinction. The best example of this is the dinosaur fossil record, which is often so patchy that it will probably take a long time to determine definitively whether they became extinct in a gradual or sudden manner, as their study is strongly influenced by what is known as the “Signor–Lipps effect” (Signor and Lipps, 1982). The foraminifera, on the other hand, due to their small sizes, wide distribution and abundance in ocean environments, are enormously useful and allow us to study their ecological patterns and strategies in detail, based on which we can then deduce the causes of extinction, especially in the Paleogene (Molina, 1995, 2006). In order to facilitate comparison among different sections and make world-wide correlations, foraminiferal taxonomy has been revised and updated according to Olsson et al. (1999) and Pearson et al. (2006). Furthermore, standard chrono-biostratigraphy has been updated (Fig. 1) and range charts (Figs. 2 to 6) have been simplified to better show the patterns of extinction.

The outcrop sections and boreholes (DSDP and ODP sites) studied, on which this paper is based, cover a wide range of locations around the world, mainly in intermediate and low latitudes. In Spain, they include the Betics (Agost, Alamedilla, Aspe, Caravaca, El Navazuelo, Fuente Caldera, Molino de Cobo, and Torre Cardela) and the Pyrenees (Arguis, Artieda, Campo, Osinaga, and Zumaya). In Italy: Gubbio, Massignano and Possagno. In France: Bidart and the Bay of Loye. In Tunisia: El Kef, Aïn Settara and Elles. In Egypt: Dababiya. In Mexico: Coxquihui, El Mimbrol, La Lajilla, and La Ceiba. In Cuba: Loma Capiro, Peñalver and Santa Isabel. In the Atlantic Ocean: DSDP sites 94, 116, 363, 366, 401, 402, and 612. In the Indian Ocean: DSDP sites 214, 216, 219, 223, 242, and 253. In the Pacific Ocean: DSDP sites 277, 292, and 462 (see Molina et al., 1993, 1998, 2009).

Detailed samplings were conducted on a metric scale, but where extinction or meteorite impact events were located, sampling density was from 2 to 20 cm. At the levels closest to the event, continuous samples were taken with a resolution of 2 cm. The samples were disaggregated with water and washed, and the fractions greater than 150 μm , 100 μm or 63 μm were studied according to the size of the foraminifera in each section and event. In many sections, quantitative studies were conducted, separating a representative fraction of more than 300 specimens in each sample, using an Otto microsplitter and also checking the rest of the sample for less frequent species.

3. The Cretaceous/Paleogene boundary event

The Cretaceous/Paleogene boundary event (K/Pg) is one of the most widely studied as it is the most recent of the 5 major mass extinctions, it has been dated to 66.04 Ma (Vandenberghe et al., 2012). The stratotype for the K/Pg boundary was defined at the base of the clay that contains the iridium anomaly in the El Kef section in Tunisia (Molina et al., 2006a, 2009). This event, which constitutes one of the most significant biological crises in geological history, is used to define the boundary between the Mesozoic and Cenozoic Eras.

Alvarez et al. (1980) proposed that the collision of a large meteorite measuring some 10 km in diameter may have produced a level abnormally rich in iridium that coincided with the sudden catastrophic mass extinction. This evidence was recorded in a thin clay interval at the K/Pg boundary in Gubbio (Italy), Stevns Klint (Denmark) and Woodside Creek (New Zealand), as well as in Caravaca (Spain) (Smit and Hertogen, 1980). In addition, other evidence at the K/Pg boundary has been found, such as microtektites, Ni-rich spinels, shocked quartz, which, combined with the discovery of a large impact crater structure in the Yucatan peninsula, the sedimentological evidence of tsunamis and gigantic gravitational flows as well as the dating by $^{40}\text{Ar}/^{39}\text{Ar}$ of the impact silica glass have enabled to confirm the validity of the impact theory (Schulte et al., 2010).

However, since the classic sections of Gubbio and Caravaca are composed of rocks that were formed in deep ocean settings, they do not

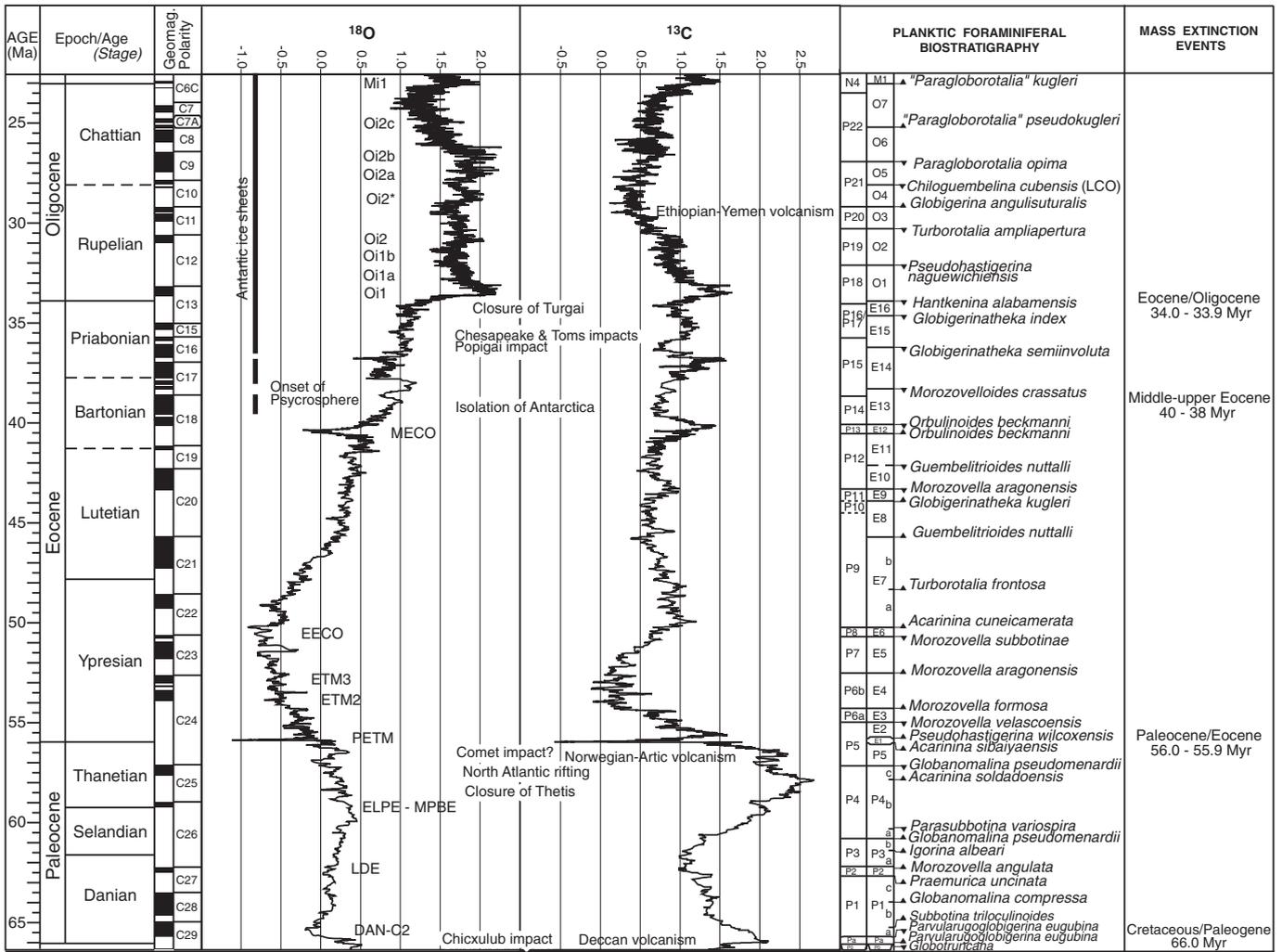


Fig. 1. Paleogene stratigraphic subdivisions, geomagnetic polarity scale, isotope curves, climatic events, tectonic and extraterrestrial events, zonations of planktic foraminifera, and mass extinction events.

Modified and completed from Vandenberghe et al. in The Geologic Time Scale (Gradstein et al., 2012).

contain remains of dinosaurs and only scant fossils of other groups: ammonites, belemnites and rudist bivalves, which also went extinct. Hence, it is the planktic foraminifera that, thanks to their abundance and small size, are allowing us to show that the impact level and mass extinction were contemporaneous (e.g., Molina, 2006, 2007).

The methodology used in the study of planktic foraminifera, both in the field (high-resolution sampling) and in the laboratory (extraction and observation techniques, quantitative studies), allows us to determine with great precision the pattern of extinction and ascertain its most probable cause. Initially, before the impact theory was put forward, the extinction pattern of the planktic foraminifera at the K/Pg event seemed to be almost total (Luterbacher and Premoli Silva, 1964). Subsequently, when high-resolution studies began, the pattern appeared to be gradual; some thought it was fairly gradual (Lamolda et al., 1983; Canudo et al., 1991) while for others it was very gradual (Keller, 1988). Currently, after a long controversy, most specialists agree that we are dealing with a sudden pattern (Smit, 1982, 1990; Molina et al., 1996, 1998, 2005; Apellaniz et al., 1997; Orue-Etxebarria, 1997; Arz et al., 1999, 2000, 2001; Kaiho and Lamolda, 1999; Arenillas et al., 2000a, 2000b, 2006; Dupuis et al., 2001; MacLeod et al., 2007). However, there are authors who maintain that the extinction pattern is one of gradual mass extinction (e.g., Keller et al., 1995; Keller, 2012).

The best sections at the K/Pg boundary for the study of the planktic foraminifera extinction pattern are found in Tunisia (El Kef, Aïn Settara,

Elles), France (Bidart) and Spain (Agost, Caravaca, Zumaya), while the best ones for studying the evidence of the meteorite impact are in the coastal area of the Gulf of Mexico and the Caribbean, specifically in Mexico (Coxquihui, El Mimbral, La Lajilla, and La Ceiba) and in Cuba (Loma Capiro, Peñalver, and Santa Isabel). Of all of these it is the El Kef section that stands out as the most reliable source of data thanks to its considerable continuity and great wealth of planktic foraminifera, as well as being the location that we have studied most intensely (Fig. 2; Arenillas et al., 2000a, 2002; Molina et al., 2002, 2006a, 2009)). We found that the planktic foraminifera display a sudden catastrophic mass extinction pattern that affected more than 70% of the species, which became extinct suddenly coinciding with the level containing the evidence of the meteorite impact. The presence in the Danian of specimens of some Cretaceous species may be due to allochronic resedimentation, since they were the smallest and most abundant species in the uppermost Cretaceous and, therefore, the most likely to be reworked; moreover, they are not found throughout the Danian in all continuous sections of the K–Pg transition and they tend to be less well preserved and different in color. If we discount these species, whose survival is very doubtful, the mass extinction would have affected about 90% of all planktic foraminifera, exactly as we have also observed in Bidart (Gallala et al., 2009).

The species that disappeared in environments of sub-tropical latitudes like El Kef amount to 91% of the species, which became extinct

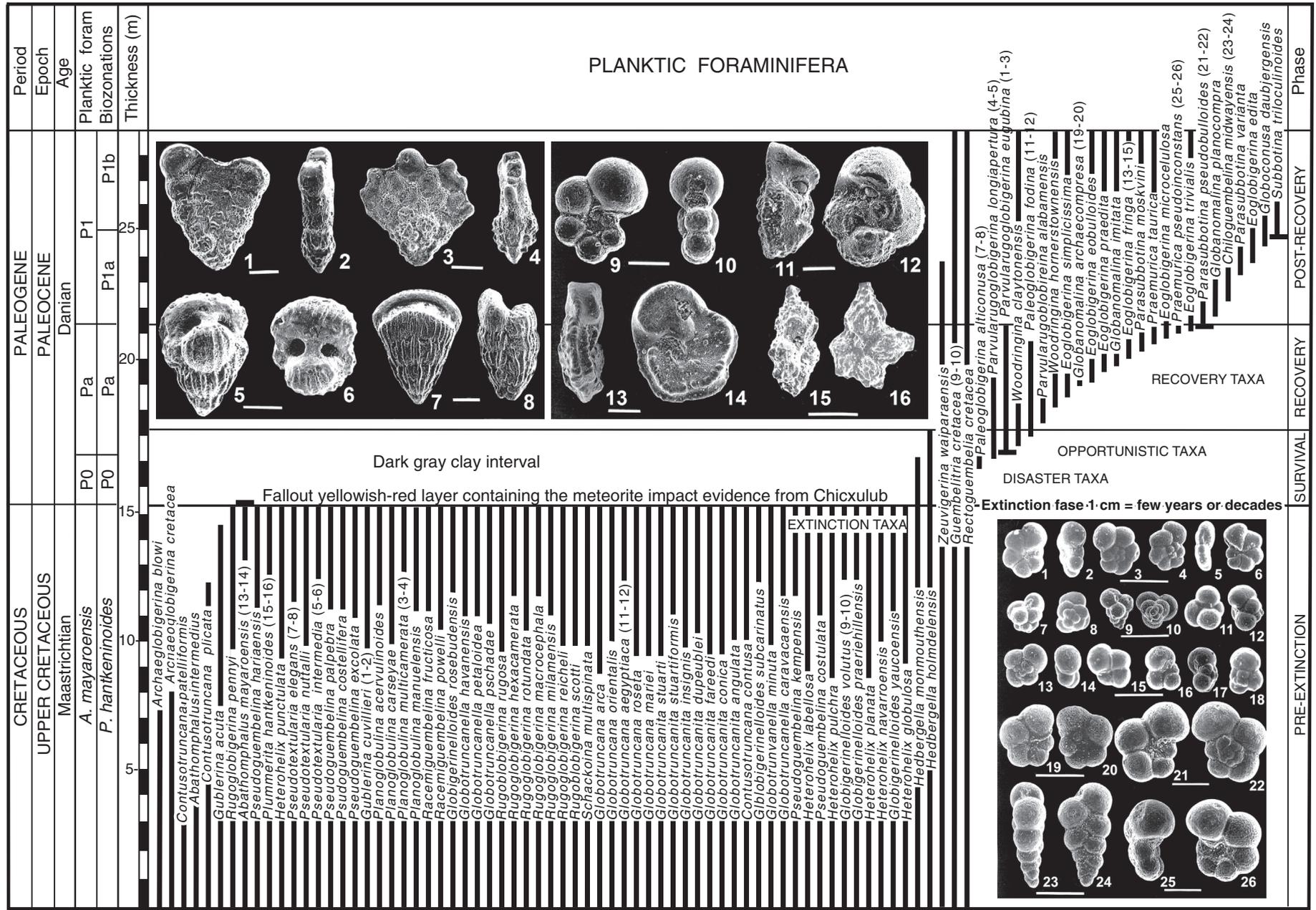


Fig. 2. Cretaceous/Paleogene sudden mass extinction pattern at El Kef, Tunisia. Some species ranges have been completed according to our studies at Ain Settara, Elles, Caravaca, Agost, and Zumaya sections. zData modified and up-dated from Arenillas et al. (2000a) and Molina et al. (2006a).

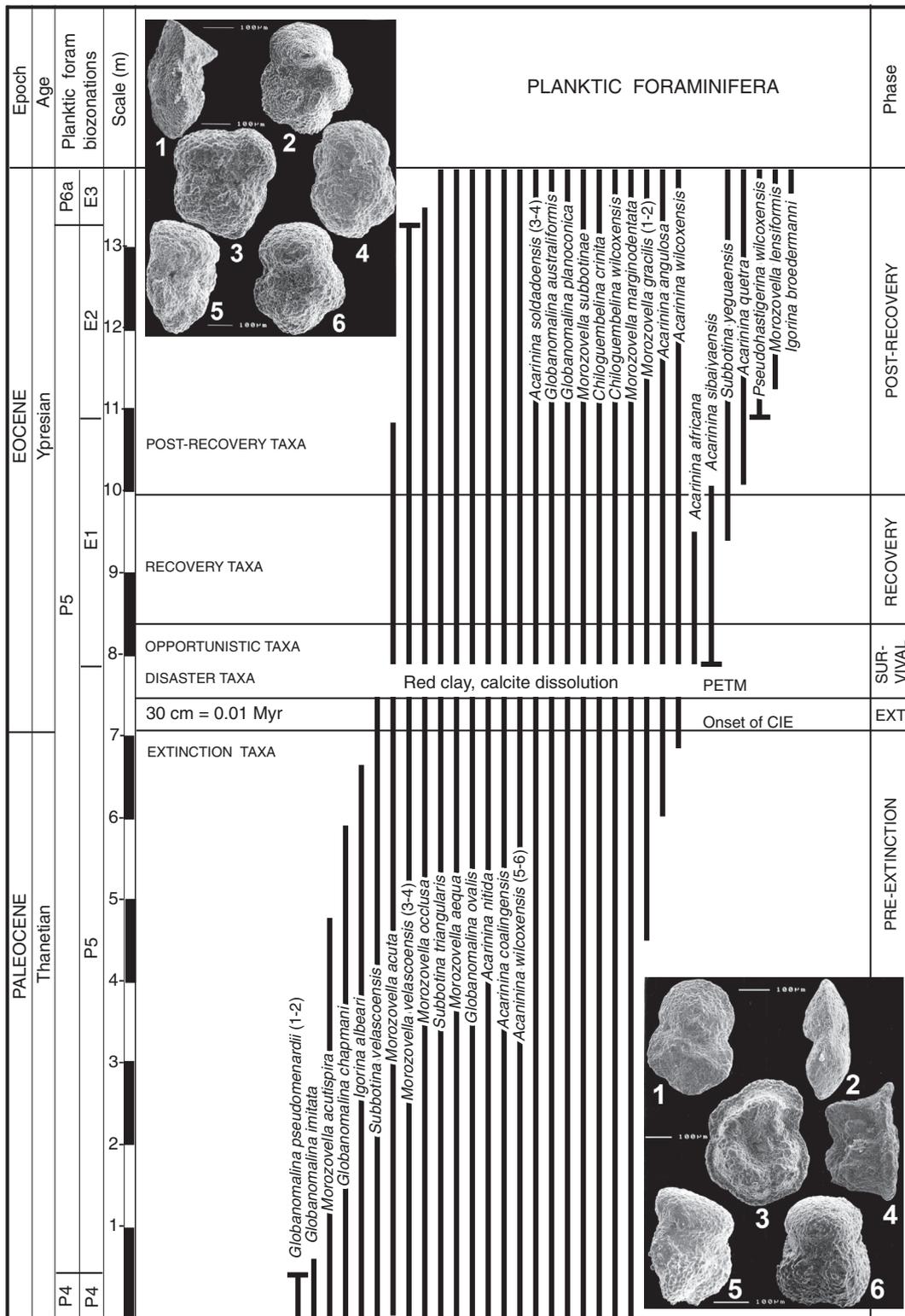


Fig. 3. Paleocene/Eocene extinction pattern of planktic foraminifera at Alamedilla, Spain. Some species ranges have been completed according to our studies of the Caravaca and Zumaya sections.

Data modified and updated from Arenillas and Molina (1996) and Molina et al. (1999).

suddenly. Most of them had large tests and complex morphologies, and were specialized forms of K-selection strategy, that had adapted to deep-water environments in warm latitudes such as *Globotruncana arca* or *Abathomphalus mayaroensis*. Therefore, this event is the most relevant and counts as the greatest morphological renewal in the entire

history of the planktic foraminifera, with the total disappearance of all forms with two keels and tegilla.

The total number fell by much larger percentages, to such an extent that in the boundary clay it is hard to find enough specimens to carry out quantitative analysis. Very few species of planktic foraminifera

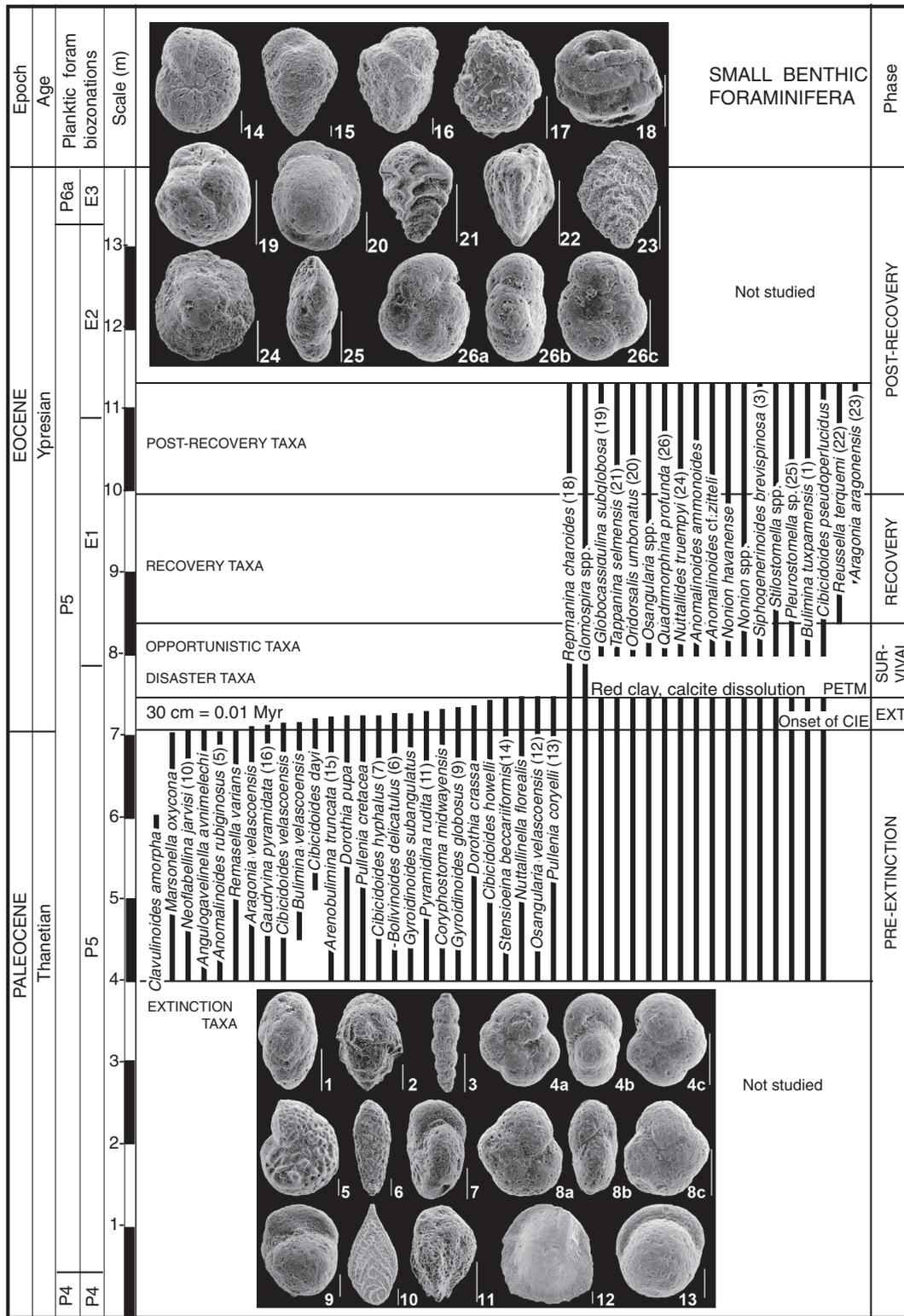


Fig. 4. Paleocene/Eocene rapid mass extinction pattern of small benthic foraminifera at Alamedilla, Spain. Numbers in brackets at the end of the species names correspond to the numbers in microphotographs. Data modified and updated from Alegret et al. (2009).

survived the K/Pg boundary event, just three delayed extinction species and two disaster species did so. The delayed extinction species *Hedbergella monmouthensis* and *Hedbergella holmdelensis*, were small in size, survived initially and became extinct shortly after the event. The disaster species *Guembeltria cretacea* and *Rectoguembelina cretacea*,

flourished in the survival phase thanks to their r-selection strategy. The progenitor species that appeared at the base of the Paleogene are: *Paleoglobigerina alticonusa*, *Parvularugoglobigerina longiapertura*, *Parvularugoglobigerina eugubina*, *Woodrighina claytonensis*, and *Paleoglobigerina fodina*. These species are widely distributed, since

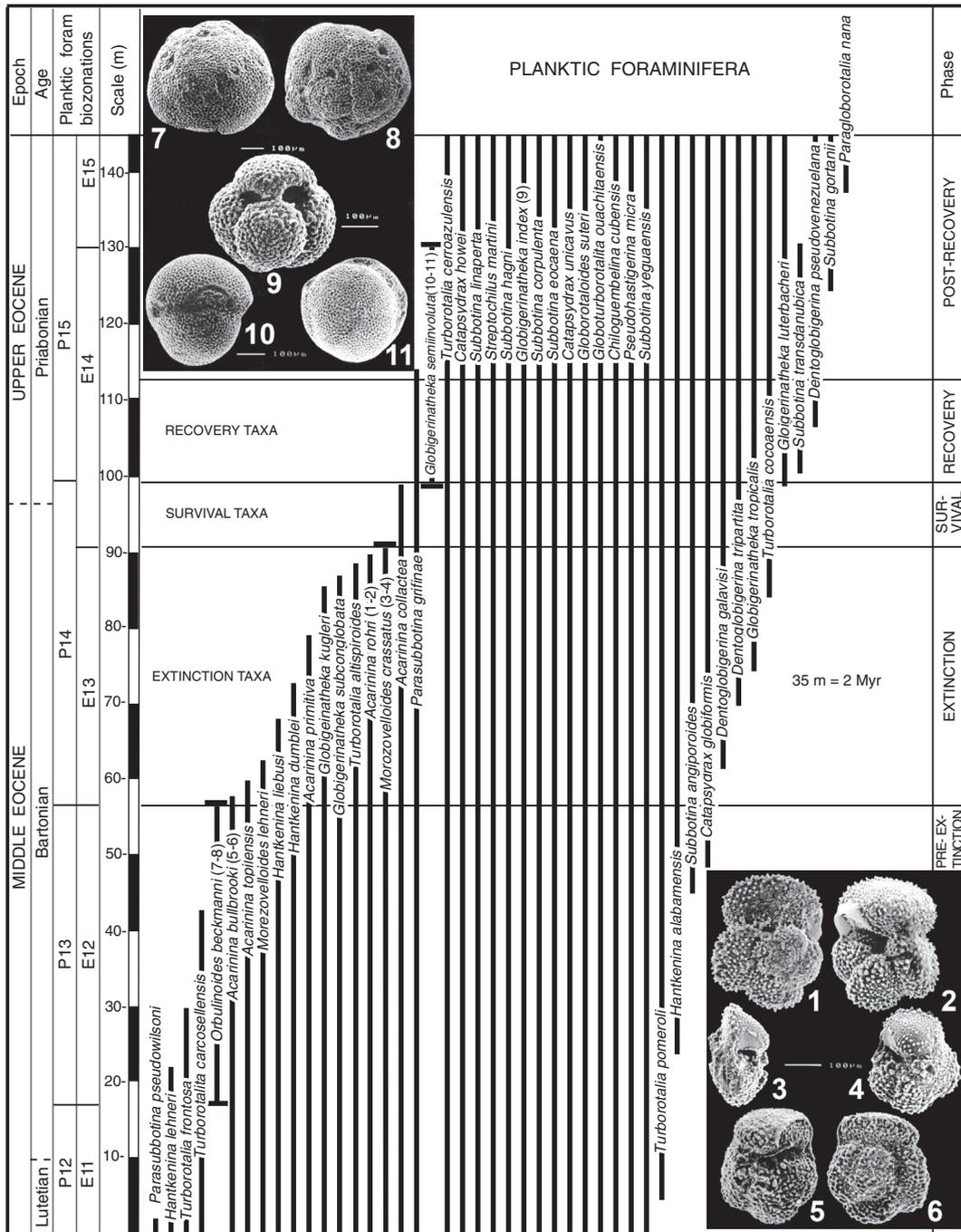


Fig. 5. Middle–Late Eocene slow mass extinction pattern at Torre Cardela, Spain. Some species ranges have been completed according to our studies in the Aspe, Arguis, and Artieda sections. Data modified and updated from Gonzalvo and Molina (1996).

almost all of them can be found in the majority of sections studied. They went extinct at the end of the recovery phase, with the exception of *W. claytonensis*.

There appear to be no Lazarus taxa among the planktic foraminifera, as the extinction was so massive that few species were left that could develop this strategy. However, it is very frequent among the small benthic foraminifera that lived in deep-ocean environments (Coccioni and Galeotti, 1994; Alegret et al., 2002; Peryt et al., 2002; Alegret et al., 2003, 2004a, 2004b). This group was less affected by the K/Pg event as its diet did not depend directly on photosynthesis since it inhabited the aphotic zone, and since before the mass extinction there was equilibrium between of infaunals and epifaunals. In Tunisia, in the El Kef

section, the sudden disappearance of 13 species of benthic foraminifera can be observed, of which the following can be considered extinct: *Cibicides beaumontianus*, *Heterostomella austiniana*, *Bolivinoidea draco*, *Praebulimina kickapooensis*, *Sitella cushmani*, and *Sitella fabilis* (Molina et al., 2006a). Following the extinction event the conditions were oligotrophic; many species behaved like Lazarus taxa and reappeared during the recovery phase. In the Gulf of Mexico and the Atlantic sections, however, this is not the case. There, the Lazarus species tend to be epifaunal, such as *Cibicidoides dayi* and *Nuttallides florealis*. However, in the Tethys there are quite a few infaunals that behaved as Lazarus species: *Arenobulimina truncata*, *Bolivinoidea delicatulus*, *Gaudryina pyramidata*, *Oridorsalis umbonatus*, and *Praebulimina reussi*

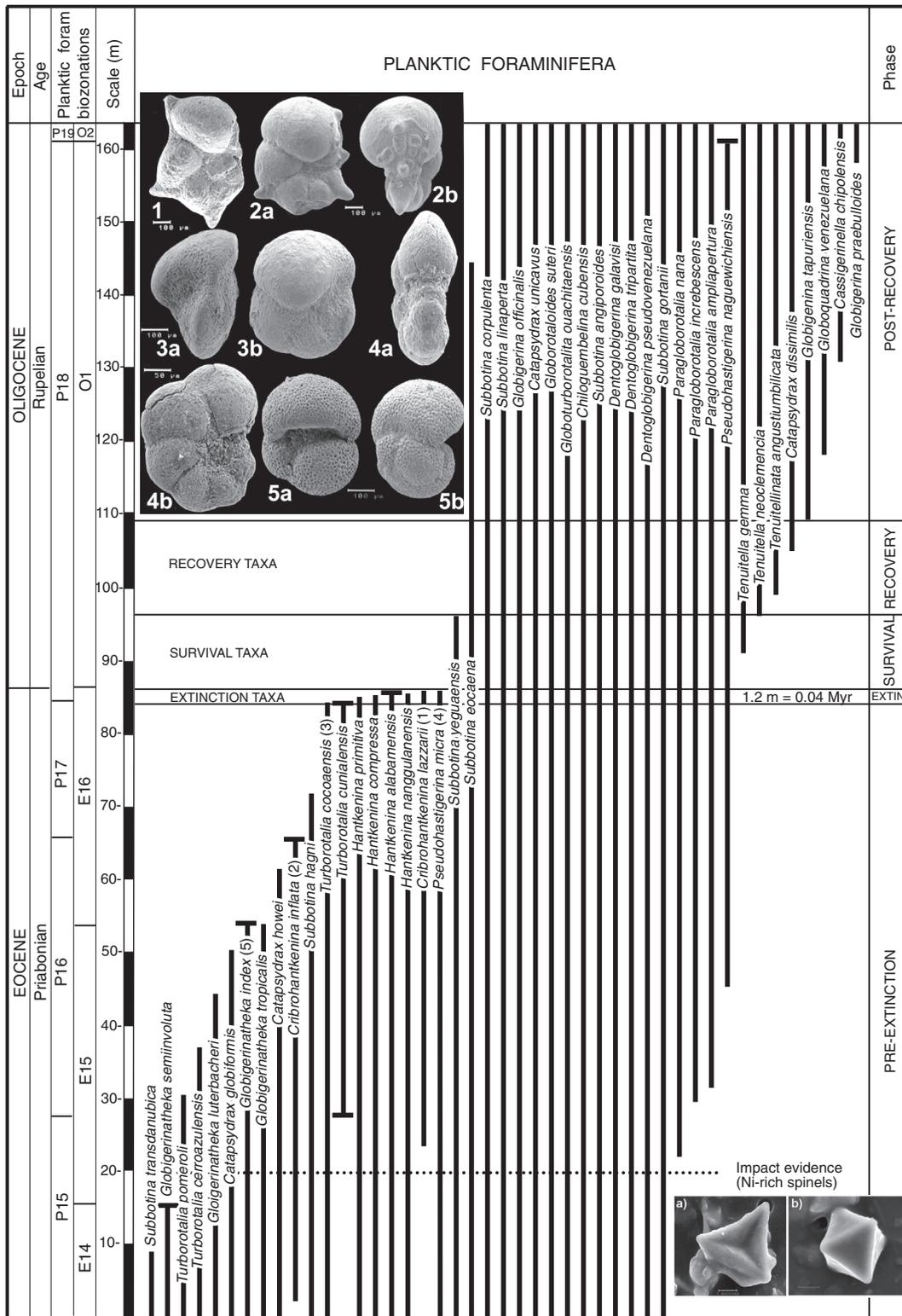


Fig. 6. Eocene/Oligocene rapid mass extinction pattern at Fuente Caldera, Spain. Some species ranges have been completed according to our studies at the Molino de Cobo and Torre Cardela sections. Data modified and updated from Molina (1986), Robin and Molina (2006), and Molina et al. (2006b).

(Peryt et al., 2002; Alegret et al., 2003). However, it has to be considered that carbonate dissolution affects the record of these species in the clay at the K/Pg boundary in deep ocean sections. In the Bidart section of the Bay of Biscay, various species, mainly epifaunal, proliferated after the extinction event: *Coryphostoma incrasata* (in the *gigantea* form),

Stensioeina beccariiiformis, *Cibicidoides hyphalus*, and *Angulogavelinella avnimelechi*, which may be regarded as opportunistic species that took advantage of the crisis (Alegret et al., 2004a). However, *S. beccariiiformis* and *A. avnimelechi* are generally regarded as indicators of stable oligotrophic deep-water settings, which can support highly diverse ecosystems

(Thomas, 2007). In the El Kef section in Tunisia, the opportunistic species that most proliferated was *Cibicidoides pseudoacutus*. Once environmental conditions began to recover, a gradual increase in epifaunal species, mainly of the genera *Anomalinoidea* and *Nuttallides* replaced the opportunists. According to Alegret et al. (2012), the end-Cretaceous marine mass extinction was not caused by a collapse in productivity in the deep sea.

The extinction pattern of the planktic foraminifera indicates a sudden mass extinction, as 91% of the species disappeared almost instantaneously in terms of geological time. The extinction phase, which was extremely short, is in the order of years or decades, and a rapid short-term cooling followed the Chicxulub impact (Vellekoop et al., 2014). In sections located far from the impact region the sediment is just about one centimeter thick, concentrates at the yellowish-red fallout layer and the interval is so short that cannot be represented in Fig. 2. The survival phase is clearly demarcated and covers the interval of dark clay of the *G. cretacea* (P0) biozone, which has been studied with high-resolution bio-magnetostratigraphic calibrations (Arenillas et al., 2004). The recovery phase was longer, as the planktic foraminifera did not regain their normal size until the lower part of the *Parasubbotina pseudobulloides* (P1) biozone and the density of accumulated sediments is much greater, producing a great diversification in the assemblages of planktic foraminifera, though never reaching the degree of diversity that existed before the extinction event.

The cause that triggered the extinction event was very probably the impact of a large meteorite in the Yucatán Peninsula, where today there is a buried crater (Chicxulub) with a diameter of some 170 km (Alvarez, 1997; Schulte et al., 2010). In the studied sections, evidence of the impact is evident (the iridium anomaly, microtektites, Ni-rich spinels, shocked quartz with impact metamorphosis) which are concentrated in a single level in the sections in areas far from the Gulf of Mexico. Since this level coincides exactly with the mass extinction, the cause-effect relationship can be established and it is the most plausible explanation. The environments most affected were terrestrial and pelagic marine environments, the catastrophe being so sudden that there was not enough time for natural selection to operate. The carbon and oxygen isotopes indicate a significant reduction in organic productivity and in water temperature. The vaporization of the meteorite and the impacted material, together with the ash from forest fires produced a global atmospheric darkening that lasted several months, which halted photosynthesis and a massive fall in temperature (the “impact winter”). The paleo-botanic record seems to show few extinctions, but sweeping paleo-environmental changes including deforestation and a brutal temporary reduction in diversity (Lazarus effect), with a few opportunistic disaster species (mainly ferns) dominating during the survival stage (Orth et al., 1981). Moreover, there is evidence of acid rain and anoxia or hypoxia in the ocean depths, acidification being the more important factor in the calcareous plankton extinctions (Ohno et al., 2014). The impact produced enormous tsunamis in the area of the Gulf of Mexico, destabilization and rupture of the marine shelf, generating a mega-turbidite mass flow, which in some Cuban sections become an enormous olistostrome reaching dimensions of hundreds of meters (Alegret et al., 2005a).

These sudden paleoenvironmental changes explain the great magnitude of the mass extinction. The catastrophic mass extinction of planktic foraminifera may possibly be extrapolated to the other groups involved in this extinction whose fossil record is not as good. Some authors have attributed this extinction event to intense volcanic activity in the Deccan (India). However, it has been shown by Venkatesan et al. (1993) that this volcanic activity began earlier, spans the K/Pg boundary, and that the injection of sulfur into the atmosphere during the main phase of Deccan flood basalt volcanism generated an only moderate climate change, as discussed in Schulte et al. (2010). However, the most significant point is that the extinction pattern observed in the foraminifera does not match this type of cause, as in this case it would have been gradual rather than massive and sudden. Furthermore, no

other major extinctions have been observed that coincide with the peak of volcanic activity, which is prior to the K/Pg boundary. Many other causes have been put forward, among which eustatic changes is a frequent contender, but this does not adequately explain the mass extinction in pelagic marine ecosystems and even less in continental environments (Brusatte et al., 2014).

4. The Paleocene/Eocene boundary event

The Paleocene/Eocene (P/E) boundary has been defined in the Dababiya section (Egypt) and is dated to 56.0 Ma (Aubry et al., 2007; Vandenberghe et al., 2012). The criterion used is a negative anomaly of the $\delta^{13}\text{C}$, the base of this anomaly corresponding to a major crisis in the smaller abyssal and bathyal foraminifera. This crisis is one of the most significant in the history of the small benthic foraminifera that lived in the bathyal and abyssal marine environments (Kennett and Stott, 1991; Thomas and Shackleton, 1996). It seems to have been caused by a massive increase in the ocean temperature (Owen and Rea, 1992; Sloan et al., 1992), and/or by multiple environmental changes, including decreased carbonate saturation, ocean acidification, lowered oxygen levels, and a globally reduced food supply, all related to a massive carbon injection (Winguth et al., 2012). The P/E boundary event coincides with the Paleocene–Eocene Thermal Maximum (PETM), the major Cenozoic global warming event. This event was identified in various sections in Spain (Canudo and Molina, 1992; Molina et al., 1994; Arenillas and Molina, 1996; Orue-Etxebarria et al., 1996, 2004).

The PETM triggered effects in continental environments that have been known not for the extinctions but for the great diversity of terrestrial flora and fauna. In the 19th century, Lemoine and later specialists in fossil vertebrates in the 20th century, such as Teilhard de Chardin, and Russell, drew attention to the existence near the P/E boundary of a great evolutionary radiation of mammals, known as the “mammal dispersion event” (Bowen et al., 2002). During this event, some Paleocene faunas became extinct, whereas the modern orders of mammals (Artiodactyla, Perissodactyla and Primates) first appeared at the P/E boundary (Gingerich, 2006). From then on, large mammals evolved and occupied many of the ecological niches that the dinosaurs had left vacant. Furthermore, there was an extensive migration of tropical and sub-tropical species to colder latitudes. The tropical–subtropical vegetation consisting mostly of tropical rainforest species extended towards the poles up to 50–60° latitude. The geographical distributions of organisms were radically rearranged by 5–8 °C of warming. Tropical species moved poleward both in marine and terrestrial realms (McInerney and Wing, 2011).

These migrations to higher latitudes have also been identified in marine environments. The planktic foraminifera diversified rapidly; *Acarinina sibaiaensis* and *Acarinina africana* reached their apogee (Fig. 3). A significant migration of tropical species into higher latitudes has been documented in several sections in Spain (Canudo et al., 1995; Arenillas and Molina, 1996; Arenillas et al., 1999; Molina et al., 1999). Something similar occurred with the dinoflagellates, which reached an apogee of the genus *Apectodinium*, and the calcareous nannofossils which underwent a marked process of diversification. Moreover, in platform environments, the larger foraminifera (e.g., *Nummulites*, *Alveolina*) diversified and many of them increased in size at the base of the Ilerdian (Orue-Etxebarria et al., 2001).

The study of a number of sections in the Iberian Peninsula has been crucial for a full understanding of the P/E event. In the Alamedilla, Caravaca, and Zumaya sections, a distinct clay layer is overlying the rapid but gradual mass extinction of the small benthic foraminifera (Lu et al., 1996; Schmitz et al., 1997; Alegret et al., 2005b, 2009; Zili et al., 2009; Alegret et al., 2010). In addition, this study is based also on sections in Possagno (Italy) and Dababiya (Egypt). The Spanish sections are very continuous and have been useful for a detailed study of the Paleocene/Eocene event, but the stratotype of the P/E boundary was finally defined in the Dababiya section, near Luxor (Egypt).

The group most affected by this event was the smaller benthic foraminifera in bathyal and abyssal oceanic environments, which suffered a crisis that can be considered a rapid mass extinction. The most representative section for this crisis is that of Alamedilla, which is where the levels that record the extinction event have been studied in the greatest detail (Fig. 4; Alegret et al., 2009, 2010). In this section, 37% of the species of benthic foraminifera became extinct in a 30 cm interval of marly sediments, coinciding with the onset of the Carbon Isotopic Excursion (CIE). The taxa which went extinct in the deep marine environments at Alamedilla are K-selection strategists, such as *A. avnimelechi*, *Anomalinoidea rubiginosus*, *A. truncata*, *B. delicatulus*, *C. hyphalus*, *Cibicoides howelli*, *Cibicoides velascoensis*, *Coryphostoma midwayensis*, *Dorothia pupa*, *Gyroidinoidea subangulatus*, *Marsonella oxycona*, *Neoflabellina jarvisi*, *Nuttallinella florealis*, *Osangularia velascoensis*, *Pullenia coryellyi*, and *S. beccariiformis*. These taxa were principally species with calcitic tests, some of which had survived the crisis at the K/Pg boundary. Only few of these species have been recorded from sections deposited in shallower environments (e.g., Dababiya). Among those that became extinct we must mention *A. avnimelechi*, which is the most characteristic of these habitats.

An example of a delayed extinction taxa is *Anomalinoidea aegyptiacus*, as can be observed in the Dababiya section (Alegret et al., 2005b). This species is regarded by Speijer et al. (2000) as an opportunistic taxon that temporarily migrated basin-downwards to greater depths during the PETM and later repopulated the vacant outer shelf ecosystem. The disaster taxa in this event, in which the dissolution of carbonates appears to have been a decisive factor, were those with agglutinated shells that grew significantly larger as they faced less competition for trophic resources and could live in environments below the calcite dissolution level. In Alamedilla, the taxa *Repmantina* (*Glomospira charoides* and *Glomospira* spp., commonly known as *Glomospira* Acme, are abundant. In deeper shelf environments (e.g., Dababiya), where benthic foraminifera were less affected, we find *Aragonia aragonensis*, whose apogee could be considered to be an indicator of hyperthermal events, although this species is rarely recorded in Egyptian shelf settings and it is difficult to evaluate its ecostratigraphic meaning. In Alamedilla, opportunist taxa appear after the disaster taxa. These are calcareous r-selection strategists, and the dominant species are *Globocassidulina subglobosa* (<45% of the assemblages), *Nuttallides truempyi*, *Osangularia* spp., *Tappanina selmensis*, *O. umbonatus*, *Reusella terquemi*, *A. aragonensis*, *Abyssamina quadrata*, and *Quadriformina profunda*. Once the environment has recovered and the levels of CaCO₃ have been restored, the recovery progenitor taxa made their appearance. In Alamedilla, *N. truempyi* and *Osangularia* spp., the buliminids, *Pleurostomella* spp., and *Stilostomella* spp. are abundant (Alegret et al., 2009). The pioneer progenitor taxon may be taken to have been *Turrilina brevispira* in Dababiya. Lazarus taxa were very frequent, since a large number of species with calcitic tests re-emerged when normal environmental conditions returned, for instance *N. truempyi*, *C. pseudoacutus*, and *Bulimina midwayensis*, which can be considered as K-selection strategists.

The P/E extinction event was very brief, as it is represented by 20 to 50 cm-thick clays in the sections (e.g., Zumaya, Alamedilla, and Caravaca), which represents a period of approximately 0.01 Myr (Alegret et al., 2010). Therefore, this is a relatively rapid but gradual mass extinction pattern produced by the hyperthermal event. The survival phase is represented by a clay interval of variable thickness (approximately 1 m in Alamedilla and Caravaca to 4 m in Zumaya). The recovery phase was relatively brief, as environmental conditions returned to normal relatively quickly and many species survived the event. This phase ended when migrations to higher latitudes and the apogee of *Acarinina* ceased, witnessing a return to normal temperatures.

Oxygen isotope analysis shows that at the P–E transition the greatest increase in temperature of the entire Cenozoic occurred (Zachos et al., 2001, 2008). Moreover, just at the P/E boundary there was a far greater increase in temperature, leading to a hyperthermal event (Thomas and Zachos, 2000; Zachos et al., 2001; Thomas, 2003, 2007; Zachos et al.,

2008; McInerney and Wing, 2011; Speijer et al., 2012). The most plausible explanation is that it was linked to plate tectonics, on the one hand the opening up of the North Atlantic, which generated a large igneous province (Norwegian–Arctic volcanism) and additionally the closure of the Tethys due to the progressive displacement of the Indian plate towards the Asiatic and the African towards the European plates. Thus the triggering mechanism could have been as follows: North-Atlantic rifting generated volcanic activity, injecting CO₂, starting a global warming, Indian rifting restricted the Tethys current and increased the salinity of this sea, modifying the global marine currents and shifting towards from a thermohaline circulation system to a halothermal one. This produced an increase in temperature in marine depths that destabilized methane hydrates, a large amount of methane gas was released and hence of organic carbon ¹²C, entering the atmosphere together with CO₂ resulting from the oxidation process, leading to an extreme greenhouse effect (Dickens et al., 1997; Svensen et al., 2004). As a result of the greenhouse effect, the highest average global temperature of the Cenozoic was reached. The strongly negative excursion of the carbon isotopes indicates that large quantities of organic carbon were released into oceanic and atmospheric reservoirs. Methane and carbon dioxide produced an intense greenhouse effect and a sudden increase in temperature, giving rise to the P/E hyperthermal event. The ocean depths became anoxic or hypoxic and the calcite compensation level rose by several hundred meters. This generated the deposition of a thick layer of shale at the P/E boundary. It is in the underlying marly levels that we find the extinction of the small bathyal and abyssal benthic foraminifera, and it is plausible to trace a cause–effect relationship between the hyperthermal event, the anoxia, the shallowing of the calcite compensation depth and the extinction of the bathyal and abyssal benthic foraminifera.

Among the possible triggers of this extinction event some authors have proposed that it was due to an extraterrestrial impact. One of the main arguments in favor of this hypothesis is the presence of a small and enigmatic iridium anomaly in the Zumaya section found by us (Schmitz et al., 1997), which some researchers (Kent et al., 2003) have interpreted as the result of a comet impact. However, at the level of the anomaly, both in Zumaya and in Alamedilla, there has been an intense search for additional evidence of an extraterrestrial impact (e.g., Ni-rich spinels, microtektites) but none have been found (Schmitz et al., 2004). The most convincing evidence is that there is no correlation between the small iridium anomaly and the extinction interval of the benthic foraminifera, as the small, enigmatic iridium anomaly occurred 40 cm below in the section. On the other hand, the extinction coincides with the carbon and oxygen isotopic changes and it would appear more plausible to attribute the extinction of the bathyal and smaller abyssal foraminifera to the sudden hyperthermal heating of the deep ocean.

5. Middle–Late Eocene transition event

The Late Eocene was a turbulent time, but two events stand out: the late Bartonian photosymbiotic crisis and the Early Rupelian cooling event Oi-1 (McGowran, 2012). Between the Middle–Late Eocene transition and the Eocene/Oligocene boundary, various events occurred which affected many groups of organisms, both marine and continental. In general terms, this could be considered to have been a long-term gradual mass extinction event (Kaiho, 1994), which would have lasted more than 6 Myr, from the Mid-Eocene to the Early Oligocene, and it is usually related to a prolonged decline in global temperature (Zachos et al., 2001). However, it is useful to analyze three events separately: the Middle–Late Eocene transition extinction event, the Eocene/Oligocene boundary extinction event, and, the Mid-Priabonian meteorite impacts. Furthermore, a single gradual mass extinction lasting more than 6 Myr seems inappropriate and according to our data (Gonzalvo and Molina, 1992, 1996; Molina, 2006, 2007), two separate extinction events seem more plausible.

Little is known about the chronology of the extinction event near the Bartonian/Priabonian (B/P) boundary, as the boundary stratotype between these two stages has not yet been officially defined: the base of the Priabonian is still unclear but in terms of absolute dating the boundary is placed at around 37.8 Ma (e.g., Vandenberghe et al. in The Geologic Time Scale) (Gradstein et al., 2012). The end of this extinction event used to be placed at the B/P boundary, but recently it has been proposed to locate it in a higher lithostratigraphic horizon at Alano, Italy (Vandenberghe et al., 2012). The planktic foraminifera suffered one of the major crises of their history, after the largest one, which occurred at the K/Pg boundary. The effect of this event on other groups is less well known, with the mollusks being one of the groups most seriously affected: on the west coast of North America, 100% of tropical species disappeared (Hickman, 2003). The radiolaria were also greatly affected, suffering a slow gradual mass extinction along Chron 17, from the middle part of the RP16 biozone to the top of the RP17 biozone (Kamikuri and Wade, 2012), lasting almost 2 Myr.

The sections we studied are located mainly in the Pyrenees (Arguis and Artieda) and in the Betic Cordillera (Torre Cardela and Aspe). In addition, we studied various boreholes of the DSDP–ODP, especially at Site 94 and Site 612 in the Atlantic Ocean. These sites show a hiatus right at the Middle–Late Eocene transition (Molina et al., 1993), which hinders a detailed study of the extinction pattern of the foraminifera, but which allows us to know what happened in between the two extinction events. The best section that has been studied, which may be considered the reference section, is the Torre Cardela section in the Betics (Gonzalvo and Molina, 1992, 1996). It illustrates very clearly the slow gradual extinction pattern, the duration of its phases and the survival strategies of the planktic foraminiferal species.

In sub-tropical latitudes, where the Torre Cardela section was located, there was an extinction of the spinose and other tropical species (Fig. 5). This involved the extinction of almost three genera (*Orbulinoides*, *Morozovelloides*, and most species of *Acarinina*) and the specific richness was reduced by 33%. Most of the extinct species were large spinose forms, with a carinated periphery and muricated wall: *Acarinina bulbrooki*, *Acarinina topilensis*, *Acarinina primitiva*, *Acarinina rohri*, *Morozovelloides lehneri*, and *Morozovelloides crassatus*. Furthermore, the extinction involved other species such as *Orbulinoides beckmanni*, *Hantkenina liebusi*, *Hantkenina dumblei*, *Globigerinatheka kugleri*, *Globigerinatheka subconglobata*, and *Turborotalia altispiroides*. In addition, there is another species (*Acarinina collactea*) that may be considered a delayed extinction species.

The disaster taxa are hard to identify. Some species such as *Dentoglobigerina eocaena* and *Globorotaloides suteri* reached their acme in the survival stage and would appear to be the disaster species, which if true would mean that those that survived were the larger forms, unlike what occurred at the K/Pg boundary. We may consider *Hantkenina alabamensis*, which inhabited warmer latitudes, to be a Lazarus species. Its temporary absence reflects a fall in temperature during the event. The survivor taxa predominate and include the most cosmopolitan forms; among the most characteristic ones are: *Subbotina hagni*, *Subbotina linaperta*, *Pseudohastigerina micra*, *Streptochilus martini*, *Chiloguembelina cubensis*, and *Dentoglobigerina corpulenta*.

The extinction stage is likely to extend from the disappearance of *O. beckmanni*, in the upper part of the E12 biozone, to the disappearance of *M. crassatus*, at the top of the E13 biozone (Gonzalvo and Molina, 1992, 1996). The long extinction stage extended over 35 m of marly sediments. It may have lasted some 2 Myr, according to the calibration of zone E13 by Wade et al. (2011) and is considered a slow mass extinction event. The extinction pattern shows two main steps at the beginning and at the end, the extinction of the spinose carinate species being the most significant.

The trigger of the extinction event could have been the separation of the Antarctic, American, and Australian plates, causing the isolation of Antarctica by the opening of the Drake Passage, with the consequent emergence of a current around the Antarctic. The warm currents from

the tropical Atlantic and Pacific oceans ceased, and a circum-Antarctic current may have led to a permanent ice cap at the South Pole; the accumulation of ice and snow would have generated an albedo effect, which would have caused a fall in the planet's average temperature. The $\delta^{18}\text{O}$ suffered a sharp decline and indicates the onset of the Antarctic glaciation (Shackleton and Kennett, 1975; Livermore et al., 2005; Tripathi et al., 2005). The $\delta^{13}\text{C}$ values, meanwhile, show a slight reduction in productivity. While the extinctions of the carinate spinose species occur during a long-term cooling trend, the biotic turnover in the muricate group could not be related to significant climatic changes, according to Wade (2004), who proposed that this turnover event was probably related to the increased surface water productivity and the deterioration of photosymbiotic partnerships with algae.

No evidence of meteorite impacts has been reported for the time interval of the Middle/Late Eocene boundary extinction event, although some researchers (Alvarez et al., 1982) on the basis of imprecise correlations have suggested that such impacts might have been the cause. Hence, the geological cause discussed in the preceding paragraph is in our view the most plausible one; as it explains the origin of the global cooling that would have caused the gradual extinction of the most specialized species of planktic foraminifera that were adapted to warm environments. In addition, this cause is a highly plausible explanation for the severe crisis experienced by radiolarians and tropical mollusks, although mollusks were probably regulated by the combined effect of cooling and sea-level fall, while radiolarians and planktic foraminifera were mostly regulated by the cooling of the ocean surface waters.

6. Eocene/Oligocene extinction event

The planktic foraminifera extinction event has served as a criterion for the definition of the Eocene/Oligocene (E/O) boundary. It coincides with the Priabonian/Rupelian boundary and has been dated to 33.9 Ma (Vandenberghe et al., 2012). The extinction of the last hantkeninids is the principal criterion for its correlation and characterization (Premoli Silva et al., 1988) while the stratotype (GSSP) of the E/O boundary has been formally defined in the section of Massignano, Italy (Premoli Silva and Jenkins, 1993). Previously, the Spanish sections of Torre Cardela, Molino de Cobo and Fuente Caldera (Molina, 1986) had been proposed as candidates. They are a richer source of data on the Eocene–Oligocene transition, allowing to study the extinction process of the planktic foraminifera with a higher resolution than in the official boundary stratotype. In addition, we have studied sites of the DSDP–ODP. The latter tend to be affected by condensation, hiatuses, and dissolution, but in sites 219 and 292 the Eocene/Oligocene boundary is recorded and the foraminifera are very well preserved (Molina et al., 1993). One of the best sections in the world is located in Tanzania, which allowed Wade and Pearson (2008) and Pearson et al. (2013) to conclude that the E/O boundary is located between two principal steps in the stable-isotope records and that the extinction of the hantkeninids preceded the maximum glacial conditions in the early Oligocene by approximately 200 kyr.

Among the most emblematic groups that were greatly affected by this extinction event were the mammals. They underwent a major renovation that is very well documented in Europe, where it is known as Stehlin's "grande coupure", which meant a major turnover in the mammalian fauna. This involved the extinction of most of the endemic European mammalian taxa, to be replaced by species migrating from Asia, a process that also affected other fauna and flora (Hartenberger, 1998). The cause of these changes would appear to be directly related to the closure of the Turgai Strait, with the consequent linking of Europe and Asia, thereby putting an end to the paleogeographical isolation of Europe and permitting migrations of species from one continent to the other (Prothero, 1994). On the west coast of the United States, evidence has been found of another sudden extinction of mollusks (Hickman, 2003). Foraminifera and mollusk extinctions seem to be more closely linked to the Oi-1 cooling event.

The reference section for the study of the planktic foraminifera is Fuente Caldera (Fig. 6; Molina, 1986; Molina et al., 2006b; Alegret et al., 2008). The boundary interval is also well exposed and extensive in Torre Cardela (Martínez Gallego and Molina, 1975) and Molino de Cobo (Molina et al., 1988). The figures included in the papers cited clearly show the duration of the phases, the extinction pattern and survival strategies of the species involved. The event is characterized by the extinction of the hantkeninids and turborotalids. Three genera became extinct: *Hantkenina*, *Cribohantkenina*, and *Turborotalia*. The species that became extinct gradually account for 31% of the assemblages. They are: *Turborotalia cocoaensis*, *Turborotalia cunialensis*, *Hantkenina primitiva*, *Hantkenina compressa*, *H. alabamensis*, *Hantkenina nanggulanensis*, and *Cribohantkenina lazzarii*. In addition, *P. micra* s.str. also seems to have gone extinct since the surviving morphotypes that have been assigned to this species are much smaller. It is very likely that they belong to a different species (Lilliput effect).

Subbotina yeguaensis and the small species *Pseudohastigerina naguewichiensis* may be considered delayed extinctions. Species whose prevalence increased and may thus be considered disaster species are *Subbotina gortanii* and *G. suteri*. The progenitor species *Tenuitella gemma*, *Tenuitella neoclemenciae*, and *Tenuitellinata angustiumbilitata* are of small size and have a micro-perforated wall. Lazarus species are rare and the only one identified so far is *Subbotina angiporoides*. The survivor taxa are the majority and include the most cosmopolitan forms, among them quite a few of those that also survived the Bartonian–Priabonian extinction: *S. linaperta*, *C. cubensis*, *D. eocaena*, and *Catapsydrax unicavus*. The extinction phase begins with the disappearance of *Turborotalia cocoaensis* and concludes with that of *C. lazzarii*. This stage was quite brief, it is recorded in 1.2 m of clay-marly sediments and may have a duration of some 0.04 Myr, according to the calibration of Wade et al. (2011). It is considered a rapid mass extinction event. In some more condensed sections such as Massignano (Gonzalvo and Molina, 1992) this stage it is more difficult to identify.

The trigger of this extinction event must have been the same that caused the progressive cooling culminating in the basal Oligocene Oi-1 glaciation. The emergence of the circum-Antarctic current would have triggered the prolonged cooling across the Late Eocene, and given rise to the forming of an ice cap in the Antarctic and to the psychrosphere, culminating in the global glaciation Oi-1 near the E/O boundary (Kennett and Shackleton, 1976). Another interpretation is that the Oi-1 was caused by a threshold response to long-term Cenozoic decline in atmospheric carbon dioxide levels (DeConto and Pollard, 2003; Pearson et al., 2009). Furthermore, the deepening of the calcite compensation depth was synchronous with the stepwise onset of Antarctic ice-sheet growth (Coxall et al., 2005). The extinction pattern is very similar to that at the B–P transition, with most of the warm-water species disappearing, some of which had managed to survive the previous event. Therefore, in the basal Oligocene the very low diversification of the fauna was limited to temperate and cold waters. Consequently, the cause that triggered this extinction event would have been a new switch to cooler climates as well. The planktic foraminifera extinction event occurs approximately 200 kyr prior to the Oi-1 glaciation and the subsequent sea level fall (Coxall et al., 2005), indicating that the cause of the extinction was the cooling, rather than the fall of the sea level fall.

No evidence of a meteorite impact has been found coinciding with the extinction event at the E/O boundary. Evidence of the impact in the Mid-Priabonian has been well known since the discovery of microtektites in the Caribbean and the Gulf of Mexico (Glass et al., 1973). Moreover, the discovery of an iridium anomaly led some researchers to suggest an impact around 34 Ma and to associate this with the extinction at the end of the Eocene (Alvarez et al., 1982; Ganapathy, 1982). The microtektites extend across the North Atlantic, as shown by numerous sites of the DSDP–ODP (Keller et al., 1987; Molina et al., 1993). A number of studies show that the impacts occurred earlier than the extinctions, and some researchers have proposed a mass stepwise extinction pattern during the Late Eocene, attributing

the stages of extinction to comet or meteorite impacts (Hut et al., 1987; Kauffman, 1988). In the Massignano (Italy) section, three layers of iridium have been identified (Montanari et al., 1993) whereas in most DSDP–ODP sites there are just one, two, or at most three levels of microtektites. However, Hazel (1989), using graphic correlation techniques, concluded that there are at least six impact levels. The study of sites in the Atlantic, Indian and Pacific Oceans, together with the Italian and Spanish sections, has enabled us to reduce the possible impact levels to three, which were dated precisely based on the presence of planktic foraminifera, finding that they did not coincide with the extinction (Gonzalvo and Molina, 1992). Therefore these impacts did not cause the extinctions of the planktic foraminifera (Molina et al., 1993, 2006b).

Evidence of meteorite impacts has been found, such as quartzes with impact metamorphosis (Clymer et al., 1996) and Ni-rich spinels (Pierrard et al., 1998; Robin and Molina, 2006; Molina et al., 2006b). Several impact craters dated as Mid-Priabonian have been located, such as Popigai in Siberia with a diameter of 100 km (Bottomley et al., 1993), Chesapeake Bay on the eastern continental platform of North America with a diameter of 90 km (Koeberl et al., 1996), and Toms Canyon, also on the eastern platform of North America with a diameter of 20 km. The correlation of these impact craters with the ejected material deposits has been established by Poag et al. (2003), confirming the impact of three large meteorites around 35.6 Ma.

These data confirm that there is no correlation between levels with evidence of impacts and levels with extinctions, as the extinctions occurred in the Middle–Late Eocene transition and at the Eocene/Oligocene boundary, whereas the evidence of impacts is in the Mid-Priabonian. Therefore, there is no coincidence and no cause–effect relationship can be established between impacts and extinctions. Some researchers have suggested that global cooling may have been accelerated by the impacts (Wonhof et al., 2000), but the isotopic data do not support any acceleration (Livermore et al., 2005). It seems evident, then, that the meteorites were not large enough to cause a global catastrophe.

The Mid-Priabonian impacts, which due to their proximity to one another were hitherto interpreted as a single event that supposedly caused a massive extinction, constitute a key argument next to the K/Pg boundary for proponents of periodicity in extinction events. There has been a great debate on the subject of periodicity in extinction events, since periodicity implies that all extinction events were triggered by meteorite impacts. The first to put forward the notion of periodicity were Fischer and Arthur (1977) who proposed a cyclical period of 32 Ma, but the debate did not commence in earnest until Raup and Sepkoski (1984) suggested a periodicity of 26 Ma. Some supporters of this hypothesis went so far as to suggest that Nemesis, a supposed twin star of our Sun, passes periodically through the Oort cloud causing a shower of meteorites to fall on the Earth (Hut et al., 1987). However, recent high-resolution studies of the geological time scale (Vandenbergh et al., 2012) allow us to rule out this supposed periodicity, since at least the Paleogene events presented here do not show any periodicity because they occurred at 66.04, 56.0, 37.8 and 33.9 Ma.

7. Discussion and conclusions

The planktic foraminifera reached the zenith of their diversity in the Late Cretaceous and suffered the greatest crisis in their history at the K/Pg boundary, after which they recovered and flourished again during the Early and Mid-Eocene climatic optimum, although their specific diversity was never as great as it had been in the Late Cretaceous. From the Mid-Eocene onward, their diversity started to decline with the extinction of the species with the most complex morphology that had adapted to warmer waters. As a result, the Early Oligocene was a period with very low diversity of planktic foraminifera and this coincides with the coldest climate of the Paleogene. The species that disappeared in these various extinction events were the most highly specialized K-selection strategists, those adapted to the deepest environments

EXTINCTION EVENTS	Cretaceous/Paleogene Maastrichtian/Danian	Paleocene/Eocene Thanetian/Ypresian	Middle/Upper Eocene Bartonian/Priabonian	Eocene/Oligocene Priabonian/Rupelian
Absolute age	K/Pg = 66.04 Ma.	P/E = 56.0 Ma	B/P – Around 37.8 Ma	E/O = 33.9 Ma
Reference section studied	El Kef	Alamedilla	Torre Cardela	Fuente Caldera
Spanish sections studied	Caravaca, Zumaya, Agost	Alamedilla, Caravaca, Zumaya	Aspe, Artieda, Arguis, Torre Cardela	Fuente Cardera, Torre C., Molino Cobo.
Other sections studied	In Tunisia, Mexico, Cuba, France	Possagno (Italy), Dababiya (Egypt)	ODP-DSDP (13 sites)	Massignano (Italy), ODP-DSDP (11 sites)
Extraterrestrial causes	Meteorite impact >10 km	Comet?	Not simultaneous with event	Not simultaneous with event
Extraterrestrial evidences	Ir, microtectite, spinel, shocked Q	Small enigmatic Ir anomaly at Zumaya	Not found just at the event	Not found just at the event
Impact craters	Chicxulub	Not found	Not found just at the event	Not found just at the event
Geological causes	Not found	Opening of North Atlantic	Isolation of Antarctica (Circumant. current)	Closure of Turgai strait (Europe-Asia)
Large Igneous Provinces	Deccan volcanism	Norwegian-Artic volcanism	Not found	Not found
Geological evidence	Megaturbidite and dark grey clay	Red or grey clay (calcite dissolution)	Grey clay	Grey clay
Eustatic factor	Sea level fall?	Sea level fall and rise	Possible sea level fall	Sea level fall
Temperature factor	Abrupt oscillation	Hyperthermal event (Ice house effect)	Strong gradual decrease	Very fast decrease
Chemical factors	Strangelove ocean, acid rain	Anoxia, methane hydrates release	CO ₂ low	CO ₂ low
Productivity factor	Strong decrease of $\delta^{13}C$	Strong decrease of $\delta^{13}C$	Low decrease of $\delta^{13}C$	Low decrease of $\delta^{13}C$
Most affected environments	Terrestrial and pelagic	Bathyal and abyssal	Neritic and pelagic	Terrestrial and pelagic
Biological causes	No time for natural selection	High competition and selection	Moderate competition and selection	High competition and selection
Most affected organisms	Dinosaurs, ammon., belemn., rudist.	Smaller benthic foraminifers	Tropical molluscs and radiolarians	Mammals (“Grand coupure”)
Extinction pattern	Sudden (<i>Globotruncanids</i>)	Rapid (Smaller benthic forams)	Slow (spinose carinated forms)	Rapid (<i>Hantkeninids</i> & <i>Turborotalids</i>)
Species extinction	91% (Planktic forams)	>37% (Smaller benthic forams)	33% (Planktic forams)	31% (Planktic forams)
Extinct taxa	56 (<i>G. arca</i> , <i>A. mayaransensis</i> , etc.)	>25 (<i>A. avnimelechi</i> , <i>A. rubiginosus</i> , etc.)	12 (<i>O. beckmanni</i> , <i>M. crassatus</i> , etc.)	8 (<i>T. cunialensis</i> , <i>H. alabamensis</i> , etc.)
Delayed extinct taxa	<i>Hedbergella holmdelensis</i> , etc.	<i>Anomalinoidea aegyptiacus</i> , etc.	<i>Acarinina collectea</i> & <i>G. subconglobata</i>	<i>S. yeguensis</i> & <i>Pseudohastigerina</i> <100µm
Disaster taxa	<i>Rugoboligerina cretacea</i> , etc.	Agglutinated forams (<i>Glomospira</i> spp.)	<i>Subbotina eocaena</i> & <i>Globorotaloides suteri</i>	<i>Subbotina gortanii</i> & <i>Globorotaloides suteri</i>
Opportunistic taxa	<i>Guembeltria cretacea</i> , etc.	<i>G. subglobosa</i> , <i>T. selmensis</i> , etc.	<i>Turborotalia cocoensis</i> , <i>G. semiinvoluta</i> , etc.	<i>Tenuitella gemma</i> , etc.
Progenitor taxa	<i>Paleoglobigerina alticonusa</i> , etc.	<i>Turrilina brevispira</i> , etc.	<i>Globigerinatheka luterbacheri</i> , etc.	<i>Tenuitella gemma</i> , etc.
Lazarous taxa	Numerous smaller benthic forams	Calcitic forams	<i>Hantkenina alabamensis</i> , etc.	<i>Subbotina angiporoides</i> , etc.
Survivor taxa	<i>Zeugligerina waiparaensis</i> , etc.	<i>Nuttallides truempyi</i> , etc.	<i>Subbotina hagni</i> , <i>Subbotina linaperta</i> , etc.	<i>Dentoglobigerina eocaena</i> , etc.
Extinction interval	Extremely short (years or decades)	Short (0.01 Myr)	Long (2 Myr)	Short (0.04 Myr)

Fig. 7. Comparative synthesis of the main Paleogene mass extinction events.

and living in the warmest latitudes. After the extinction events, the generalized r-selection strategists predominated and gradually specialized again and recolonized the deepest habitats. Consequently, we find an alternation of polytaxic periods with large numbers of specialized species (Late Cretaceous, Late Paleocene–Mid Eocene) and oligotaxic periods with small numbers of generalistic species (Early Paleocene and Early Oligocene).

The extinction events in the Paleogene (K/Pg boundary, P/E boundary, B/P transition, E/O boundary) occurred at 66.04, 56.0, 37.8, and 33.9 Ma, respectively and, therefore, do not fit into periodic extinction models (Fig. 7). Evidence of meteorite impacts indicates that the greatest meteorite impacts occurred at 66.04 and around 35 Ma. The large meteorite impacts were mass extinction triggers, as at the K/Pg boundary. However, there are no other mass extinction events during the Paleogene for which a cause–effect relationship can be traced between meteorite impacts and mass extinctions.

The examples presented in this study indicate that the causes are different for each extinction event. However, the temperature factor proves to be the most relevant and omnipresent one: global falls in water temperature tend to lead to extinction while temperature increases tend to result in greater diversity of species. Since the tropics have a greater abundance of specialized forms, these zones become a lethal trap during global falls in temperature: the species that inhabit them cannot migrate to maintain their optimal temperature, unless they colonize deeper niches, though this phenomenon requires some time for evolution to enable adaptation to greater hydrostatic pressure. In contrast, increases in temperature can be overcome mainly by migration of species to higher latitudes. In some environments, the increase in temperature may also lead to extinctions, as occurred in the deep ocean at the P/E boundary.

In general, there are three kinds of triggers for mass extinctions: biological, geological and extra-terrestrial. Biological causes (competition, endemism) operate mainly at the level of background extinction, while mass extinctions tend to be triggered by geological causes (e.g., plate

tectonics generating volcanic activity, greenhouse effect, glaciations, and eustatic sea-level) and by extra-terrestrial causes (e.g., large meteorite or comet impacts and possibly cosmic and solar radiation).

The terminology generally used to name patterns of mass extinction (gradual, step-wise, catastrophic) is imprecise and does not reflect well enough the processes involved. The step-wise mass extinction pattern, which was proposed for extinctions in the Late Eocene and was supposedly produced by a series of meteorite or comet showers, has been refuted (see above). The step-wise pattern could be the result of conflating different events or it could amount to one slow extinction pattern that may not have been constant in its intensity. Hence, a new terminology is proposed: sudden mass extinction, rapid mass extinction, and slow mass extinction. According to the events in our study, sudden mass extinction would have occurred almost instantaneously, the process taking just years or decades (K/Pg boundary). This can only be confirmed by studies of continuous and expanded sections. Rapid mass extinction is characteristic of events of relatively short duration of around 100 kyr (P/E and E/O boundaries) and can be best observed in continuous and data-rich sections, while in more condensed sections it may appear to have been sudden. Finally, slow mass extinction would take around 1 Myr (B/P transition) and could extend even to a few million years.

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