Trace fossils after the K–T boundary event from the Agost section, SE Spain

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Abstract – Palaeogene trace fossils penetrate the uppermost Cretaceous sediments in the Agost section, Betic Cordillera, SE Spain. *Chondrites* ?*targionii*, *Zoophycos* isp., *Planolites* isp. A, *Planolites* isp. B, ?*Thalassinoides* isp. A, *Thalassinoides* isp. B, *Thalassinoides* isp. C, *Alcyonidiopsis longobardiae*, and *Diplocraterion* ?*parallelum* have been identified. A well-developed endobenthic tiering pattern is interpreted. The uppermost tier (A) represents major benthic activity in the shallowest sediments at or just below the seafloor, recorded as bioturbated background (only discrete rare *Planolites*). The next upper tier (B) displays the highest trace-fossil diversity, with *Planolites* in the shallow levels, and *Thalassinoides* and *Alcyonidiopsis* at slightly deeper ones. The intermediate tier (C) contains randomly distributed *Thalassinoides* and *Alcyonidiopsis*, cross-cut by *Zoophycos* and large and medium-sized *Chondrites*. The deepest tier (D) contains *Zoophycos*, cross-cut by medium- and mainly small-sized *Chondrites*. Two interpretations are proposed: (1) vertical partitioning of a singled multi-tiered community under steady-stable conditions in well-oxygenated water bottom, reflecting gradual changes deep into the sediment, with decreasing oxygen pore water and benthic food, and increasing substrate consistency, and (2) sequential colonization and community replacement, reflecting the work of two successive communities. The first community, mainly represented by *Planolites*, *Alcyonidiopsis* and *Thalassinoides*, was produced in a shallow, oxygenated soft substrate. Probably related to decreasing oxygen content and benthic food availability, this community was replaced by deeply burrowing organisms that produced *Zoophycos* and *Chondrites*. This sequential colonization can be determined by changes in environmental parameters related to the Cretaceous–Palaeogene (K–T) event, or may have resulted from normal ecological and early diagenetic processes.

Keywords: Cretaceous–Tertiary boundary, trace fossil, palaeoenvironmental change, Spain.

1. Introduction

Ever since the classic paper by Alvarez *et al*. (1980), numerous studies have focused on the Cretaceous–Palaeogene (K–T) boundary mass-extinction event. The event is generally ascribed to a large bolide impact that produced the Chicxulub crater in Yucatán, Mexico (e.g. Sharpton *et al*. 1993; Kettrup *et al*. 2000). The impact is considered to be the cause of relatively rapid and dramatic environmental changes that strongly affected marine and terrestrial life. However, the occurrence of extinction and turnovers before and after the K–T event, the possible existence of event survivors, other biological changes and their causes, and the rate of the changes (catastrophic v. rapid but not catastrophic) are controversial (see MacLeod *et al*. 1997, for an extended review).

The environmental consequences of the K–T boundary event on marine ecosystems have been documented mainly in planktonic microfossil biota, while changes in the benthic assemblages are comparatively poorly recognized. Although trace fossils are important tools

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for studying benthic life, especially where shelly benthic fauna is scarce, their application to K–T boundary problems is relatively rare (but see Ekdale & Bromley, 1984; Savrda, 1993; Ekdale & Stinnesbeck, 1998). The ichnological analysis at the Agost section (Alicante Province, Spain) provides the opportunity to ascertain how trace fossil assemblages looked after the K–T boundary event. Trace-fossils description and interpretation are the main aims of this paper.

2. Location and geological setting

The K–T boundary profile described here is located about 1 km north of the town of Agost (Alicante Province), in the Betic Cordillera of SE Spain (Fig. 1). The K–T boundary section was sampled in a roadcut near the 13 km marker post, and the Upper Cretaceous (Maastrichtian) sequence was sampled closer to the town, in a small gully opposite the cemetery. The Maastrichtian sediments consist of intercalated grey marlstone and marly limestone beds. The K–T boundary is marked by a 10 cm thick, dark clay layer with a basal rust-red layer 2 mm thick.
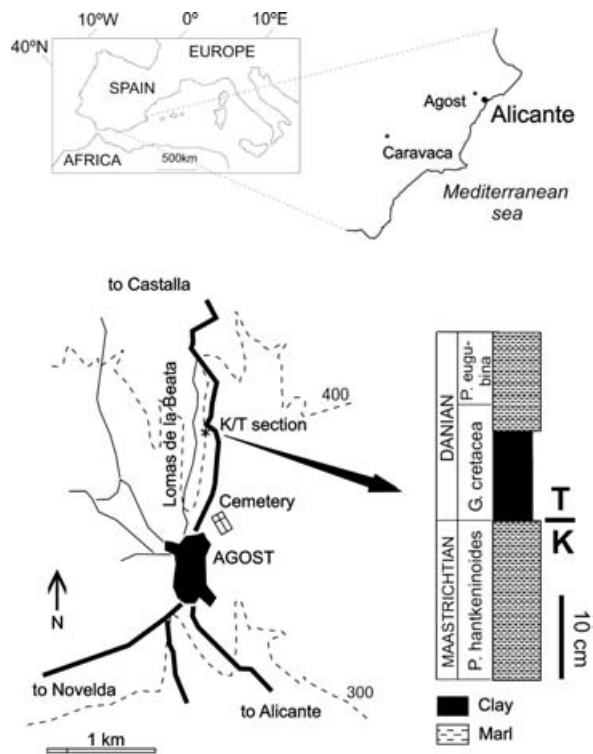
Figure 1. Location, planktic foraminiferal biostratigraphy, and lithological column of the K–T boundary section at Agost (Alicante Province, southeast Spain).

This red layer contains the evidence of impact (K–T boundary spherules, Ir and other Platinum-Group Elements anomalies in Ni, Co, Cr and Fe) and is interpreted as distal ejecta of the Chicxulub impact (Smit, 1990; Martínez-Ruiz *et al*. 1992, 1997; Martínez-Ruiz, Ortega-Huertas & Palomo, 1999). Lateral continuity of the red layer is difficult to estimate due to the small thickness and outcrop limitations. The lowermost Palaeogene (Danian) sediments are composed of marly claystones with gradually increasing carbonate contents, giving way to marlstones and marly limestones (Fig. 1). Benthic foraminiferal assemblages indicate a subtropical, low-latitude, upper-bathyal to outer-neritic environment for the uppermost Maastrichtian–lowermost Danian section at Agost (Canudo, Keller & Molina, 1991; Keller, 1996; Pardo, Ortiz & Keller, 1996), which is shallower than the neighbouring Caravaca (Murcia Province) section (middle-bathyal environment, 600–1000 m deep: Coccioni & Galeotti, 1994).

The Agost section is considered one of the most complete K–T boundary sections known. It includes an expanded and continuous sedimentary record across the boundary, as is common in continental-shelf to upper-slope sections, such as those at El Kef, Brazos River and Caravaca (MacLeod & Keller, 1991*a*), and is characterized by the absence of any thin, condensed interval, or any hiatus at the K–T boundary, nor is there

any evidence of erosional surfaces (MacLeod & Keller, 1991*a*; Pardo, Ortiz & Keller, 1996).

Three biozones have been differentiated through the K–T boundary transition at the Agost section (Fig. 1). The *Plummerita hantkeninoides* Biozone (latest Maastrichtian: Pardo, Ortiz & Keller, 1996) corresponds to the top 3.45 m of the Maastrichtian section. The *Guembelitria cretacea* Biozone (earliest Danian: Canudo, Keller & Molina, 1991; Canudo, 1994; Molina, Arenillas & Arz, 1996, 2001), correlated with the P0 Zone (Keller, 1988, 1993; Pardo, Ortiz & Keller, 1996), is recognized in the dark-clay layer and in the overlying 5 cm thick layer of light marly claystones (Molina, Arenillas & Arz, 2001). The *Parvularugoglobigerina longiapertura* Biozone (Canudo, Keller & Molina, 1991), correlating with P1a (P1a(1) and P1a(2)) or *P. eugubina* Biozone (Keller, 1988, 1993; Pardo, Ortiz & Keller, 1996; Molina, Arenillas & Arz, 2001), corresponds to the interval 60 to 65 cm above the *Guembelitria cretacea* Biozone.

Previous work at the Agost K–T boundary section has focused mainly on magnetostratigraphy (Groot *et al*. 1989), chronostratigraphy (MacLeod & Keller, 1991*a,b*), and mineralogy/geochemistry (e.g. Smit, 1990; Martínez-Ruiz *et al*. 1992). Palaeontological approaches have been based primarily on planktonic foraminifers, especially biostratigraphic and palaeoecological analyses of the K–T boundary extinction and faunal turnover (e.g. Canudo, Keller & Molina, 1991; Molina, Arenillas & Arz, 1996, 2001), and occasionally on benthic foraminifers (Pardo, Ortiz & Keller, 1996).

3. Trace fossils

3.a. Previous ichnological work on the K–T boundary

Papers on trace fossils from the K–T boundary are uncommon. Some emphasize the stratigraphic blurring effect of bioturbation (Officer & Drake, 1983; Smit & Romein, 1985; Pospichal *et al*. 1990). Only a few give relatively detailed ichnological information (Ekdale & Bromley, 1984; Savrda, 1993; Stinnesbeck *et al*. 1993, 1996; Keller, Stinnesbeck & Lopez-Oliva, 1994; Ekdale & Stinnesbeck, 1998), providing evidence of complex and protracted palaeoenvironmental changes across the boundary. None recognize ichnological evidence for rapid catastrophe.

Bioturbation has been viewed as an important agent for redistribution of Cretaceous and Palaeogene sediments, nannofossils and geochemical constituents (e.g. iridium) above and below the K–T boundary. Analyses from Gubbio (Officer & Drake, 1983), El Kef and Caravaca sections, South Atlantic DSDP cores (Smit & Romein, 1985), and East Antarctic ODP cores from the Weddell Sea (Pospichal *et al*. 1990) show evidence of several centimetres of vertical

mixing above and below the boundary. As an extreme case, Pospichal *et al*. (1990) estimated that Palaeogene nannofossils were displaced a minimum of 1.3 m below the boundary by large-bodied bioturbators. By contrast, in the Caravaca and/or the Agost sections, previous research revealed that mixing due to bioturbation is not a critical factor (Smit & ten Kate, 1982), and some researchers even failed to find any evidence of this mixing (Canudo, Keller & Molina, 1991; Molina, Arenillas & Arz, 1996).

Ekdale & Bromley (1984) analysed trace fossils from the K–T boundary marine deposits of Denmark on a high-latitude distal continental shelf (Keller, 1996). In those materials, the uppermost Maastrichtian chalk is totally bioturbated (mostly with *Thalassinoides, Zoophycos, Chondrites*), and the basal Danian clays contain abundant *Planolites*, *Thalassinoides*, and 'small *Chondrites*-like forms' that are now recognized as *Phycosiphon*. The trace fossil assemblages indicate shallowing and local anoxia in the shallower part of the basin during sedimentation of the famous boundary Fish Clay.

Savrda (1993) analysed ichnosedimentological evidence at or near the K–T boundary at various sites in Alabama, corresponding to a very proximal continental shelf at depths shallower than 150 m (Olsson & Liu, 1993; Keller, 1996). Savrda recognized *Thalassinoides*, *Ophiomorpha* and *Planolites* penetrating sands of earliest Danian age.

Stinnesbeck and collaborators presented several papers on the K–T boundary sections of northeastern Mexico. These sections, represented by the lower Tertiary Velasco Formation, accumulated in a low-latitude neritic setting in which water depths were probably shallower than 200–350 m (Keller, Stinnesbeck & Lopez-Oliva, 1994; Stinnesbeck *et al*. 1996). Notably, Ekdale & Stinnesbeck (1998) documented diverse trace fossil assemblages, which mainly include well-developed burrows of deposit feeders (e.g. *Chondrites, Ophiomorpha, Planolites* and *Zoophycos*), and interpreted tiered ichnocoenoses.

3.b. Occurrence and preservation

The outcrops were trenched and cleaned to provide fresh exposures. Locally the rock surface was wetted to accentuate ichnological features. Because of outcrop limitations, continuous observations are possible only to 20 cm below the K–T boundary, and only occasionally were isolated samples collected from lower intervals. Rock samples and polished blocks perpendicular to bedding were studied in the laboratory, either directly without treatment or after impregnation with water and/or light-weight oil ('modified Bushinsky oil technique': Bromley, 1981). Thin sections were prepared and analysed for microfacies, especially in order to see burrow margins and fill. Their preparation was made difficult by the unconsolidated character

of the sedimentary rocks. Ichnological analysis was focused on ichnotaxonomy, vertical distribution of trace fossils, and cross-cutting relationships. The limited lateral continuity of outcrops, together with difficulties of analysing the internal structure of the sediments, precluded an ichnofabric characterization.

A relatively abundant and conspicuous trace fossil assemblage occurs in the Maastrichtian sediments (*Plummerita hantkeninoides* Biozone), including dark- and light-coloured structures. Some of the trace fossils therein are filled with dark-coloured sediment similar to that of the lowermost Danian marly claystones, which contrast strongly with the light colour (grey to cream) of the Maastrichtian host sediment. These include abundant *Chondrites* and *Zoophycos*, common *Thalassinoides* and *Planolites*, and rare *Alcyonidiopsis*, *Diplocraterion* and unidentified structures (Rodríguez-Tovar, 2001). This interval also includes less contrasting trace fossils filled with sediments that are only slightly darker than the host sediments. Those trace fossils filled with light-coloured sediment include *Chondrites*, *Zoophycos*, *Planolites* and other unidentified structures. All the trace fossils cross-cut a diffuse, burrow-mottled background.

Due to the comparative abundance of darker structures and the poor visibility of the lighter traces, we focused our ichnological analysis on the dark-filled, better-defined trace fossils. Recently, carbon-isotope analysis of trace-fossil infill across the K–T boundary transition at the Agost section enabled us to discriminate between different phases of macrobenthic colonization. Thus, light-filled traces show $\delta^{13}C$ values consistent with those from uppermost Maastrichtian sediments, while dark-filled trace fossils show $\delta^{13}C$ in accordance with those from lowermost Danian materials. Thus, dark-filled trace fossils in the uppermost Maastrichtian interval reveal a colonization subsequent to the K–T boundary event, during earliest Danian time (Rodríguez-Tovar, Martínez-Ruiz & Bernasconi, 2004).

In the lowermost Danian part of the section (*Guembelitria cretacea* Biozone), trace fossils are indistinct. This part of the section is composed of dark marly claystones, in which sedimentary structures have been not recognized, except for occasional fine lamination. The dark-filled trace fossils were produced during the earliest Danian deposition of dark, marly claystones. Features of these claystones, that is, the unconsolidated character, near-absence of sedimentary structures and dark colour, impede, for now, the recognition of biogenic structures. We can only assume that the claystones are bioturbated, as no record of ichnofabric is evident, and, in consequence, no convincing ichnological interpretation is possible. Moreover, the absence of cross-cutting relationships between the dark-filled trace fossils and the K–T boundary red
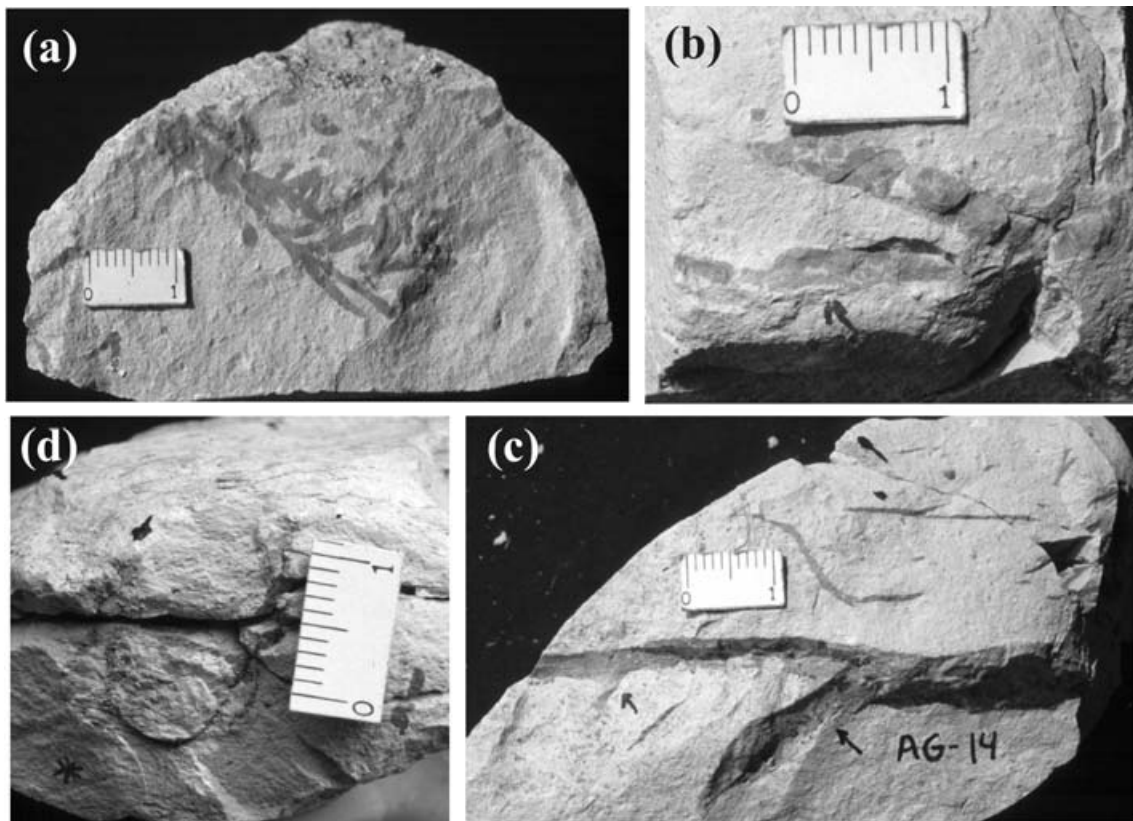
Figure 2. Trace fossils from the Agost section. (a) *Chondrites* ?*targionii*, tunnels are crowded and confined to a narrow zone. (b) *Alcyonidiopsis longobardiae* filled with small ovoid pellets. (c) ?*Thalassinoides* isp. A with branches at acute angle to straight main tunnel. (d) *Diplocraterion* ?*parallelum*.

layer is another important limitation (Rodríguez-Tovar, Martínez-Ruiz & Bernasconi, 2004).

3.c. Synopsis of ichnotaxa

Trace fossils belonging to six ichnogenera are recognized. They are described in order of abundance, from most abundant to rare.

Chondrites ?*targionii* (Brongniart, 1828) (Fig. 2a) is preserved as horizontal to inclined, straight to gently curved, strongly flattened, branched tunnels filled with dark-grey argillaceous sediment. First- and second-order successive branches *sensu* D'Alessandro & Bromley (1987) occur. Size differences between specimens are recognized, with large *Chondrites* being more than 40 mm long and tunnels 1.0 to 2.0 mm wide, and small *Chondrites*, less than 10 mm long and tunnels ≤ 1.0 mm wide. In some specimens (Fig. 2a), the tunnels are crowded and confined to a narrow zone. More steeply inclined tunnels occur on horizontal parting surfaces as oval dots or short bars, and are interpreted as fragments of burrow system. Branch width is in the lower range of *Chondrites targionii* (cf. Uchman, 1999). Therefore, the ichnospecies is identified only with reservations.

Chondrites is a feeding system of unknown tracemakers related to infaunal deposit-feeders (e.g.

Osgood, 1970). According to Kotake (1991a), this ichnogenus is produced by surface ingestors that pack their faecal pellets inside burrows. According to Seilacher (1990) and Fu (1991), the tracemaker of *Chondrites* may have been able to live at the oxic/anoxic interface as a chemosymbiont. *Chondrites* is present in Tommotian (Crimes, 1987) to Holocene strata (e.g. Werner & Wetzel, 1981).

Zoophycos isp. (Fig. 3f) occurs in small slabs as horizontal to oblique planar spreite structures. Some slabs contain elongated lobes that are 18–30 mm wide and encircled by a cylindrical marginal tunnel 3–5 mm wide. One lobe is wider in its distal part. The lobes are filled with arcuate spreite laminae. Small (< 1 mm long) dark, oval pellets are distributed along the laminae. A single, very complete specimen was found, composed of five lobes spaced vertically 20–70 mm apart, with maximal length increasing downwards from about 40 mm to more than 140 mm.

Zoophycos *s.l.* is generally assumed to be the trace of an as yet undiscovered deposit-feeder. Their producers have been hypothesized to have been sipunculids (Wetzel & Werner, 1981), polychaete annelids, arthropods (Ekdale & Lewis, 1991) and echiuran worms (Kotake, 1992). According to Kotake (1989, 1991b), *Zoophycos* is produced by surface ingestors of organic detritus. The precise ethological

interpretation of *Zoophycos* remains controversial. This is probably due to the assignment to *Zoophycos s.l.* of diverse structures generated by different tracemakers with different behaviours, or even a single tracemaker with diverse behaviours (Kotake, 1989, 1994; Bromley, 1991; Locklair & Savrda, 1998; MacEachern & Burton, 2000). Lately, Bromley & Hanken (2003) suggested that the upper helical part of a large Pliocene *Zoophycos* from Rhodes, Greece, is a deposit-feeding structure, and lateral lobes developing from its lower part are sulphide wells for chemosymbiotic bacteria.

Planolites isp. (Fig. 3b) is preserved as horizontal to subhorizontal, unbranched, straight to slightly curved, strongly flattened cylinders filled with dark argillaceous sediment. Burrow diameters range from 1.5–2.5 mm in *Planolites* isp. A, and 4.5–6 mm in *Planolites* isp. B.

Planolites is a eurybathic, extremely facies-crossing form referred to polyphyletic vermiform deposit-feeders producing active backfilling (e.g. Pemberton & Frey, 1982; Fillion & Pickerill, 1990, and references therein). However, it has also even been interpreted as passively filled in some cases (Locklair & Savrda, 1998).

Thalassinoides is preserved as horizontal (straight to slightly curved in *Thalassinoides* isp. B), strongly flattened branched cylinders, filled with dark argillaceous sediment. Burrow diameters are 3.0–4.5 mm in ?*Thalassinoides* isp. A, 3 mm in *Thalassinoides* isp. B, and 5–8 mm in *Thalassinoides* isp. C. Sparse, poorly preserved dark muddy pellets occur in the fill, probably as a constituent of passive fill rather than belonging to the tracemaker. In *Thalassinoides* isp. B the irregular distribution of these pellets contrasts with the dense, regular distribution of pellets in the *Alcyonidiopsis* fill. In ?*Thalassinoides* isp. A (Fig. 2c) the straight main tunnel has secondary branches, more or less parallel, at an acute angle, and branch junctions are not enlarged. In *Thalassinoides* isp. B the branches are T-shaped with slight enlargements at branch junctures, while in *Thalassinoides* isp. C the branches are Y-shaped, without any enlargement in the branching point.

Thalassinoides is a facies-crossing form, most typical of shallow-marine environments, and is produced mainly by crustaceans (e.g. Frey, Curran & Pemberton, 1984; Bromley, 1996). *Thalassinoides* is generally interpreted as a fodinichnion, passively filled, usually found in oxygenated, soft but fairly cohesive substrates (Bromley & Frey, 1974; Kern & Warme, 1974; Ekdale, Bromley & Pemberton, 1984; Bromley, 1996). The origin and palaeoenvironmental significance of *Thalassinoides* were summarized recently by Ekdale (1992).

Alcyonidiopsis longobardiae Massalongo 1856 (Fig. 2b) is represented by horizontal to subhorizontal, unbranched, straight to slightly curved, strongly flattened cylinders that are 3–4 mm wide and filled with small oval pellets composed of dark, argillaceous

sediment. *Alcyonidiopsis* has been regarded as a feeding burrow of polychaetes (Chamberlain, 1977; Uchman, 1999), but arguments are without convincing evidence.

Diplocraterion ?*parallelum* Torell 1870 (Fig. 2d) occurs as single specimens of vertical or oblique trace fossils composed of a U-shaped cylindrical tube linked by a spreite structure. The size of the trace fossil is up to 10–15 mm wide and at least 30 mm deep. U limbs are about 2 mm in diameter. The spreiten contain fine, elongated dark pellets less than 1 mm in diameter. Though most of the specimens are filled with dark sediment, occasional light-green fill is registered (Fig. 2d). All specimens represent protrusive forms *sensu* Goldring (1962). Size differences with typical *Diplocraterion parallelum* from the Cambrian or Jurassic (distinctly larger than the Agost material) prevent a conclusive ichnotaxonomical assignation.

Diplocraterion is interpreted as the domichnion of suspension-feeders, mostly polychaetes and crustaceans (e.g. Fillion & Pickerill, 1990). In Jurassic shallow-marine siliciclastics, *Diplocraterion parallelum* commonly occurs in very shallow subtidal to intertidal facies (e.g. Fürsich, 1974, 1981). In Jurassic sediments, at least, this trace fossil is common at transgressive surfaces (e.g. Mason & Christie, 1986; Dam, 1990; Taylor & Gawthorpe, 1993; Goldring *et al.* 1998). Horizons rich in *D. parallelum* in the Kimmeridgian of Spain have been used by Olóriz & Rodríguez-Tovar (2000) to identify facies representing more energetic and unstable environments during sea-level fall, and thus used for the recognition of sequence boundaries. The occurrence of both *D. parallelum* and *Zoophycos* together is unexpected (Bromley, pers. comm.), due to the different palaeoecological requirements of the tracemakers. *Diplocraterion* rarely occurs in Palaeogene deeper water facies (Crimes *et al.* 1981; Leszczynski, Uchman & Bromley, 1996; Gibert *et al.* 2001), where *Zoophycos* is expected, or even together with *Zoophycos* isp. (L. A. Buatois and others, unpub. data, 1999, http://www.kgs.ukans.edu/Current/1999/buatois/buatois1.html), or it could be related to a possible environmental change between colonization by the two tracemakers (see Section 4).

3.d. Vertical distribution

The vertical distribution of trace fossils with dark fill enabled us to recognize two intervals (Fig. 3).

The first interval represents the topmost 1.5 cm of the Maastrichtian sediments. The contact between the light-green youngest Maastrichtian and the darker oldest Danian sediments is poorly defined and irregular (Fig. 3a), probably due to the tracemaker activity in the contact between two different sediments, that is, marls and clays. On the irregular parting surface, discrete trace fossils are barely visible. Only sparse *Planolites* isp. and very small *Chondrites*
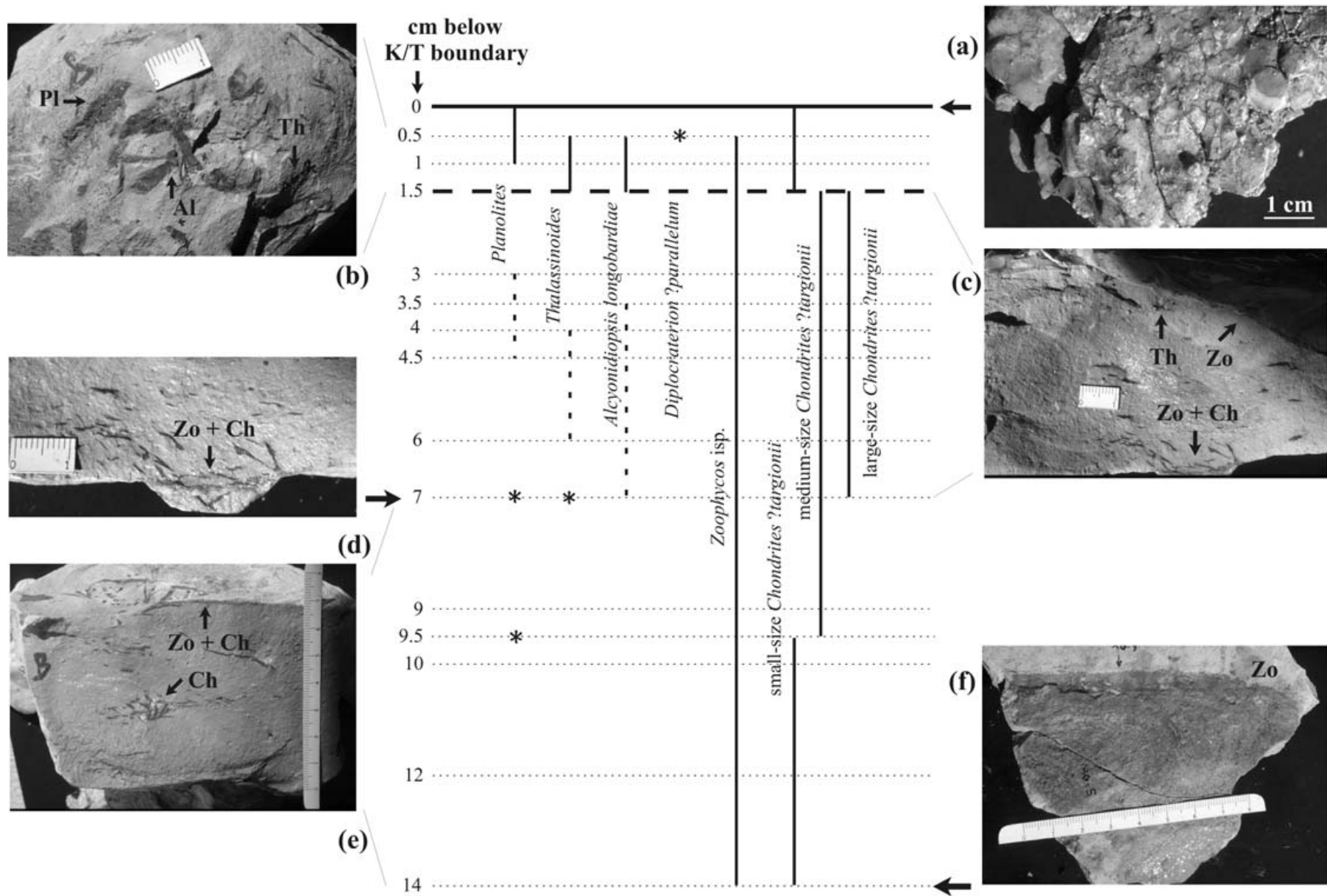
Figure 3.   For legend see facing page.

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?*targionii* were identified. Below the surface, trace fossils are abundant and relatively diverse. *Planolites* and *Thalassinoides* are the dominant ichnogenera (Fig. 3b), but their abundance decreases markedly downwards. *Planolites* isp. B is noted up to 1 cm below the surface, while *Thalassinoides* appears from −0.5 to −1.5 cm. Thus, *Planolites* and *Thalassinoides* occur together in a very narrow vertical interval from −0.5 to −1 cm. *Alcyonidiosis longobardiae* is present in the same interval as *Thalassinoides* but is less abundant (Fig. 3b). *Diplocraterion* ?*parallelum* (Fig. 2d), registered in the uppermost part of this interval, and oblique structures of *Zoophycos* (Fig. 4b), are rare. Locally, small *Chondrites*? *targionii* occurs in high concentrations, both within the fill of other trace fossils (see cross-cutting relationships; Fig. 4a,b) as well as in background sediments (Fig. 4a).

The second interval is defined from 1.5 cm to 20 cm below the K–T boundary (Fig. 3c–f). In this interval, *Zoophycos* and *Chondrites* are most abundant. However, other ichnogenera such as *Planolites*, ?*Thalassinoides* and *Alcyonidiopsis* also occur, dispersed throughout the upper part of this interval (from 3 to 7 cm below the K–T boundary). *Planolites* isp. A is located predominantly from −3 to −4.5 cm, ?*Thalassinoides* between −4 and −6 cm (Fig. 3c), and *Alcyonidiopsis longobardiae* from −3.5 to −7 cm. Locally, straight and unbranched unidentified structures (probably *Planolites* or *Thalassinoides*) occur around −7 cm. Some structures assigned to *Planolites* isp. B extend to −9.5 cm. *Zoophycos* and *Chondrites* show a continuous vertical distribution throughout the interval. A homogeneous distribution is recognized for *Chondrites* ?*targionii*, except in a few intervals with higher concentrations, mainly between −6 and −9 cm, and between −10 and −12 cm (Fig. 3c–e). *Chondrites* specimens show a clearly diminishing downward size trend, with the largest and least abundant *Chondrites* between −1.5 and −7 cm. Medium-sized *Chondrites* occurs from −1.5 to −9.5 cm, and the smallest *Chondrites* occurs from −9.5 cm downwards. Oblique (Fig. 3c) to horizontal (Fig. 3c–f) *Zoophycos* isp. are registered throughout the entire interval (from 1.5 to 17 cm below the K–T boundary), showing a progressively greater helical whorl size downwards.

3.e. Cross-cutting relationships

In accordance with the vertical distribution outlined above, some cross-cutting relationships between the ichnotaxa described were recognized (Fig. 4). In the top Maastrichtian surface, due to the scarcity of discrete trace fossils, only a few small *Chondrites* ?*targionii* within *Planolites* fill were found. As much as 1.5 cm below the K–T boundary, clear cross-cutting relationships were discerned. *Planolites*, *Thalassinoides* and *Alcyonidiopsis* were not registered cross-cutting other trace fossils. *Zoophycos* cross-cuts *Diplocraterion*, and small *Chondrites* ?*targionii* cross-cuts the other trace fossils, including *Planolites* isp. B (Fig. 4b), *Diplocraterion*, *Thalassinoides* (Fig. 4a) and *Zoophycos* (Fig. 4b).

In the second interval, from 1.5 to 20 cm below the K–T boundary, cross-cutting relationships were very similar to those noted above, with *Zoophycos* and *Chondrites* cutting across the remaining trace fossils. *Zoophycos* isp. cross-cuts *Planolites* isp. A and *Thalassinoides* (Fig. 3c) between −4 and −6 cm. *Chondrites* of different sizes cross-cutting the remaining trace fossils is usual. Between −3 and −7 cm, medium-sized *Chondrites* cross-cuts *Planolites* (Fig. 4d), *Thalassinoides* (Fig. 4c), *Alcyonidiopsis* and *Zoophycos* (Figs 3c–e, 4e). Small *Chondrites* cross-cuts *Zoophycos* between −10 and −14 cm (Fig. 4f).

3.f. Tiering pattern

Ichnotaxonomic analysis of trace fossils with dark fill, their vertical distribution, and cross-cutting relationships support the interpretation that a well-developed endobenthic multi-tiered assemblage existed during the early Danian interval. Four tiers (A to D) were distinguished downwards:

The uppermost tier (A) corresponds to the shallowest sediments at or just below the seafloor during the earliest Danian, when the dark boundary layer was deposited. It represents an important benthic activity of unknown organisms recorded as a bioturbated background between the topmost layer of the Maastrichtian section and the oldest Danian sediment. The irregularities and slightly diffuse character of the boundary surface, together with the scarcity of discrete trace fossils immediately below the surface (only rare

Figure 3. Vertical distribution of dark-filled trace fossils from the K–T boundary to 14 cm below (*Plummerita hantkeninoides* Biozone, late Maastrichtian) at the Agost section (stars for isolated records, discontinuous vertical line for discontinuous record). (a) Topmost Cretaceous sediments showing irregular surface and the absence of discrete structures. (b) Interval from 0.5 to 1.5 cm below the boundary surface with *Planolites* (Pl), *Thalassinoides* (Th) and *Alcyonidiopsis* (Al). (c) Interval from 1.5 to 7 cm below the boundary surface, with oblique *Zoophycos* (Zo), *Thalassinoides* (Th) and cross-cutting relationships between horizontal *Zoophycos* (Zo) and medium-size *Chondrites* (Zo + Ch). (d) Close-up view of the cross-cutting relationship from C. (e) Interval from 7 to 14 cm below the boundary surface showing distribution of medium- and small-sized *Chondrites* (Ch), and *Zoophycos* cross-cut by *Chondrites*. (f) Horizontal *Zoophycos* at 14 cm below the boundary surface.
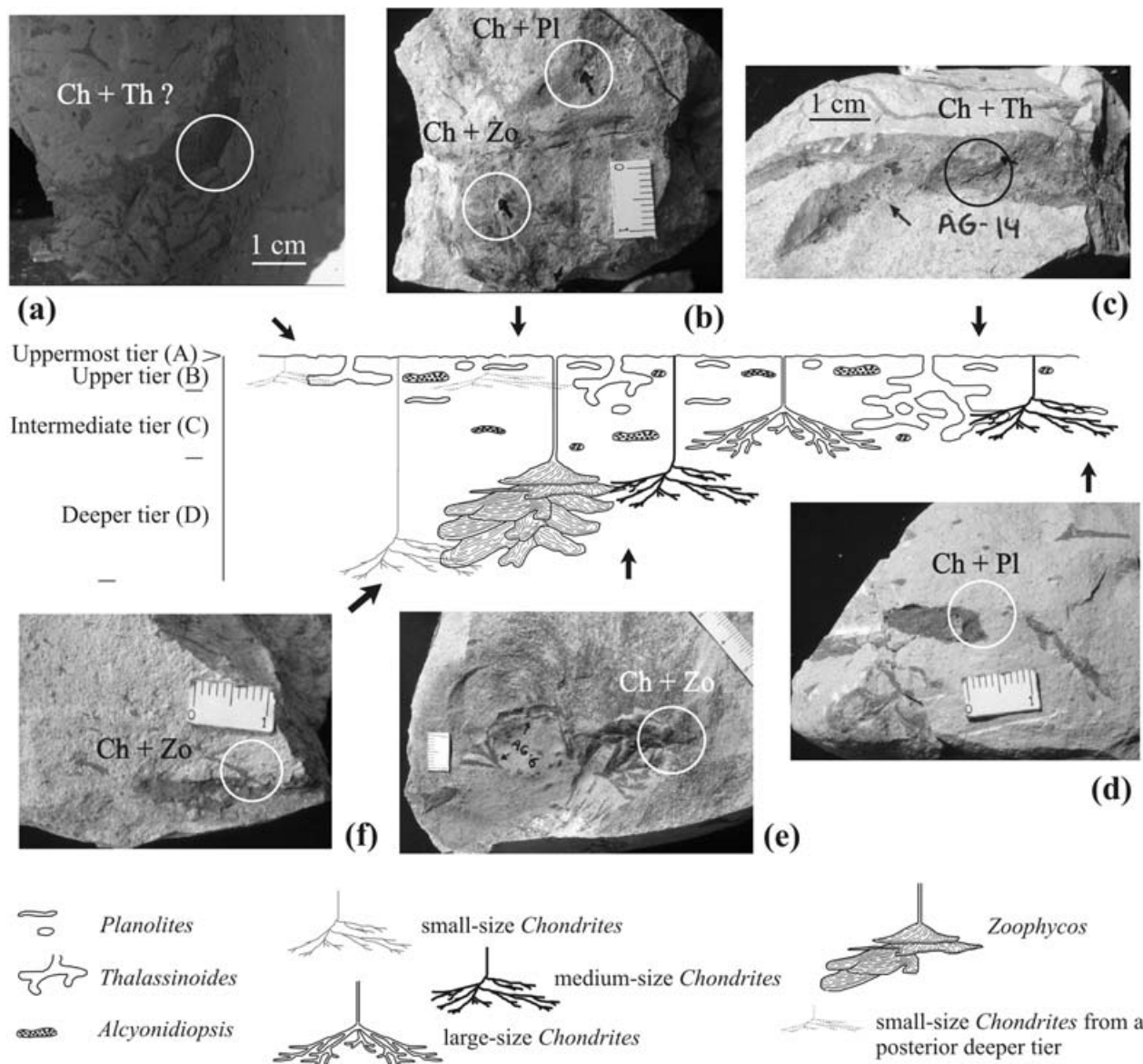
Figure 4. Cross-cutting relationships and tiering pattern of the dark-filled trace fossil assemblage. Photographs illustrate these relationships: Upper tier shows small-size *Chondrites* cross-cutting *Thalassinoides* (a), *Planolites* and *Zoophycos* (b). Intermediate tier showing medium-size *Chondrites* cross-cutting *Thalassinoides* (c), and *Planolites* (d). Deeper tier showing medium- (e) and small-size (f) *Chondrites* cross-cutting *Zoophycos*.

Planolites), are related to this activity, which caused mixing of oxygenated soft sediment.

The next upper tier (B) displays the highest trace-fossil diversity. *Planolites* represents the activity of shallow (up to 1 cm below the boundary surface), vagile deposit-feeders. *Thalassinoides* was produced by mobile crustaceans feeding at slightly a deeper level (−0.5 to −1.5 cm). *Alcyonidiopsis* represents a vagile deposit-feeder acting at the same level as the *Thalassinoides* producer. Comparatively high diversity, including *Planolites*, can be related to oxygenated soft-ground. The high concentration of small *Chondrites* ?*targionii* that cross-cut the remaining trace fossils in this tier can be related to a younger tiered assemblage penetrating from a higher colonization surface.

The intermediate tier (C) is recorded from 3 to 7 cm below the K–T boundary. It contains randomly distributed trace fossils known from tier B, mainly *Thalassinoides* and *Alcyonidiopsis*, which are cross-cut here by *Zoophycos* as well as large- and medium-sized *Chondrites*. *Chondrites* probably was made in slightly firmer, and dysoxic substrates below the oxygenated shallower layer.

The deepest tier (D), recorded from 7 to 20 cm below the boundary surface, contains *Zoophycos*, medium- and mostly small-sized *Chondrites*, which represent sessile to semisessile deposit-feeding or farming and chemichnial structures, respectively. Cross-cutting relationships lead us to infer later endobenthic colonization by *Zoophycos* producers and final colonization

by *Chondrites* tracemakers occupying the deepest tier. *Chondrites* of different sizes could correspond to several sub-tiers within the tier D, with the smallest forms invariably at the greatest depths below the seafloor.

4. Interpretation

The tiering pattern from the Agost section is similar to others recognized in Cretaceous chalk from Denmark and Alabama (Ekdale & Bromley, 1984, 1991; Ekdale, Bromley & Pemberton, 1984; Frey & Bromley, 1985; Bromley & Ekdale, 1986; Ekdale, 1988; Bromley, 1996). Many environmental factors determine the trace-fossil types and tiering pattern of deep-sea trace-fossil communities (Wetzel, 1991), with special attention to oxygenation, benthic food content, sedimentation rate, and substrate consistency. From these limiting eco-sedimentological factors, no clear changes in sedimentation rate during the dark clay-layer deposition have been discerned in the Agost section, and thus the tiering pattern characterized may be the consequence primarily of changes in oxygenation as well as substrate consistency, and secondarily in the benthic food content.

After the K–T boundary event and during the beginning of sedimentation of the darker, clayey oldest Danian sediments, the soft oxygenated substrate was colonized by the shallow, probably very diverse benthos. This benthos was responsible for the intense bioturbation observed in tier A. At the same time or shortly afterwards, *Planolites*, *Alcyonidiopsis* and *Thalassinoides* tracemakers (probably polychaetes and crustaceans) colonized the deeper layer of sediments at the top of the Maastrichtian section (tier B). As oxygen decreased, these animals were replaced by a stationary deposit-feeding or agrichnial *Zoophycos* tracemaker (possibly echiuran worm) and chemichnial *Chondrites* tracemaker (unknown worm) (tiers C and D). It is interesting that larger *Chondrites* was apparently supplanted by smaller *Chondrites*. The diminishing size could result from an intensification of environmental stress, which, in turn, may be related to a further decrease in oxygen and to increased cohesiveness of the substrate due to early diagenetic processes. It would be expected that the shallowest layers of the dark clay were reworked continuously by shallow infauna producing a bioturbated background, but their activity was limited. Changes registered from tiers A to D in the dominant ichnotaxa, and in diminishing degree of bioturbation, diversity, and size of trace fossils may also be indicative of waning benthic food availability.

Two models can be envisaged to interpret the data gathered and the proposed tiering pattern:

(1) Vertical partitioning of a single multi-tiered community in a well-oxygenated floor. In this scenario, steady-stable conditions without significant changes in, for example, oxygen in bottom waters existed after the K–T boundary event. The tiering structure could respond to gradual changes in the sediment. Ichnological features from tiers A to D (variations in trace fossils assemblage, and diminishing in diversity, abundance and size), could be related to decreasing oxygen in pore waters and increasing substrate consistency deeper in the sediment. In this situation, the ichnological tiering registered is a consequence of the vertical zonation within the Upper Maastrichtian sediments. Cross-cutting relationships could also be related to a gradational change in the tier structure from tiers A to D, according to a deoxygenation model (Savrda & Bottjer, 1989; Wignall, 1994; Taylor, Goldring & Gowland, 2003). However, this model is difficult to prove because of the absence of any convincing record of bioturbation in the dark early Danian sediments.

(2) Sequential colonization, reflecting the work of two different communities, one of which replaced the other in time. This interpretation considers the dynamics of the changing tiering patterns registered to be best described by a model of sequential colonization (Wetzel & Uchman, 2001), especially where sedimentation is affected by depositional or other environmental events. These two successive communities could be related to environmental changes in the early Danian interval. Thus, colonization of several levels in the sediment at different times (change from tiers A–B to C–D) indicate diminishing oxygenation, changes in substrate consistency, and probably decreasing benthic food content. Changes in these factors need not have been related directly to the K–T event, but could well have resulted from normal ecological and early diagenetic processes that took a far longer time, such as exploitation of food and oxygen by the first community, or decomposition of refractory organic matter due to oxygenation. However, we cannot rule out the existence of environmental alterations occurring during the early Danian interval, shortly after the K–T event, such as the appearance of oxygen-deficient bottom waters that could influence colonization by *Chondrites* and *Zoophycos* belonging to the second community. In the neighbouring Caravaca section a drastic and marked decrease in dissolved oxygen was postulated close to the K–T boundary, and related to an important and sudden influx of nutrients to the seafloor (Coccioni & Galeotti, 1994; Kaiho *et al*. 1999).

5. Conclusions

Trace fossils from the K–T Agost section enable the recognition of a well-developed, oldest Danian endobenthic community that was emplaced at the top layer of Maastrichtian age deposits. In order of abundance, the following ichnotaxa are recognized: *Chondrites* ?*targionii*, *Zoophycos* isp., *Planolites* isp. A, *Planolites* isp. B, ?*Thalassinoides* isp. A,

Thalassinoides isp. B, *Thalassinoides* isp. C, *Alcyonidiopsis longobardiae*, and *Diplocraterion ?parallelum*. *Alcyonidiopsis* and *Diplocraterion* are described for the first time from K–T boundary intervals. The trace fossils studied indicate that infaunal communities were established shortly after the K–T event. The diverse common tracemakers (different polychaetes, crustaceans, ?echiurans) were registered after the K–T boundary event.

The registered trace fossil assemblage displays a tiered pattern with clear cross-cutting relationships, that can be interpreted as: (1) a single multi-tiered community under steady-stable conditions in well-oxygenated water bottom, but with decreasing oxygen pore water and benthic food, and increasing substrate consistency deeper into the sediment, or (2) two successive communities established after the K–T event as a sequential colonization and community replacement indicating diminishing oxygenation, changes in substrate consistency, and probably decreasing benthic food content. These changes determining the sequential colonization appear to be the consequence of environmental alterations related directly to the K–T event, or could well have resulted from normal ecological and early diagenetic processes that took place over a much longer time.

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