



Evaluating tracemaker recovery after the Cretaceous–Paleogene (K–Pg) boundary event: different biotic responses at the Caravaca section

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Abstract

Trace fossils are an aid to characterize major extinction events, enriching evolutionary paleoecology research. Ichnological analysis at the Cretaceous–Paleogene (K–Pg) marine boundary interval, worldwide, points to a relatively minor disruption in the macrobenthic tracemaker community; that is, trace-fossil assemblages do not change significantly across the K–Pg boundary, showing relatively rapid recovery, locally in just a few years post-impact. To evaluate the incidence of this event and the rapid recovery of the tracemaker community afterwards, the evolution of planktic and benthic groups at the K–Pg boundary interval was analysed in the Caravaca section (Betic Cordillera) based on the integration of available data. In general terms, planktic foraminifera and calcareous nannoplankton dropped in abundance and diversity at the K–Pg boundary, whereas benthic foraminifera did not show significant extinction, but rather a sudden and dramatic decrease in diversity and reorganization. After the K–Pg boundary event, planktic communities exhibit a prolonged delay in recovery—mainly occurring above the dark boundary layer—with respect to benthic foraminifera. The K–Pg boundary event did not induce a severe crisis for the burrowing macroinfauna, as revealed by the similarity between pre- and post-event ichnotaxa, showing a comparatively rapid first colonization phase, less than 2 ky after the event. The record of *Zoophycos* and *Chondrites* at the base of the dark boundary layer evidences an opportunistic behaviour of tracemakers and a high independence from oxygen in pore waters and food in the sediment, allowing for the colonization of an overall unfavorable environment.

Keywords Cretaceous–Paleogene (K–Pg) bio-event · Recovery · Temporal calibration · Benthic and pelagic ecosystem · Trace fossils · Caravaca

Resumen

En los últimos años las pistas fósiles se han revelado como una herramienta fundamental para caracterizar eventos de extinción mayores, mejorando la investigación sobre paleoecología evolutiva. El análisis icnológico del intervalo Cretácico–Paleógeno (K–Pg) en secuencias marinas muestra una menor incidencia del evento sobre la comunidad macrobentónica bioturbadora, las asociaciones de trazas no cambian significativamente a lo largo del límite K–Pg, así como una recuperación relativamente rápida, localmente en el rango de los pocos años, tras el impacto. En esta investigación se estudia el intervalo del límite K–Pg en la sección distal y continua de Caravaca (Subbético Externo, Cordillera Bética) con el objetivo de evaluar la incidencia del evento y la recuperación comparativamente rápida de la comunidad bioturbadora tras el mismo, comparándola con la evolución de diferentes grupos planctónicos y bentónicos. La zonación bioestratigráfica de alta resolución junto con la calibración temporal existentes facilitan este estudio. En términos generales, foraminíferos planctónicos y nanoplancton calcáreo colapsan en abundancia y diversidad en el límite K–Pg, mientras los foraminíferos bentónicos no muestran una extinción significativa sino una caída brusca en la diversidad y la reorganización de la comunidad. Tras el evento del límite K–Pg, las comunidades planctónicas experimentan una recuperación prolongada, registrada, fundamentalmente, por encima

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de la capa oscura del límite, en comparación con los foraminíferos bentónicos. En este contexto de una incidencia comparativamente menor del evento del límite sobre el hábitat bentónico en Caravaca, es particularmente interesante la respuesta de la comunidad macrobentónica bioturbadora. El evento del límite no induce una crisis severa para la comunidad bioturbadora, como se refleja en la similitud entre las asociaciones de pistas antes y después del evento, mostrando una comparativamente rápida primera fase de colonización en menos de 2 ka. El registro de *Zoophycos* y *Chondrites* en la base de la capa oscura del límite evidencia el comportamiento oportunista de los productores y la alta independencia del oxígeno entre poros y del alimento en el sedimento, permitiendo la colonización de ambientes poco favorables.

Palabras clave Bio-evento del Cretácico–Paleógeno (K–Pg) · recuperación · calibración temporal · ecosistemas bentónico y pelágico · pistas fósiles · Caravaca

1 Introduction

The Cretaceous–Paleogene (K–Pg) bio-event is one of most dramatic phenomena during the Phanerozoic, determining rapid environmental changes that affected biota. This event, related with the impact of an asteroid at the end of the Cretaceous Period (66.0 Ma) on the Yucatan Peninsula (the Chicxulub crater, Mexico), caused the extinction of some 75% of the marine species (Schulte et al., 2010), likewise affecting terrestrial communities (plants, reptiles, primitive mammals) (Kauffman & Hart, 1996). The extinction has been profusely studied, focusing on the adverse environmental conditions involved, especially variations in temperature, ocean acidification, and marine productivity (Alegret et al., 2012; Henehan et al., 2019; Hull et al., 2020). In recent years, particularly after the International Ocean Discovery Program (IODP)–International Continental Scientific Drilling Program (ICDP) Expedition 364, more attention has been paid to the immediate aftermath of the impact (Bralower et al., 2020; Gulick et al., 2019; Lowery et al., 2018, 2021). Detailed study at ground zero in the Chicxulub crater revealed a rapid recovery of life in the basin just years after the impact, with a high-productivity ecosystem established within 30 kyr (Lowery et al., 2018). Planktic foraminifera, calcareous nannoplankton, calcispheres (calcareous dinoflagellate resting cysts), and cyanobacteria reappeared within a few years post-impact (Lowery et al., 2021 and references therein). Of special significance, the ichnological record shows the presence of discrete, small, isolated *Planolites* (initial recovery) in the first few years after the extinction, and the establishment of a well-developed multitiered community ~ 640–700 ky after the K–Pg boundary (Rodríguez-Tovar et al., 2020).

The post-extinction recovery observed in the Chicxulub crater is hardly known for K–Pg boundary sections worldwide. Most analyses of marine recovery after the K–Pg event have been conducted on particular groups, giving only a partial interpretation of the phenomenon. An integrative paleontological analysis of the different communities affected—micro and macro, in complete and continuous K–Pg sections—is essential for understanding recovery as a whole.

Out of all the K–Pg boundary sections worldwide, several features make the Caravaca section (External Subbetic Zone, Betic Cordillera; Figs. 1, 2) very appropriate for undertaking research of biotic recovery: (a) the high completeness of the K–Pg boundary interval, with an absence of condensed intervals and hiatuses (MacLeod & Keller, 1991; Smit, 2005), leading this section to be chosen as an auxiliary of the Global Boundary Stratotype Section and Point (GSSP) for the base of the Danian Stage (Molina et al., 2009); (b) the high-resolution planktic foraminiferal biostratigraphy of the lower Danian at Zone and sub-Zone level, together with the biomagnetostratigraphic correlation and calibration of the biostratigraphic data (Arenillas et al., 2004; Arz et al., 2000); and (c) previously performed detailed paleontological research, focusing on biodiversity patterns, including data from planktic (foraminifera, calcareous nannofossils) and benthic communities (foraminifera, trace fossils) (see references below).

Here, a comparative study of available, published, data from paleontological records of diverse groups (micro and macro) along the K–Pg boundary interval at the Caravaca section is presented, in order to evaluate both the incidence of the impact event and the recovery pattern of the different marine communities affected. Paleontological data were compiled and integrated under recent biostratigraphic and calibration proposals.

1.1 Trace fossils and the K–Pg boundary event

Interest in ichnology as a tool to improve evolutionary paleoecology research has been growing in recent years (Márgano and Buatois, 2016). Exploring the relationship between trace fossils and major evolutionary events can provide for a better understanding of the organic history of the Earth. In turn, the usefulness of trace fossils as a tool to characterize the “Big Five” mass extinction events has been recognized to some extent. Ichnological analyses of the end-Ordovician event (Herringshaw & Davies, 2008; McCann, 1990; Nicholls, 2018; Twitchett & Barras, 2004), end-Devonian event (Boyer et al., 2014; Buatois et al., 2013; Haddad et al., 2013; Stachacz et al., 2017; Wang et al., 2006), and the end-Triassic event (Barras & Twitchett, 2007, 2016; Twitchett & Barras, 2004) are relatively scarce. Better known are the

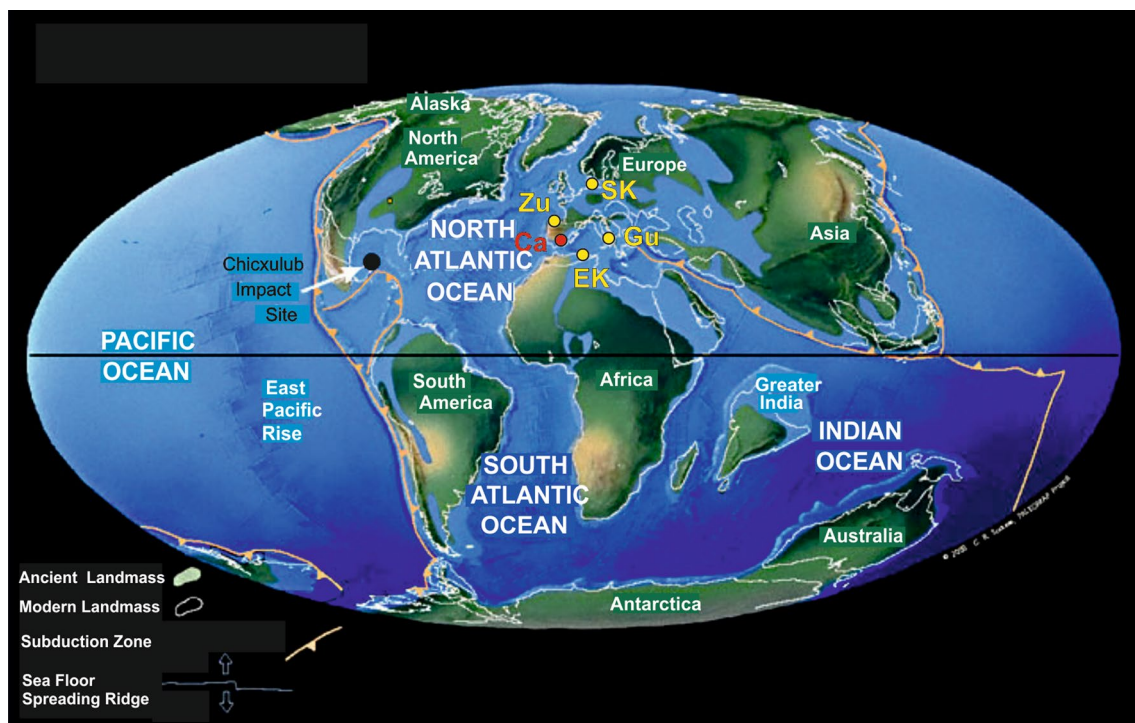


Fig. 1 Global paleogeography at the K–Pg boundary (modified from Scotese, 2001) with location of the Chicxulub impact site (black circle), the Caravaca section (Ca; red circle) and other distal sites (yellow circles; EK—El Kef, Zu—Zumaya, Gu—Gubbio, SK—Stevns Klint)

contexts of the end-Permian event (i.e., Chen et al., 2012; Foster et al., 2018; Hofmann et al., 2015; Knaust, 2010; Luo et al., 2020, 2021; Rodríguez-Tovar et al., 2021; Twitchett, 1999, 2006; Twitchett & Wignall, 1996; Twitchett et al., 2004; Zhang et al., 2019; Zhao et al., 2015), and the end-Cretaceous event (Alegret et al., 2015; Labandeira et al., 2016; Łaska et al., 2017; Lowery et al., 2018; Monaco et al., 2015; Rodríguez-Tovar, 2005; Rodríguez-Tovar & Uchman, 2004a, 2004b, 2006, 2008; Rodríguez-Tovar et al., 2004, 2006, 2010, 2011, 2020, 2022; Sosa-Montes de Oca et al., 2013, 2016, 2017, 2018).

Detailed ichnological analysis at the K–Pg boundary interval worldwide (outcrops and drilling cores) reveal particular features linked to selectivity during the mass extinction, minor disruption, or rapid recovery, among others (see Labandeira et al., 2016). Especially interesting for the marine setting is the relatively minor disruption among the macrobenthic tracemaker community—trace-fossil assemblages do not change significantly across the K–Pg boundary, and show a relatively rapid recovery. Recent ichnological studies conducted on cores from the Chicxulub impact crater, Yucatán Peninsula, Mexico (IODP/ICDP Site M0077), evidence a similarity in trace fossil assemblage and the size of traces in Upper Cretaceous and early Paleocene sediments in the crater area, in agreement with the absence of major effects (i.e., extinction) on the global marine macrobenthic tracemaker community. Moreover, a

rapid recovery of the macrobenthic tracemaker community was characterized, the first trace fossils appearing just years after the impact (Lowery et al., 2018; Rodríguez-Tovar et al., 2020, 2022).

2 Geological setting: the Caravaca section

The K–Pg boundary within the Caravaca section ($38^{\circ}04'36.39''\text{N}$, $1^{\circ}52'41.45''\text{W}$) is found in the Barranco del Gredero, 4 km SE from the town of Caravaca de la Cruz (Murcia province), in the External Subbetic Zone of the Betic Cordillera, SE Spain. This section belongs to a 225 m thick succession of intercalated marls, marly limestones and occasional turbidites (the Jorquera Formation; lower Maastrichtian–lower Eocene) (Figs. 1, 2).

The topmost Maastrichtian in the Caravaca section consists of light grey marls grading into a green transitional layer (3 mm thick) (Fig. 2). The K–Pg boundary is sharp and overlain by a black grey clay interval (the dark boundary layer; 7–10 cm thick) with a rusty layer (the ejecta layer; 2–3 mm thick) at the base, containing evidences of the impact event (K–Pg boundary spherules, Ir, other platinum-group elements, and Ni, Co, Cr and Fe anomalies; Smit, 2005). The dark boundary layer comprises four parts (Rodríguez-Tovar & Uchman, 2006) (Figs. 2, 3, 4): (a) the lowermost (14 mm thick) is laminated, more clayey and dark

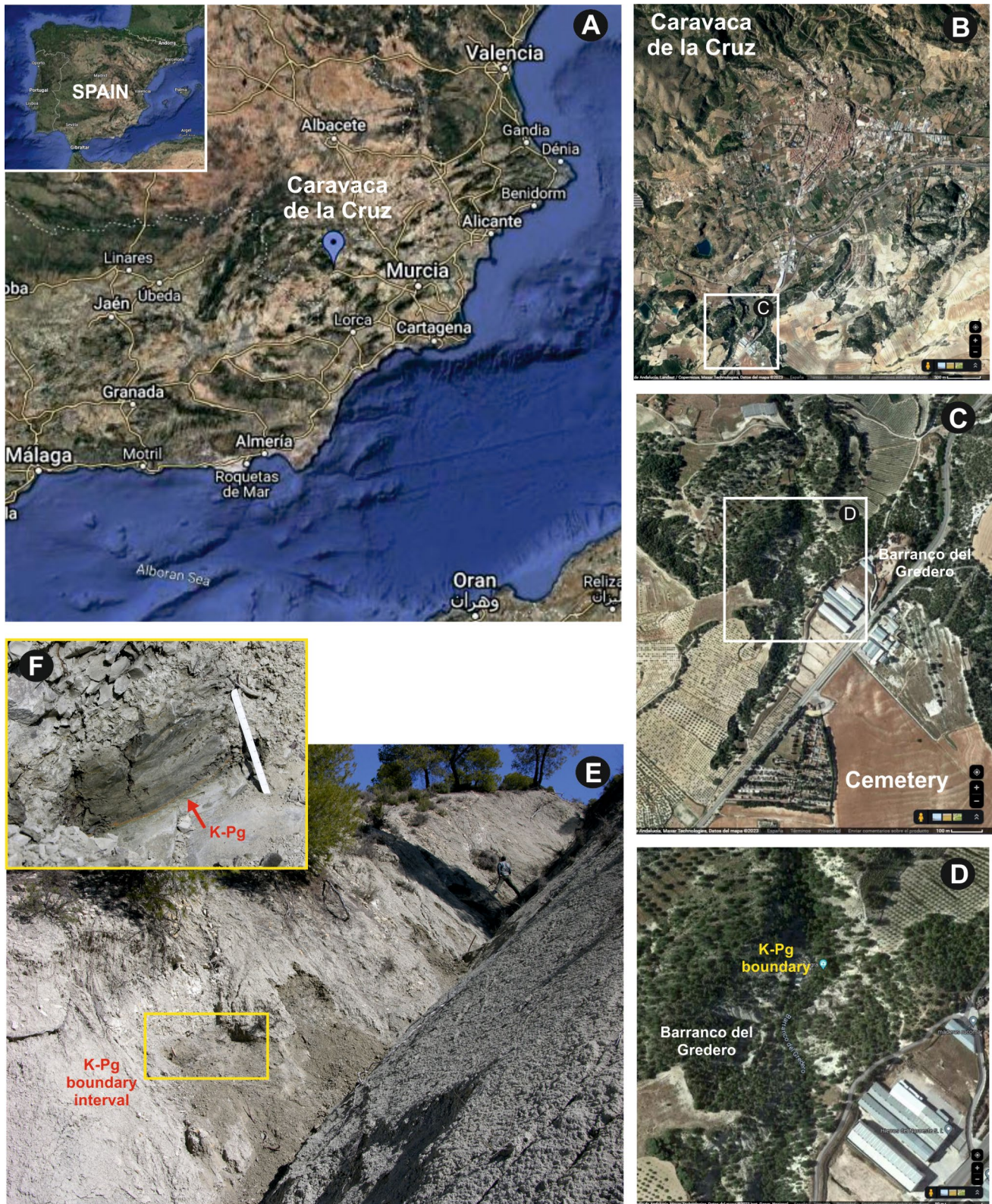


Fig. 2 Location of the Caravaca section. **A** General location of Caravaca. **B–D** Close-up views of Caravaca village (**B**), Barranco del Gredero and cemetery (**C**) and K–Pg outcrop at the Barranco del

Gredero (**D**). **E, F** K–Pg Caravaca outcrop, and close-up view of the K–Pg boundary and dark boundary layer (scale bar: 10 cm)

grey; (b) a light grey bioturbated interval (26 mm thick); (c) a more clayey interval (35 mm thick) with convolute, sinuous disturbances and loaded lighter lensoidal bodies, separated by discontinuous lighter sediments with discontinuous lamina; and (d) a greenish grey, bioturbated interval (25 mm thick) at the top. This dark boundary layer is overlain by grey clayey marls (Figs. 2, 3, 4).

Mainly based on benthic foraminifera assemblages, the terminal Maastrichtian-basal Danian sediments are usually interpreted as deposited in a middle bathyal environment, at around 30° N (MacLeod & Keller, 1991). A bathymetry at 600–1000 m (Coccioni & Galeotti, 1994, 1998; Coccioni et al., 1993), around 800 m (Widmark & Speijer, 1997a, 1997b), or more than 1000 m (Smit, 2005) has been evoked.

The K–Pg boundary interval at the Caravaca section has been profusely studied through high-resolution micropaleontological, ichnological, and geochemical analyses, allowing for the characterization of variations in oxygenation, temperature, and productivity, and consequent paleoenvironmental,

paleoclimatic, and paleoceanographic reconstructions (Gilbert et al., 2021a and references therein, see below).

3 Faunal (micro and macro) distribution patterns at the K–Pg boundary interval

At the Caravaca section, detailed paleontological analyses focused on particular groups pertaining to pelagic and benthic communities. The pelagic community is represented by planktic foraminifera and calcareous nannofossils, while the benthic community consists of benthic foraminifera and macro-tracemakers.

Before offering any comparative analysis of the main paleobiological and evolutionary episodes at the Caravaca section, it is necessary to consider the variations in thicknesses, in biostratigraphic zonation, and in temporal calibrations described from the first paleontological studies (late 1970's) to recent ones. For the sake of uniformity,

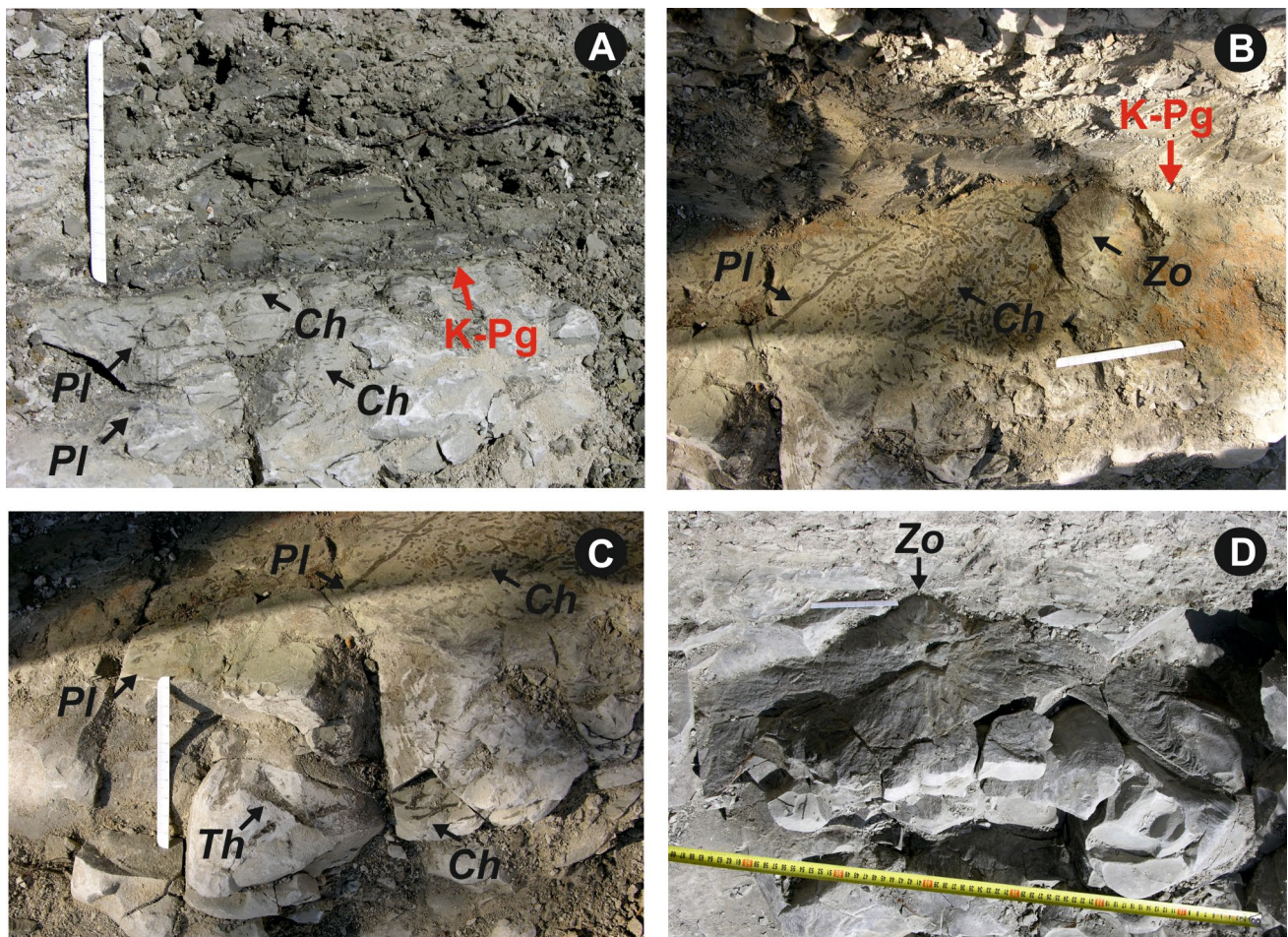


Fig. 3 Trace fossils registered in the uppermost Maastrichtian light sediments with location of the K–Pg boundary. **A** Dark *Planolites* (*Pl*) and *Chondrites* (*Ch*). **B** Dark *Planolites*, *Chondrites* and *Zoophy-*

cos (*Zo*). **C** Dark *Planolites*, *Chondrites* and *Thalassionoides* (*Th*). **D** *Zoophycos*. Scale bar: 10 cm

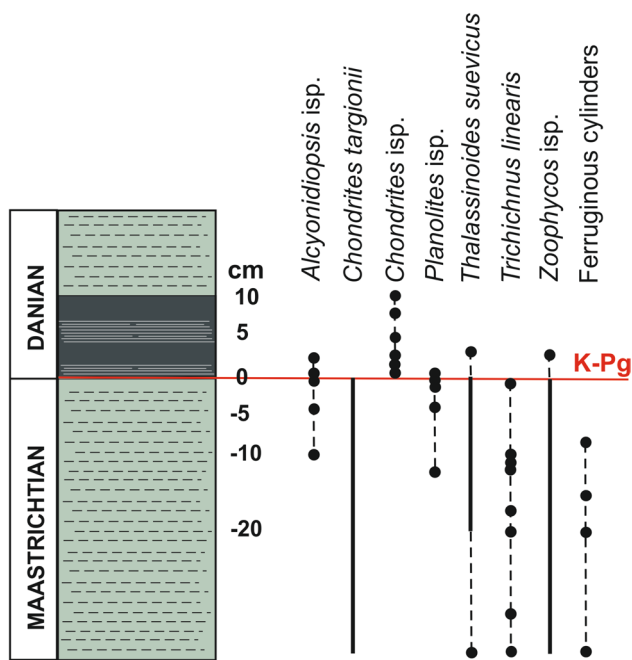


Fig. 4 Vertical distribution of trace fossils of the Danian boundary assemblage in and below the dark boundary layer. Solid lines indicate continuous range and the dots punctuated observations (after Rodríguez-Tovar & Uchman, 2006)

and to avoid misinterpretations related to different biozonations of the lowermost Danian (see Arenillas et al., 2004, 2021 for a recent update), all correlations of the paleontological data herein will refer to position with respect to the dark boundary layer (rather than a concrete Zone and/or subzone), taking into account the differences in thickness assigned to the dark boundary layer between 6.5 cm (Coccioni & Galeotti, 1994; Smit, 1990) and roughly 10 cm (Arinobu et al., 1999, 2005; Kaiho et al., 1999; Rodríguez-Tovar & Uchman, 2006) (Table 1). Given the similar thickness of the dark boundary layer considered here, and that of Arinobu et al. (1999), in calibrating and correlating the time recovery of different communities we adopt their proposal of an average sedimentation rate of 3.1 cm/kyr for the Maastrichtian part of C29R, 0.8 cm/ky for the dark boundary layer (total duration of 12.5 ky)—except for the red layer which is usually considered as instantaneous—and 1.7 cm/ky for the Paleocene part of C29R above the dark boundary layer (Arinobu et al., 1999, 2005; Kaiho et al., 1999), will be followed. Thus, those temporal data based on other averaged sedimentation rates for the dark boundary layer (i.e., 0.77–0.9 cm/ky, considering a duration about 5–6 ky; Smit, 1990; Coccioni & Galeotti, 1994, or around 0.76–0.65 cm/ky; Arenillas et al., 2004) will be adapted to the proposal applied here (Table 1).

Arenillas et al. (2021) proposed new biochronological scales of planktic foraminifera for the early Danian, based on qualitative data, and including four biozones, and on quantitative data, including three acme-zones. The planktic foraminiferal key-biohorizons of the proposed qualitative biozonation are those from Arenillas et al. (2004), characterized by updated magnetostratigraphical and astronomical calibrations. Arenillas et al. (2021) consider a ~6 cm thick dark clay bed, with a ~2 cm thick darker layer at its basal part. The base of these dark clay marls marks the K–Pg boundary, and consists of a 1 to 2 mm thick red airfall layer that coincides with the planktic foraminiferal mass extinction horizon. The above authors assign an age of 66.001 Ma to the K–Pg boundary and 65.991 Ma to the top of the K–Pg boundary dark clay, considering a duration of ~10 kyr for the deposition of the ~6 cm K–Pg boundary dark clay bed (Table 1 in Arenillas et al., 2021). The proposed average sedimentation rates at Caravaca are 0.60 cm/kyr for the K–Pg boundary dark clay bed, and 1.67 for the Danian part of C29r. In this particular case, because of the differences in thickness/duration between this proposal and that used here (Arinobu et al., 1999), data from Arenillas et al. (2021) were not adapted but maintained without modifications, and included close to the biostratigraphic ranges in Fig. 5.

3.1 Planktic foraminifera

Planktic foraminifera assemblages in the K–Pg boundary interval at the Caravaca section have been profusely studied to assess extinction and recovery patterns (i.e., Arenillas et al., 2021; Arz et al., 2000; Gilabert et al., 2021a, 2021b; Smit, 1982). General planktic foraminiferal stability in the upper Maastrichtian and a synchronous catastrophic mass extinction at the K–Pg boundary have been proposed, the occurrences of Cretaceous planktic foraminiferal species in lower Danian sediments being interpreted as the result of reworking (Kaiho & Lamolda, 1999; Smit, 1990). A more graduated extinction spanning over an extended time period has also been evoked (Canudo et al., 1991).

A five-stage pattern of extinction and radiation was previously proposed (Smit, 1982, 1990, 2005; Smit & Romein, 1985) (Fig. 5): (a) the first stage corresponds to the topmost zone of the Maastrichtian, showing few changes in the composition of the planktic assemblage; (b) at the ejecta layer (i.e., the K–Pg boundary), the mass-extinction is registered with the disappearance of most species; (c) the dark boundary layer contains poor remnants of dwarfed foraminifera and non-specialized species; (d) the initial recovery stage, recorded at the transition from the dark boundary layer to foraminifer-rich marls, is defined by the first occurrence of new Paleocene planktic foraminifera, having abundant faunas and reflecting the first explosive development of planktic biota; and (e) the adaptative radiation stage, at about

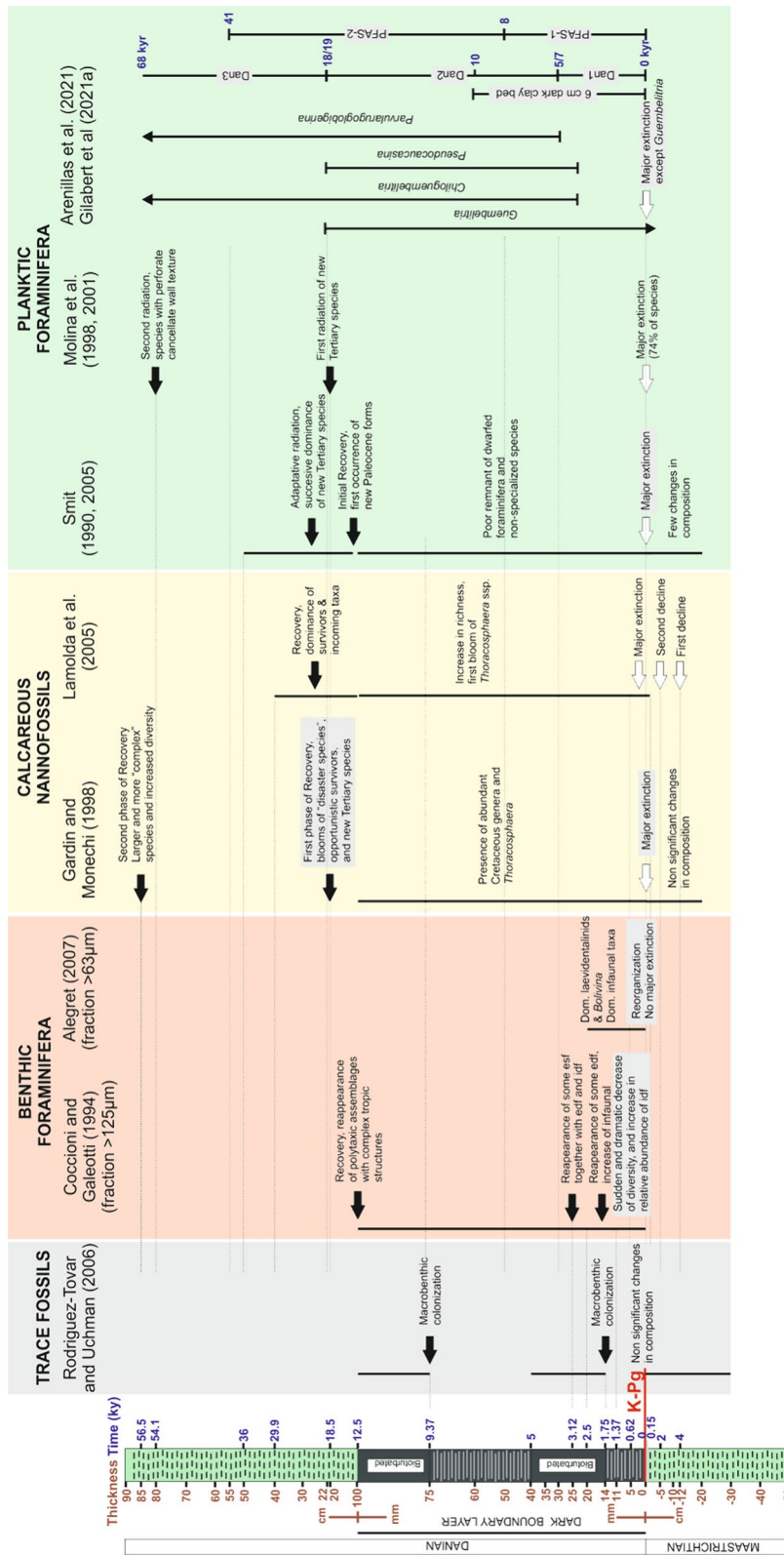


Fig. 5 Lithological column of the Caravaca section from the uppermost Maastrichtian to the lowermost Danian, with sedimentological horizons differentiated in the black boundary layer (after Rodríguez-Tovar & Uchman, 2006). Main extinction and recovery data in trace fossils, benthic and planktic foraminifera and calcareous nannofossils, and correlation with thickness and time values. Note difference in the scale of the dark boundary layer (mm) with respect to the rest of the lithological column (cm), idf=infaunal deposit feeders, edf=epifaunal deposit feeders, esf=epifaunal suspension feeders

0.5 m above the K–Pg boundary and corresponding to 36 ky according to the proposal here applied, represents the successive dominance of the new Tertiary species.

Molina and collaborators interpreted a catastrophic mass extinction in the planktic foraminiferal assemblage in coincidence with the K–Pg boundary (around 74% of the species went extinct), most of them large, complex, tropical-subtropical and deep-intermediate dwelling forms (Arenillas et al., 2000; Arz et al., 2000; Molina et al., 1998, 2001). After the K–Pg boundary, two evolutionary radiations of new Paleogene species were discerned (Fig. 5): (a) the first radiation of new opportunistic species (initial appearance of small species of *Parvularugoglobigerina*, *Globoconusa*?, *Woodringina* and *Chiloguembelina*) occurred above the dark boundary layer, in the white Tertiary marls, around 20 cm above the K–Pg rusty layer, corresponding to 18.4–21.5 ky (Arenillas et al., 2004); and (b) the second radiation occurred at about 80 cm above the K–Pg rusty layer, corresponding to 54.1–63.4 ky (Arenillas et al., 2004), with the first appearance of species showing perforate cancellate wall texture (figs. 3 and 2 in Molina et al., 1998, 2001 for thickness, and Arenillas et al., 2004 for temporal calibration).

Gilabert et al., (2021a, 2021b), recognized planktic-foraminiferal acme-assemblages (PFAS) correlated with the planktic foraminiferal zonation of Arenillas et al. (2004). The PFAS-1 span the first 5 cm of the lower Danian of the Caravaca section, hence included in the 6 cm-thick dark clay bed, corresponding to the first 8 kyr after the K–Pg boundary (Gilabert et al., 2021a) (Fig. 5). This PFAS-1 is dominated by triserial taxa, mainly *Guembelitra*, the only genus that survived the K–Pg boundary mass extinction, increasing its abundance after the K–Pg boundary, and to a lesser extent, its descendant *Chiloguembelitra*. Moreover a bloom of *Pseudocaucasina antecessor*, which starts within PFAS-1 and ends at the lowermost part of PFAS-2 is identified (Gilabert et al., 2021a). PFAS-2 is found 5 to 55 cm above the K–Pg boundary, corresponding to the interval between 8 and 41 kyr after the K–Pg event (Gilabert et al., 2021a). This acme-stage is dominated by parvularugoglobigerinids (i.e., *Parvularugoglobigerina* and *Palaeoglobigerina*) (Gilabert et al., 2021a).

3.2 Calcareous nannofossils

Calcareous nannofossils at the Caravaca section were first studied by Romein (1977) and later by Gardin and Monechi (1998). Acmes of nannofossils in the basal part of the Paleocene are recorded about 0.5 m above the K–Pg boundary, being characterized by the bloom of *Thoracosphaera* and *Braarudosphaera* (Romein, 1977 in Smit, 2005) (Fig. 5). Afterwards, the acme of *Biscutum* occurs. Gardin and Monechi (1998) register insignificant changes in nannofossil assemblages below the K–Pg boundary, the drastic

decrease in almost all Cretaceous species taking place just at the boundary (Fig. 5). At the 10 cm thick dark boundary layer, the calcareous assemblage is still dominated by the presence of abundant Cretaceous genera and *Thoracosphaera*. Two major phases in the recovery of the nannofossil community were recognized (Fig. 5), well above the dark boundary layer (see Figs. 4 and 8 of Gardin & Monechi, 1998). The first phase is characterised by blooms of “disaster species” (*Thoracosphaera* spp.), opportunistic survivors (i.e., *Braarudosphaera bigelowii*, *Markalius inversus*, *Cyclagelosphaera reinhardtii*), and new Paleogene species (dwarf *Biscutum*); this phase is around 20 cm above the K–Pg boundary, corresponding to 18.5 ky in our proposal. The second phase consists of the appearance of larger and more “complex” species (i.e., *Cruciplacolithus primus*) and increased diversity, interpreted as indicating a long return to more stable conditions, and informally fixing the recovery of the calcareous nannofossil community; this phase is around 85 cm above the K–Pg boundary, corresponding to 56.5 ky in our proposal.

Lamolda et al. (2005) record the main extinction event of the Cretaceous taxa in the K–Pg boundary, but reveal previous phases of decline among the calcareous nannofossils at 12 cm (about 4 ky prior to the boundary) and within the top 5 cm of the Maastrichtian (Fig. 5). An especially important nannofossil shift, with a marked drop in diversity, is registered at the transitional layer (Lamolda et al., 2005), from 0.3 cm below to 0.5 cm above the K–Pg boundary, spanning from around 0.1 ky prior to 0.62 ky after the K–Pg boundary event. At the base of the Danian, two successive blooms —of *Thoracosphaera* spp., followed by that of *Braarudosphaera bigelowii*— were recognized (Fig. 5). The first bloom, showing an increase in richness, is registered between 0.5 cm and 10 cm above the K–Pg boundary (from around 0.62 ky to 12.5 ky), corresponding to the rest of the dark boundary layer. Between 10 and 40 cm, well above the dark boundary layer, covering the period from approximately 12.5 to 29.9 ky, minor changes in diversity are registered. The recovery is interpreted about 25 ky after the K–Pg boundary mass extinction event, when the nannofossil assemblage is dominated by survivors as well as by incoming taxa, representing an early pioneer calcareous nannofossil ecosystem (Lamolda et al., 2005).

3.3 Benthic foraminifera

A four-step pattern of benthic foraminiferal decimation, survival, and recovery throughout the K–Pg boundary at Caravaca was proposed (Coccioni & Galeotti, 1994; Coccioni et al., 1993) (Fig. 5): (a) the first step represents the immediate dramatic consequence of the K–Pg boundary event, showing a sudden and marked decrease in diversity associated with a concurrent bloom of infaunal deposit-feeding

(*Bolivina*, *Spiroplectammina*), described as low-oxygen-tolerant forms; this phase lasted on the sea floor for 0.5–0.6 ky, correlating to 1.37 ky and 1.1 cm according to the proposal applied in this paper; (b) during the second step, from 0.6 to 1.2 ky after the K–Pg boundary, correlating to 2.12 ky and 2.4 cm, some epifaunal, deposit feeding taxa reappeared (i.e., *Anomalinoides*, *Gavilinella*), and the relatively abundant presence of infaunal deposit-feeding organisms continued; (c) in step three, particularly interesting is the reappearance of epifaunal suspension feeders (*Bathysiphon*) at about 1.5 ky, correlating to 3.62 ky and 2.9 cm, together with some epifaunal and infaunal deposit feeders; and (d) in step four, just above the top of the dark boundary layer, epifaunal, attached suspension-feeder forms reappeared (*Rhabdammina*, *Rhizammina*). The recovery is registered at the end of the dark boundary layer, about 7 ky after the K–Pg boundary, correlated in this proposal to around 12.5 ky, when assemblages are K-selected and polytaxic, with complex trophic structures (Coccioni & Galeotti, 1994; Coccioni et al., 1993).

Alegret (2007) conducted a detailed analysis of the Upper Cretaceous and lower Paleogene benthic foraminiferal assemblages (> 63 µm) from the middle bathyal Loya section (Basque–Cantabrian Basin, southwestern France), comparing the obtained results to data from the Agost and Caravaca sections (southeastern Spain). She indicated the reorganization of the benthic foraminiferal community structure—but no major extinctions—starting at the K–Pg boundary in the southeastern Spain sections (Fig. 5). Results from Alegret (2007) are based on the fraction > 63 µm and cannot be directly compared to the study by Coccioni et al. (1993) based on the fraction > 125 µm. Even so, Alegret (2007) analysed some scattered samples of the fraction larger than 63 µm at Caravaca (see Fig. 6 in Alegret, 2007); assemblages from the lowermost 2 cm of the Danian are mainly, but not exclusively, dominated by laevidentalinids and *Bolivina* (*Coryphostoma*). Other taxa, such as *Gavilinella* (*Stensioeina*), *Gyroidinoides depressus*, *Valvalabamina lenticula*, *Anomalinoides*, *Pleurostomella*, *Stilostomella*, and *Fursenkoina* are common components of the assemblages. Moreover, assemblages from the lowermost 2 cm of the Danian are dominated by infaunal taxa (62% of the assemblages), which may indicate low oxygen conditions at the sea floor.

3.4 Trace fossils

Detailed ichnological analysis of the K–Pg boundary interval at Caravaca section reveals the existence of a well-developed trace fossil assemblage, consisting of *Alcyonidiopsis* isp., *Chondrites targionii*, *Ch.* isp., *Planolites* isp., *Thalassinoides suevicus*, *Trichichnus linearis*, *Zoophycos* isp., and ferruginous cylinders (Rodríguez-Tovar & Uchman, 2006) (Figs. 3, 4). The uppermost Maastrichtian, lower Danian boundary

dark layer and lower Danian post-boundary dark layer trace fossil associations are very similar, with dark-coloured *Ch. targionii*, *Planolites* isp., *T. suevicus*, *Zoophycos*, and some *Alcyonidiopsis* penetrating into light Maastrichtian marls. Thus, no ichnological evidence of a severe macroinfaunal crisis is recognized. Dark-coloured traces come from two bioturbated horizons in the dark boundary layer separated by two horizons with primary lamination. Recovery of tracemakers is comparatively rapid after the K–Pg boundary event (Fig. 5), with an initial horizon of colonization just above the first laminated bed, 1.4 cm thick, at the base of the dark boundary layer, representing around 1.75 ky after the K–Pg boundary event, while a second phase of macrobenthic colonization is registered in the dark boundary layer, about 7.5 cm from the K–Pg boundary rusty layer, corresponding to 9.37 ky (Rodríguez-Tovar & Uchman, 2006).

4 Environmental changes across the K–Pg boundary: a variable impact on the microfaunal community

As indicated in previous papers, the selective effect of the K–Pg impact event on ecosystems and therefore on involved biota, has been demonstrated (i.e., Schulte et al., 2010). Regarding microfossils, the planktic foraminifera and nannoplankton collapsed in abundance and diversity at the K–Pg boundary, while benthic foraminifera did not display significant extinction (Alegret & Thomas, 2005; Alegret et al., 2001; Culver, 2003; Thomas, 1990). This pattern, registered worldwide, is similarly observed in the Caravaca section, showing no major extinction in the benthic foraminifera yet sudden and dramatic decreases in diversity and reorganization (Alegret, 2007; Coccioni & Galeotti, 1994).

Hence, recovery also reveals a variable response of the different microfaunal communities with respect to the involved environmental changes, entailing a post-crisis recovery phase that is clearly non-synchronous, with heterogeneity in the response and different rates of recovery (Coxal et al., 2006; Hull et al., 2011; Alegret & Thomas, 2013; Alvarez et al., 2019; Brich et al., 2021). This variable recovery is also observed in the Caravaca section. Planktic communities (i.e., planktic foraminifera and calcareous nannoplankton) exhibit major extinction associated to the K–Pg impact event. Accordingly, only *Thoracosphaera* spp., in the case of the calcareous nanoplankton (Gardin & Monechi, 1998; Lamolda et al., 2005) and planktic foraminifera *Guembelitria* are registered in the first centimeters of the dark boundary layer (Arenillas et al., 2021; Gilabert et al., 2021a). After that, a prolonged delay in recovery is observed, with the initial recovery occurring above the dark boundary layer, around 18.5 ky after the event, and the total recovery around 80 cm above, around 54 ky later. Recovery of the planktic foraminifera was related to improvement

in oxygen conditions (Smit, 1982, 2005). Paleoenvironmental, paleoclimatic and paleocenographic reconstruction of the early Danian from the Caravaca section, as proposed by Gilabert et al. (2021a), suggest very volatile environmental conditions during the first 230 ky of the Danian, indicating that eutrophication, warming, ocean acidification, low oxygenation, and the remobilization of pollutants and toxic heavy metals all occurred potentially in the aftermath of Chicxulub impact.

Benthic foraminifera show a comparatively rapid diversification early in the Paleocene. The initial marked decrease in diversity, but not extinction, together with the bloom of infaunal deposit-feeding during the first kilo year (< 1 cm) was related to an exceptionally large nutrient influx that suddenly reached the sea floor (Martínez-Ruiz, 1993), together with quasianaerobic sea-bottom conditions (Coccioni & Galeotti, 1994, 1998; Coccioni et al., 1993). A rapid decrease in oxygen levels from low to medium oxic to low oxic, along with an important mass mortality just after the K–Pg boundary, was also interpreted for the Caravaca section by Kaiho et al. (1999). The decrease in dissolved oxygen in the intermediate waters can be explained by an abruptly increased influx of terrestrial organic matter into the marine environment (Arinobu et al., 2005). After this initial decrease in diversity associated with the concurrent bloom of infaunal, low-oxygen-tolerant deposit feeders, the initial reappearance of epifaunal suspension feeders, together with some epifaunal and infaunal deposit feeders, is comparatively rapid in the lower part of the dark boundary layer—below 2.9 cm and correlating to 3.62 ky. The recovery is also rapid, at the end of the dark boundary layer, around 12.5 ky after the K–Pg boundary event according to the applied proposal.

According to the above data, the interpreted pattern of recovery reveals significant differences in the environmental perturbation of the marine ecosystem, resulting especially severe for the planktic community with respect to the benthic one. This determined a gradual reestablishment of the ecosystem; the recovery of the marine ecosystem structure locally at the Caravaca setting could be situated when eco-sedimentary parameters—particularly oxygenation—returned to more stable, normal conditions, at around 80–90 cm from the K–Pg boundary, corresponding to 54–56 ky.

5 Tracemakers as the inhabiting pioneers

In the context of the relatively minor incidence of the K–Pg boundary event on the benthic habitat at the Caravaca setting, particularly interesting is the comparatively rapid recovery of the macrobenthic tracemaker community. The K–Pg boundary event did not induce a severe crisis for the burrowing macroinfauna, as revealed by the

similarity between pre- and post-event ichnotaxa. The rapid first colonization phase, less than 2 ky after the event, could reflect the strategies of *Zoophycos* and *Chondrites* tracemakers, allowing for a high independence from oxygen in pore waters and food in the sediment and the colonization of unfavorable environments. *Chondrites* tracemakers can colonize sediments poor in oxygen in pore waters, constructing open burrows (e.g., Bromley & Ekdale, 1984), as can be envisaged for *Zoophycos*. The *Chondrites* tracemaker benefits mostly from chemosymbiosis (cf. Baucon et al., 2020; Seilacher, 1990), whereas the *Zoophycos* tracemaker is known to collect material from the sea floor and actively put it inside its own burrow (e.g., Bromley, 1991; Kotake, 1991, 1994; Löwemark et al., 2004; Monaco et al., 2017; Zhang et al., 2015 for review). The interpreted abundant nutrient input supplied to the sea floor after the K–Pg event could benefit *Zoophycos* tracemaker through placement of the organic matter deep within the burrow, beyond the range of other competing consumers. The similarity between the time recovery of the burrowing macroinfauna and that of the bloom of infaunal deposit-feeding benthic foraminifera (aprox. 1 kyr; < 1 cm) could be related to the availability of new habitats for the infaunal deposit-feeder foraminifera provided by the burrowing activity.

Integration of geochemical and isotopic analysis with ichnological information support the relatively rapid recovery of the macrobenthic tracemaker community, within horizons a few millimeters above the K–Pg boundary event, and the instantaneous reestablishment—some 10² years—of pre-impact conditions in terms of oxygenation (Rodríguez-Tovar & Uchman, 2006; Sosa-Montes de Oca et al., 2013, 2016; Vellekoop et al., 2018), suggesting a probable rapid recovery of deep-sea ecosystems at bottom and in intermediate waters.

6 Conclusions

The comparative responses of micro (calcareous nannoplankton, planktic and benthic foraminifera) and macro (tracemakers) communities to the K–Pg impact event at the Caravaca section (External Subbetic Zone, Betic Cordillera) has been analysed. Planktic foraminifera and calcareous nannoplankton collapsed in abundance and diversity at the K–Pg boundary; and although benthic foraminifera did not undergo significant extinction, they show a sudden and dramatic decrease in diversity and reorganization. After the K–Pg boundary event, planktic communities reflect a prolonged delay in recovery: the initial recovery occurs above the dark boundary layer, around 18.5 ky after the event, and total recovery around 80–90 cm above, around 54–56 ky later. Benthic foraminifera display a comparatively rapid reestablishment, involving a bloom of infaunal,

low-oxygen-tolerant, deposit feeders, and the initial reappearance of epifaunal suspension feeders, together with some epifaunal and infaunal deposit feeders, in the lower part of the dark boundary layer, below 2.9 cm and correlating to 3.62 ky. The recovery is also rapid, at the end of the dark boundary layer, some 12.5 ky after the K–Pg boundary event. The macrobenthic tracemaker community is less affected by the K–Pg boundary event, though a rapid first colonization phase occurs less than 2 ky after the event, probably related to the opportunistic behaviour of *Zoophycos* and *Chondrites* tracemakers. The comparatively minor incidence of the K–Pg boundary event on the benthic habitat with respect to the planktic one at the Caravaca setting may be associated with the nearly instantaneous reestablishment of pre-impact oxygen conditions at bottom and in intermediate waters.

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Conflict of interest The corresponding author states that there is no conflict of interest.

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