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ABSTRACT

A bed-by-bed ichnological analysis at the classic Bottaccione section (Gubbio area, Italy), reveals an unusual response of ichnofauna to the environmental changes associated with the Cretaceous-Paleogene (K-Pg) boundary event. The trace fossil assemblage, consisting of *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., *Trichichnus* isp., and *Zoophycos* isp., is similar to that registered during Cenomanian and Turonian times, showing persistence of the same community for a long time interval in deep-sea carbonate deposits. Absence of significant changes through the K-Pg boundary confirms that the extinction did not touch the ichnofauna. The decline of trace fossils occurs at 6 cm above the K-Pg boundary, with the total absence of biogenic structures in a 3 cm-thick layer showing parallel laminations. A gradual record of *Zoophycos* and *Planolites* resumes in the overlying layers. This suggests a progression of inhospitable conditions for the macrobenthos, followed by a delayed response of ichnofauna to drastic diminution of available food starting about 15 k.y. after the K-Pg boundary event, and then a gradual recovery leading to pre-event environmental conditions.

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1. Introduction

The Cretaceous-Paleogene (K-Pg) boundary event (~ 65.5 m.y.) resulted in one of the major Phanerozoic mass extinctions (Schulte et al., 2010). A large bolide impact represented by the Chicxulub crater in Yucatan, Mexico, is widely accepted. Environmental effects of this event include acid rains, wildfires, elevated atmospheric temperatures, dust and aerosols in the atmosphere, destruction of ozone layer, and the increase of greenhouse gases (Wolbach et al., 1985; Gale et al., 2001; Beerling et al., 2002; Kring, 2007). The catastrophic vs. gradual disappearance or change of biota or recovery of the involved communities is still a matter of debate and controversy (Kring, 2007; MacLeod et al., 1997; MacLeod, 1998).

Some authors (Kring, 2007; Keller et al., 2009; Schulte et al., 2010) point out the absence of a similar reaction of different biota at the boundary, suggesting influences of several factors leading to variable effects on marine *vs.* continental communities, vertebrates *vs.* invertebrates, planktonic *vs.* benthic, K- *vs.* r-strategists,

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http://dx.doi.org/10.1016/j.geobios.2015.02.001 0016-6995/© 2015 Elsevier Masson SAS. All rights reserved. or deposit vs. suspension feeders (Powell and MacGregor, 2011; Labandeira et al., in press). Marine deposit-feeders living in deepsea substrates and feeding upon detritus or dead organisms (Arthur and Zachos, 1987; Twichett, 2006) were less affected by the extinction episode than suspension and filter feeders living in the shallow water conditions, having more direct trophic links to photosynthesis (Sheehan and Hansen, 1986). However, Levinton (1996) suggested that extinction levels of deposit and suspension feeders are consistent with a near simultaneous extinction, possibly within a maximum of 3 to 6 months.

The response of marine infaunal invertebrates to the K-Pg boundary event can be deciphered from ichnological data. Trace fossil analysis of the deep-marine K-Pg boundary sections from the Czech Republic, southern (Agost and Caravaca) and northern (Sopelana) Spain, and in southwestern France (Bidart), reveals little ichnotaxonomic variation between pre- and post-event ichnoassemblages (Rodríguez-Tovar and Uchman, 2004a,b; Uchman et al., 2005; Rodríguez-Tovar et al., 2011; Table 1). This indicates a minor influence of the K-Pg boundary event on deep-sea ichnofauna. In the Agost section, isotopic analysis of trace fossil fillings allowed characterization of different phases of colonization during the earliest Danian (Rodríguez-Tovar et al., 2002, 2004, 2006). The presence of iron-oxide spherules in fillings of *Thalassinoides*

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Table 1

Pre- and post-K-Pg boundary trace fossils in selected marine sections.

Section	Pre-K/Pg (Upper Maastrichtian) boundary traces	Post-K/Pg (Lower Danian) boundary traces	References
Stevns Klint (Denmark)	Chondrites, Thalassinoides, Zoophycos	Phycosiphon (former "small Chondrites-like forms), Planolites, Thalassinoides	Ekdale and Bromley (1984)
Millers Ferry (Alabama)	Chondrites, Planolites, Thalassinoides, Zoophycos	Ophiomorpha, Planolites, Thalassinoides	Savrda (1993)
Los Ramones, El Mimbral, etc. (NE Mexico)	Chondrites, Ophiomorpha, Planolites, Zoophycos		Ekdale and Stinnesbeck (1998)
Agost (SE Spain)	Chondrites, Planolites, Zoophycos, unidentified structures	Alcyonidiopsis, Chondrites, Diplocraterion, Planolites, Thalassinoides, Zoophycos, unidentified structures	Rodríguez-Tovar and Uchman (2004a,b)
Caravaca (SE Spain)	Chondrites, Planolites, Thalassinoides, Trichichnus, Zoophycos	Alcyonidiopsis, Chondrites, Planolites, Thalassinoides, Zoophycos	Rodríguez-Tovar and Uchman (2006)
Bidart (SW France) & Sopelana (N Spain)	Planolites, Thalassinoides	Chondrites, Planolites, Thalassinoides, Trichichnus, Zoophycos	Rodríguez-Tovar et al. (2010, 2011)
Gubbio (Italy)	Chondrites, Planolites, Thalassinoides, Zoophycos	Chondrites, Planolites, Thalassinoides, Trichichnus, Zoophycos	This paper

K-Pg: Cretaceous-Paleogene; NE: northeast; SE: southeast; SW: southwest; N: north.

confirms nearly contemporaneous macrobenthic colonization with deposition of the red iron-rich layer (Rodríguez-Tovar, 2005). In the Caravaca section, the red iron-rich boundary layer at the base of the dark boundary layer is crosscut vertically by *Zoophycos* and *Chondrites*, and penetrated horizontally by *Chondrites*, confirming rapid re-colonization of the substrate after the K-Pg boundary event by opportunistic tracemakers (Rodríguez-Tovar and Uchman, 2006, 2008; Kędzierski et al., 2011).

The aim of this paper is to present a particular response of deepsea ichnofauna to the K-Pg event in the Bottaccione section at Gubbio, Italy. Our objective is not to address the catastrophic *vs.* gradual debate, but rather to present new data revealing an alternative to the traditional hypotheses on the evolutionary and ecological dynamics associated with the K-Pg boundary event, including the recovery of marine biota.



Fig. 1. Location map of the Gubbio Cretaceous-Tertiary (GBKT) boundary section and Cretaceous-Paleogene (K-Pg) boundary. Modified from Coccioni et al. (2012).

2. Geological setting

From the numerous K-Pg boundary sections available worldwide, the Bottaccione section at Gubbio in the Umbrian Apennines, Central Italy, represents the classic and probably most important and intensely studied one (Bonarelli, 1890; Renz, 1936; Luterbacher, 1964; Luterbacher and Premoli Silva, 1964; Premoli Silva, 2012; Fig. 1). This section is located along the state road SR298, crossing the Bottaccione Gorge on the slope west of the GPS point N43°21.923'-E012°34.958' \pm 11 m (see Coccioni et al., 2012, for a geology of the Gubbio area). This section is a reference section of the K-Pg boundary, being the first where the iridium anomaly, together with other trace elements, were discovered and interpreted as evidences of a large extraterrestrial impact (Alvarez et al., 1980; Montanari and Koeberl, 2000; Alvarez, 2009).

The Maastrichtian-Danian sediments belong to the Scaglia Rossa Formation (early Turonian-middle Eocene; Fig. 2(A)). A 117 cm-thick interval of uppermost Maastrichtian, including \sim 62 cm of red to white calcilutites with abundant microbioclasts, and the lowermost Danian interval, dominated by \sim 55 cm-thick red calcilutites and red marlstones on top, were studied. The K-Pg boundary is marked by a 5 mm-thick black to red clay layer (Fig. 2(B, C)). The K-Pg boundary layer is well exposed at m 382.6, in the upper part of Chron 29r (Coccioni et al., 2012). At the top of the red limestones, there is a 60 cm-thick bed of white pelagic limestone (Maastrichtian) containing abundant *Zoophycos* (Montanari and Koeberl, 2000; Fig. 3(G)). This is the first report of ichnological data from the section.

Recent bio-magnetostratigraphic study of the upper Campanian-Maastrichtian from the Bottaccione and Contessa sections of the Gubbio sections revealed a 425 k.y.-long hiatus within Chron C31n at Bottaccione (well below the studied interval). The sedimentation rate for Chron C29r (topmost Maastrichtian) is estimated at 1.23 cm/ k.y. (Gardin et al., 2012). Previous studies revealed low sedimentation rates in the Gubbio area, i.e., 6-10 mm/k.y. for the top of the Cretaceous and 2-5 mm/k.y. for the lowermost Paleocene (Montanari and Koeberl, 2000). Other authors indicate 4–6 mm/k.y. for the latest Cretaceous and 2–3 mm/k.y. for the early and middle Paleocene (Mukhopadhyay et al., 2001; Cronholm and Schmitz, 2007). Upper Cretaceous and Paleocene sediments from the Gubbio, Umbria Marche Basin were deposited in a deep bathyal position with a water depth of 1500-2500 m, according to agglutinated foraminifera assemblages (Kuhnt, 1990; Cronholm and Schmitz, 2007). Coccioni et al. (2012) indicated that Cretaceous and Paleogene



Fig. 2. The Cretaceous-Paleogene (K-Pg) boundary section at Bottaccione. **A.** General view; the K-Pg boundary is marked by the dash line. The measuring stick is 1 m long. **B.** Detail of the boundary, which is located just at the top of the white calcilutite. **C.** Cross section of the boundary in a polished slab. *Thalassinoides (Th)* filled with darker sediment and transformed by stylolithization. Scale bars: 1 cm (B, C).

pelagic successions of the Contessa Valley were deposited at middle to lower bathyal depths (1000–1500 m).

3. Trace fossil assemblages

The ichnological analyses focused on characterization of the Maastrichtian and Danian trace fossil assemblages, based on outcrop and laboratory studies. An ichnofabric approach was difficult due to problems in recognizing the bioturbation index, crosscutting relationships or tiering patterns. Samples were collected bed-by-bed, cut in different oriented sections, polished, and photographed. They are housed in the Earth Science Department of Perugia University (labeled GBKT). Five ichnotaxa were recognized: *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., *Trichichnus* isp., and *Zoophycos* isp. (Fig. 4). Poor preservation and common stylolitization prevents a determination at the ichnospecies level.

Chondrites isp. appears as small groups of patches that are usually darker than the host rock (Fig. 5(B)). This contrasts with the abundant light *Chondrites* characterizing the Bonarelli Event in the same Bottaccione section (Monaco et al., 2012). Patches have circular to elliptical cross sections; short, vertical or oblique segments with occasional branches 0.5–0.8 mm-wide (Fig. 3(A, B, E)) can be present. *Chondrites* is a deep-tier trace fossil probably produced by an organism most likely living in dysaerobic conditions, that is, a chemosymbiont (Seilacher, 1990; Fu, 1991). *Chondrites* is usually related to an opportunistic behavior (r-strategy) of a tracemaker tolerant of very low oxygen conditions



Fig. 3. Trace fossils from the Cretaceous-Paleogene (K-Pg) boundary section at Bottaccione. Samples indicated in the lower part of the photographs. Trace fossils: *Ch: Chondrites*; *PI: Planolites*; *Th: Thalassinoides*; *Tr: Trichichnus*; *Zo: Zoophycos*. **A–D**. Horizontal cross sections of polished slabs. **E,F**. Vertical cross sections of polished slabs. **G.** Large *Zoophycos* below the K-Pg boundary with a distinct apex and at least two whorls (*Zo* 1 and *Zo* 2). **H**. *Zoophycos* truncated by stylolith; vertical cross sections of polished slab. **I.** Sample GBKT12 with possible primary laminations (lam); vertical cross sections of polished slab. **J.** *Zoophycos* transformed by stylolithization; vertical cross sections of polished slab. Scale bars: 1 cm.

(Bromley and Ekdale, 1984; Savrda and Bottjer, 1986, 1989, 1991; Tyszka, 1994; Wetzel, 1994) and/or organic-rich sediments (Vossler and Pemberton, 1988).

Planolites isp. is assigned to horizontal/oblique, straight, simple flattened cylinders. They have a dark color that differs from the host sediment. They present a sharp boundary (Fig. 3(F)), and they are up to 150 mm long when occurring in plane surfaces. Long specimens usually occur with an endichnial/epichnial stratinomic position in limestone beds. When observed in cross sections, they appear as 2–3 mm-wide elliptical spots (Figs. 3(A–D, F), 5(B)). *Planolites* is a facies-crossing form, interpreted as a pascichnion (i.e., a grazing trace), produced by a number of different softbodied invertebrates (Pemberton and Frey, 1982; Keighley and Pickerill, 1995).

Thalassinoides isp. occurs as straight, horizontal to oblique, locally vertical branched cylinders, up to 20 mm-wide in plane view (immediately below the K-Pg boundary; Fig. 5(A)). They occur usually as epichnial specimens, although some hypichnial and endichnial positions can be observed in many mudstones. They can be observed mostly in cross sections as 4.5–11 mm-wide elliptical spots (Figs. 2(C), 3(A–C)). *Thalassinoides* occurs in a great variety of marine environments, being mostly interpreted as a domichnial (i.e., dwelling) and fodinichnial (i.e., feeding) structure produced by arthropods, most commonly decapod crustaceans (Frey et al., 1984; Ekdale, 1992; Schlirf, 2000).

Trichichnus isp. appears as a vertical, often branched structure. The rarity of oblique to flat forms in the Scaglia Rossa Formation, compared to other formations in the Northern Apennines (Monaco and Trecci, 2014), can be due to a slow sedimentation rate of pelagic carbonates in contrast with siliciclastic turbidites (MacBride and Picard, 1991; Monaco and Trecci, 2014). This ichnotaxon appears as thread-like cylinders filled with a ferruginous substance, with a whitish, diagenetic halo around the cylinder (usually less than 1 mm in diameter; Fig. 3(D)). *Trichichnus* is a eurybathic marine trace fossil, common in fine-grained deposits (Fillion and Pickerill, 1990). *Trichichnus* is regarded as domichnial burrows of marine meiofaunal deposit-feeders (Frey, 1970). The producer of *Trichichnus* has also been suggested as a chemosymbiont (Uchman, 1995).

Zoophycos isp. is observed in cross section as horizontal or subhorizontal spreiten stripes, 2–3 mm-thick (Fig. 3(E, F, H, J)). In the outcrop, fragments of the burrow systems are observed as planar spreite lobes surrounded by a marginal tunnel and arranged in helical whorls (at least two) with a distinct apex (Fig. 3(G)). The outer diameter of the whorls at the top of Maastrichtian can reach 35–40 cm, while the Paleogene specimens are smaller, from 5 to 20 cm (exceptionally up to 25 cm). A progressive increase in dimensions and complexity of *Zoophycos* in the Gubbio area resumes from the Late Paleocene/Eocene (Fig. 5(C)), and especially in Oligocene to early Miocene times (upper Scaglia Rossa, Scaglia



Fig. 4. The studied interval with bed-by-bed indication of samples, ranges of trace fossils and number of ichnotaxa. Intervals referred to ichnofauna crises are shadowed in grey.

Variegata, Scaglia Cinerea, Bisciaro, and Marnoso-arenacea Formations), with helicoidal to lobate forms up to 120 cm wide (L. Bracchini, personal communication). *Zoophycos* has been interpreted as a feeding structure (fodinichnia; Seilacher, 1967; Wetzel and Werner, 1981; Ekdale and Lewis, 1991; Olivero and Gaillard, 1996). Other ethological interpretations, however, consider that *Zoophycos* may have been produced by surface ingestors of organic detritus that accumulate fecal pellets in a



Fig. 5. Ichnological features of the studied section. **A.** Bioturbated limestone at the top of the Maastrichtian carbonates, with *Thalassinoides* (*Th*). **B.** Bioturbated limestone beds at the top of the Maastrichtian carbonates (sample GBKT 10 on Fig. 2), with *Planolites* (*Pl*) and *Chondrites* (*Ch*) in different levels; scale bar: 2 cm. **C.** A gradual record of large *Zoophycos* (*Zo*) resumes in the overlying late Paleocene-early Eocene layers of the Bottaccione section.

subsurface structure (Kotake, 1989, 1991; Löwemark et al., 2007), or as a combination structure of deposit feeding and chemosymbiotics (Bromley and Hanken, 2003).

The composition of the trace fossil assemblage in the studied interval shows no significant differences below and above the K-Pg boundary (Figs. 3, 4). Only the questionable Trichichnus above the boundary is absent below. However, the diversity and abundance of trace fossils vary throughout the investigated interval. A concentration of large, superimposed *Zoophycos* isp, is present in the white limestones at the top of the Cretaceous (in the same stratigraphic position as in the Contessa section, which is 2.5 km away; Montanari and Koeberl, 2000). The decline of trace fossils (only sporadic Zoophycos and Planolites) in an 18 cm-thick level (sample GbKT12-GbKT16A) starting at 6 cm above the K-Pg boundary is most striking. At the base of this interval, primary parallel lamination is present in a thin 3 cm-thick layer (Figs. 3(I), 4), in and around which trace fossils are absent. Above, the diversity increases and drops again. Below the K-Pg boundary, the diversity drops in three levels, which do not show any primary lamination (Fig. 4). At the K-Pg boundary and just above and below it, the diversity of trace fossils is high and their record is continuous (Fig. 4).

4. Discussion

The studied trace fossil assemblage (*Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., *Trichichnus* isp., and *Zoophycos* isp.) is typical of the *Zoophycos* ichnofacies that characterizes pelagic sediments below the range of storm currents and beyond flysch sedimentation (Wetzel and Uchman, 2012). It is very similar to the ichnoassemblage in the Bonarelli Level (uppermost Cenomanian) in the same area (Monaco et al., 2012), suggesting a persistence of the same ichnofauna over a long time interval. Environmental change, such as fluctuation in oxygenation and food supply, apparently had a minor effect on the ichnofauna, causing only a variation in abundance and diversity, but without extinction. The analysis of the trace fossil assemblage reveals several significant points.

4.1. Rhythmic pattern

In general, the fluctuations of diversity and abundance of trace fossils through the studied interval show a more or less developed rhythmic pattern (Fig. 4), which may be related to fluctuations of environmental conditions. Cyclostratigraphic analysis conducted on the Contessa and Bottaccione sections revealed an orbital control on the Maastrichtian sedimentation, with the identification of precession and eccentricity cycles (Husson et al., 2014). Thus, it is possible that the ichnological fluctuations are related to the Milankovitch cyclicity, though the data are, at present, insufficient to prove this hypothesis. However, taking into account that the fluctuations in trace fossil diversity and abundance are in 20-30 cm-thick intervals (Fig. 4), and the rate of sedimentation during the latest Maastrichtian was 1.23 cm/k.y. (Gardin et al., 2012), the periodicity of changes ranges from 16 to 24 k.y., fitting well within the precession cycle. A much smaller sedimentation rate postulated for the lower Paleocene (2-3 mm/k.y.; Mukhopadhyay et al., 2001; Cronholm and Schmitz, 2007) still gives periodicity within the range of duration of the orbital cycles.

4.2. Continuous distribution

Distribution of trace fossil taxa across the studied Cretaceous-Palaeogene interval shows an evident continuity, with only a brief absence of discrete trace fossils (see below). This ichnotaxonomic continuity suggests that the catastrophic phenomena interpreted for the K-Pg boundary event (acid rain, wildfires, elevation and subsequent drop of atmospheric temperatures, dust and aerosols in the atmosphere, ozone destruction, and greenhouse gases, among others) did not significantly affect the deep-sea macrobenthos during or immediately after the boundary event. Only the large Zoophycos that is very abundant in white sediments of the upper Maastrichtian Scaglia Rossa (Fig. 3(G)) disappears above the K-Pg boundary, probably due to a decrease in sedimentation rate after the event (Mukhopadhyay et al., 2001) or a change in food supply. A discontinuous record of smaller Zoophycos is present above the boundary. The absence of ichnofaunal extinction in the K-Pg boundary interval of the Bottaccione section agrees with observations in other K-Pg boundary sections (Rodríguez-Tovar, 2005; Uchman et al., 2005; Rodríguez-Tovar and Uchman, 2006, 2008). This could be related to the opportunistic character of some tracemakers (e.g., Chondrites and Zoophycos producers), as well as the dominance of deep-tier feeding traces, interpreted as mainly produced by deposit-feeders obtaining food from the sediment or by chemichnia benefiting from sulfids below the redox boundary. Therefore, deposit-feeders were less affected by the K-Pg event extinction than suspension and filter feeders (Arthur and Zachos, 1987; Jablonski, 2005; Twichett, 2006). The presence of Chondrites, Planolites, and Thalassinoides across the boundary, the former usually associated with low oxygen conditions and the latter two related to comparatively oxygenated environments, would allow us to discard significant changes in oxygenation at the K-Pg boundary interval.

4.3. Disappearance of ichnotaxa

A sudden disappearance of trace fossils is observed at the levels located 6 and 17 cm above the K-Pg boundary. The former is especially significant, because the decline of trace fossils at around 6 cm above the K-Pg boundary in limestones is associated with parallel laminae, reflecting the absence of biodeformational structures. In this interval the diversity and abundance of biodeformational structures and trace fossils were influenced negatively. Causes of this disappearance are difficult to interpret, but they may be attributed to a decrease in the rate of deposition of food and sediment to the sea floor (Fig. 4). This negative flux of food to the deep-sea floor influenced the ichnofauna. A drastic decrease in oxygenation (anoxic conditions) could have caused the local disappearance of macrobenthic tracemakers, including the Chondrites producers. However, no changes were observed in the sediment features, such as a darker/black colour suggesting anoxic depositional environments. Trace fossils do not provide information about conditions during sedimentation of their host sediments, only about the colonization surface (Goldring, 1995), so their absence is significant.

4.4. Recovery phase

After the major disappearance recorded around 6 cm above the K-Pg event, an initial return to previous conditions of the ichnofaunal community took place with the appearance of a nearly monospecific assemblage (*Zoophycos* at around 12 cm above the K-Pg boundary); then there was a full recovery with development of an ichnoassemblage similar in composition and abundance to that of the pre-event at about 32 cm above the K-Pg boundary. The occurrence of *Zoophycos* as the first trace fossil after the ichnofaunal crisis can be misleading, however. *Zoophycos* can be the deepest tier trace fossil, as in the K-Pg of Caravaca section (Rodríguez-Tovar and Uchman, 2006), meaning the colonization level is much higher than its level (tier) of occurrence. The average sedimentation rate was around 3–4 mm/k.y. for the lowermost Paleocene (between 2–5 mm/k.y. in Montanari and Koeberl, 2000,

and 2–3 mm/k.y. in Mukhopadhyay et al., 2001; see also Cronholm and Schmitz, 2007). This demonstrates several points:

- the change in the trace fossil assemblage starting at 6 cm was initiated at around 15 k.y. after the K-Pg boundary event;
- the 3 cm-thick interval without bioturbational sedimentary structures but presenting primary laminate had a duration around 7.5 k.y.;
- the recovery of the pre-event trace fossil assemblage (but without large *Zoophycos*), noted about 32 cm above the K-Pg boundary, initiated around 70 k.y. after the K-Pg event.

This recovery sequence may reflect the survivor of benthic deposit-feeders after the K-Pg crisis, showing a delayed response due to decreasing storage of organic matter in the sediment. A sudden, drastic change in the palaeoenvironmental conditions affecting macrobenthic habitat during the initial phase of the recovery, determining total disappearance of bioturbational sedimentary structures, is feasible.

According to Coccioni et al. (2012), the observed change registered at the Bottaccione section between large (up to 1 mm) planktonic foraminifera from the last Cretaceous limestones and the small (less than 0.1 mm) globigerinids from the first Paleogene limestones (Premoli Silva et al., 1974) is a clear palaeobiologic signature of the mass extinction event in planktonic foraminifera. A brief episode of anoxic bottom waters, rich in organic matter, is interpreted on the abyssal sea floor immediately after the mass extinction of marine plankton (Coccioni et al., 2012). In the case of ichnofauna, previous ichnological analysis of the K-Pg interval revealed that oxygenation levels were not a significant limiting factor for the macrobenthic tracemacker assemblage, especially for opportunistic taxa such as those producing Zoophycos and Chondrites (Rodríguez-Tovar, 2005; Rodríguez-Tovar and Uchman, 2006, 2008). Moreover, recent geochemical analysis from the K-Pg boundary at the Caravaca section supports the hypothesis that the recovery to pre-impact levels of oxygenation occurred quite rapidly, perhaps as quickly as about 100 years (Sosa-Montes de Oca et al., 2013). Thus, a significant improvement of oxygenation was probably not the major factor influencing the macrobenthic tracemaker community.

Generally, trace fossils in the study section are less abundant than in the other K-Pg boundary sections in Spain or France (Rodríguez-Tovar and Uchman, 2004a, b; Rodríguez-Tovar et al., 2011). This may be due to more oligotrophic conditions in the Gubbio area. In such conditions, the ichnofauna would be more sensitive to changing food supply, making the changes in trace fossil diversity and abundance clearer at Gubbio than in other sections.

5. Conclusions

A trace fossil assemblage in the Bottaccione section consists of *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., *Trichichnus* isp., and *Zoophycos* isp. This assemblage, found also in many other places in the world (Table 1), is typical of deep-sea carbonate depositional systems (*Zoophycos* ichnofacies). This remarkable assemblage contrasts with assemblages of siliciclastic flysch deposits of the same depth range, which typically contain graphoglyptids (*Nereites* ichnofacies; Uchman, 1995; Monaco and Trecci, 2014).

Ichnological changes in the Bottaccione section confirm the delayed response of the macrobenthic tracemaker community to the K-Pg crisis. Changes of trace fossils across the studied K-Pg boundary interval show four significant features:

- a rhythmic pattern, that could be related to the Milankovitch cyclicity;
- the continuous distribution across the boundary, suggesting a minor influence of the K-Pg event on the deep-sea macrobenthos during or immediately after the boundary event;
- a sudden disappearance of ichnotaxa several centimeters above the K-Pg boundary suggests a delayed response of ichnofauna, which is registered as a sharp, major change occurring within a few 100 to 1000 years after the event;
- a gradual recovery phase characterized initially by the appearance of *Zoophycos* and then by a full recovery, with the development of an ichnoassemblage similar to that of the preevent part of the section.

No significant changes in the palaeoenvironmental parameters, including oxygen conditions, can be envisaged during the K-Pg boundary event, with only slight variations in sedimentation rate or food supply after the event.

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