Changes in the composition of trace fossil assemblages across the Paleocene–Eocene transition in the north-western Tethys (Untersberg section, Austria)

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Abstract: The Untersberg section (Northern Calcareous Alps, Austria) provides an expanded and biostratigraphically well constrained deep-sea record of the Paleocene–Eocene transition in the north-western Tethyan realm. At the base of the Eocene, massive carbonate dissolution and a shoaling of the calcite compensation depth (CCD) by at least 1 km is recorded by 5.5 m-thick red claystone, which is intercalated into a grey marlstone succession. Previous studies documented the benthic foraminifera extinction event (BEE) in this claystone. Now biodeformational structures and trace fossils were investigated in this interval to evaluate the impact of the extinction event on the macrobenthic tracemaker fauna. Using the stratigraphic distribution pattern of trace fossils, the lowermost Eocene claystone can be subdivided into three parts: (1) the lower part shows a trace fossil assemblage consisting of *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., and *Zoophycos* isp., (2) the middle part is characterized by primary sedimentary lamination and exceedingly rare ichnofossils, and (3) the upper part shows a less abundant and less diverse trace fossil assemblage than the lower part, indicating a slow recovery of the macrobenthic tracemaker community. This pattern demonstrates that macrobenthic communities were severely affected by the ecological perturbations in the earliest Eocene. The change in sediment colouration towards red colour in the middle part of the Paleocene–Eocene transition at the Untersberg section, together with decrease in bioturbation degree indicate that oxygen consumption was rather reduced during the PETM, and the loss in bioturbation is thus unrelated to oxygen limitation. Trace fossils can be used to improve the resolution of the benthic extinction interval and provide an excellent proxy for the precise determination of timing of the climax of this global event.

Keywords: North-western Tethys, Eastern Alps, Paleocene–Eocene boundary, benthic extinction event, trace fossils.

Introduction

At the Paleocene–Eocene boundary (P–E boundary), around 56 Ma ago, an increase in Earth's atmospheric temperature by 5–8 ºC occurred (Kennett & Stott 1991; Sluijs et al. 2007; McInerney & Wing 2011). This hyperthermal event (The Paleocene–Eocene Thermal Maximum; PETM) is associated with a massive perturbation of the global carbon cycle, as indicated by a negative carbon isotope excursion (CIE) in marine and terrestrial settings with a magnitude between 2.4 ‰ and 7 ‰ (e.g., Handley et al. 2008; McCarren et al. 2008). This is interpreted as the result of a massive release of isotopically light carbon into the carbon cycle sourced by a release of methane hydrates (Dickens 1999, 2011) or by a major emission of volcanic gases (Gutjahr et al. 2017). Based on X-ray fluorescence core-scanning of precessional cycles the duration of the whole event is estimated approximately as 170 ka (Röhl et al. 2007).

The CIE is associated with severe carbonate dissolution and a shoaling of the calcite compensation depth (Egger et al. 2005; Zachos et al. 2006; Penman et al. 2014) as well as an increase in terrigenous input into marginal ocean basins, which led to enhanced surface productivity in marginal ocean

settings (e.g., Egger et al. 2003; Thomas 2007; Speijer et al. 2012). The ecological perturbations at the P–E boundary also affected deep-sea microfaunal biota and caused the global extinction of 35–50 % of benthic foraminifera species within the first 10 kyr of the Eocene (Benthic Foraminiferal Extinction Event, BEE; Thomas 1998, 2003; Alegret et al. 2009a,b). The benthic foraminifera assemblages at the top of the BEE-interval show the predominance of opportunistic species (Arreguín-Rodríguez et al. 2018). Several causes have been proposed to explain the mass extinction, including low oxygenation, carbonate corrosion, changes in oceanic productivity and increasing temperatures of deep ocean waters (Giusberti et al. 2016 for a review).

McInerney & Wing (2011) stressed that benthic macroinvertebrate assemblages were not affected by the perturbations during the BEE. However, effects on macrofossil communities are indicated by the composition of trace fossil assemblages, which reflect very well the activities of macrofaunas, even if they are not preserved as body fossils (Nicolo 2008; Nicolo et al. 2010; Cumming & Hodgson 2011a,b; Rodríguez-Tovar et al. 2011a). The PETM seems to have had minor long-lasting evolutionary impacts on benthic macrofauna inhabiting shelf environments (Ivany et al. 2018). However, the effects of

the PETM event on microbenthic fauna in bathyal and deep-sea environment remain poorly explored.

In the latest years, ichnological analysis has been revealed as a tool for the interpretation of major bioevents, such as those associated with the Frasnian–Famennian boundary (Stachacz et al. 2017), the T-OAE (Rodríguez-Tovar & Uchman 2010; Rodríguez-Tovar & Reolid 2013; Reolid et al. 2014; Miguez-Salas et al. 2017; Rodríguez-Tovar et at. 2017), the Cenomanian–Turonian boundary (Uchman et al. 2008, 2013a,b; Rodríguez-Tovar et al. 2009a,b; Monaco et al. 2012, 2016b), the latest Hauterivian (Rodríguez-Tovar & Uchman 2017), the Paleocene–Eocene (Rodríguez-Tovar et al. 2011a), and, especially the Cretaceous–Paleogene (K–Pg) boundary (Rodríguez-Tovar & Uchman 2004a,b, 2006, 2008; Rodríguez-Tovar et al. 2004, 2006, 2010, 2011b, 2016; Rodríguez-Tovar 2005; Kędzierski et al. 2011; Sosa-Montes de Oca et al. 2013, 2016, 2017; Alegret et al. 2015; Monaco et al. 2015; Labandeira et al. 2016; Łaska et al. 2017; Lowery et al. 2018).

In this paper we present a high resolution trace fossil record for the Paleocene–Eocene transition at a section in the north-western Tethys and demonstrate that macrobenthic communities there were severely affected by the ecological perturbations during the BEE.

Material and methods

The Untersberg section is located southwest of Salzburg (Austria) in a forested stream gorge (47°44'21" N, 12°59'09" E) in the Northern Calcareous Alps, which form a 500 km-long fold and thrust belt on the north-eastern margin of the Alps (Fig. 1). The P–E boundary lays within the Nierental Formation (upper Santonian–Lutetian) of the Gosau Group and accumulated in a lower bathyal slope environment at a paleodepth of about 2000 m in the north-western Tethyan realm (Egger et al. 2005). General plate tectonic reconstructions by the ODSN Plate Tectonic Reconstruction Service (http://www.odsn.de) suggest a position of this section at a paleolatitude of c. 44° N in the early Paleogene.

Thanetian and Ypresian deposits consist essentially of marl-stone, displaying $CaCO_3$ contents between 40–50 wt. %. Within the dominantly marlstone succession, a 5.5 m-thick intercalation of red and green claystone and marly claystone indicates the CIE, which is used to recognize the P–E boundary. At Untersberg, the CIE was associated with a shallowing of the calcite compensation depth by at least one kilometre (Egger et al. 2005).

High-resolution planktonic biostratigraphy of the section was presented in Egger et al. (2005). Calcareous nannoplankton assemblages of the entire now studied section indicate the *Discoaster multiradiatus* Zone (Zone NP9) in the zonation scheme of Martini (1971). Beneath the claystone the zonal marker fossil co-occurs with common fasciculithids (*F. tympaniformis*, *F. involutus*, *F. schaubii*). Close to the base of the claystone the first specimens of *Rhomboaster cuspis* were found, a species, which is indicative for the upper part of Zone

NP9. Above the claystone, which is devoid of calcareous plankton, *R. cuspis* co-occurs with *Discoaster araneus* and *D. mahmoudii*. The stratigraphic ranges of both species are restricted to the CIE interval within the Zone NP9 (see Egger et al. 2005, 2017). Planktonic foraminifera assemblages from the base of the section contain *Morozovella subbotinae* and were assigned to the *Morozovella velascoensis* Zone (Zone P5 of Berggren & Pearson 2005 and Wade et al. 2011). The claystone contains an agglutinated fauna dominated by *Glomospira* spp. The marlstone overlying the claystone is also assigned to Zone P5.

Bioturbation structures, consisting of biodeformational structures and trace fossils (Uchman & Wetzel 2011), were studied directly on parting surfaces in the field during "bed-by-bed" inspection and sampling. In the laboratory, the samples were polished mechanically in different plains with use of abrasive paper. Features of ichnofabrics have been observed on the polished and wet surfaces of collected rock samples. Their visibility on photo-images was intensified using Adobe® Photoshop® software. Collected specimens are housed in the Nature Education Centre of the Jagiellonian University (CEP) — Museum of Geology, labelled as Ft.

Results

Trace fossil assemblage

In general, the trace fossil assemblage of the Untersberg section is poorly diverse and consists only of four ichnotaxa (Fig. 2): *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., and *Zoophycos* isp. They are mostly visible in cross section which precludes determinations at the ichnospecies level for most of them.

Chondrites isp. was observed as patches of circular to elliptical cross sections and short segments, occasionally with branches, 0.4–2 mm wide (Figs. 3A–F and 4B). They are cross sections of root-like burrow systems. Smaller forms, with burrows less than 1 mm in diameter (Fig. 3A), probably belong to *Ch. intricatus* and the larger forms (Fig. 3B) to *Ch. targionii* (for morphometric parameters of *Chondrites* see Uchman 1999; Uchman et al. 2012). *Chondrites* is a deep-tier trace fossil that was most likely produced in dysaerobic conditions by chemosymbiotic organisms (Seilacher 1990; Fu 1991).

Planolites isp. is represented by circular or elliptical spots or bars, which 1.4–4 mm wide (Fig. 3C, E). They represent horizontal/oblique, straight, simple flattened cylinders without any wall. *Planolites* is a pascichnion produced by several different soft-bodied invertebrates in marine and non-marine environments (Pemberton & Frey 1982; Keighley & Pickerill 1995).

Thalassinoides isp. is visible as circular or oval spots and bars, 4–21 mm wide (Fig. 3C–E), which represent straight, horizontal to oblique, locally vertical, branched cylinders. *Thalassinoides* is a domichnial (i.e. dwelling) and fodinichnial (i.e. feeding) structure produced by arthropods, mostly

decapod crustaceans; it occurs in a great variety of different marine environments (Frey et al. 1984; Ekdale 1992; Schlirf 2000).

Zoophycos isp. is represented by horizontal or subhorizontal stripes, 1.5–3.5 mm, filled with arcuate structures, locally with elliptical pellets (Fig. 3F). They are cross sections of planar spreite structures with a marginal tunnel and represent a larger, three-dimensional, probably helical trace fossil. *Zoophycos* has been interpreted either as a feeding structure (fodinichnia; Seilacher 1967; Werner & Wetzel 1982; Ekdale & Lewis 1991; Olivero & Gaillard 1996), or a combination structure produced by deposit-feeding and chemosymbiotic (Bromley &
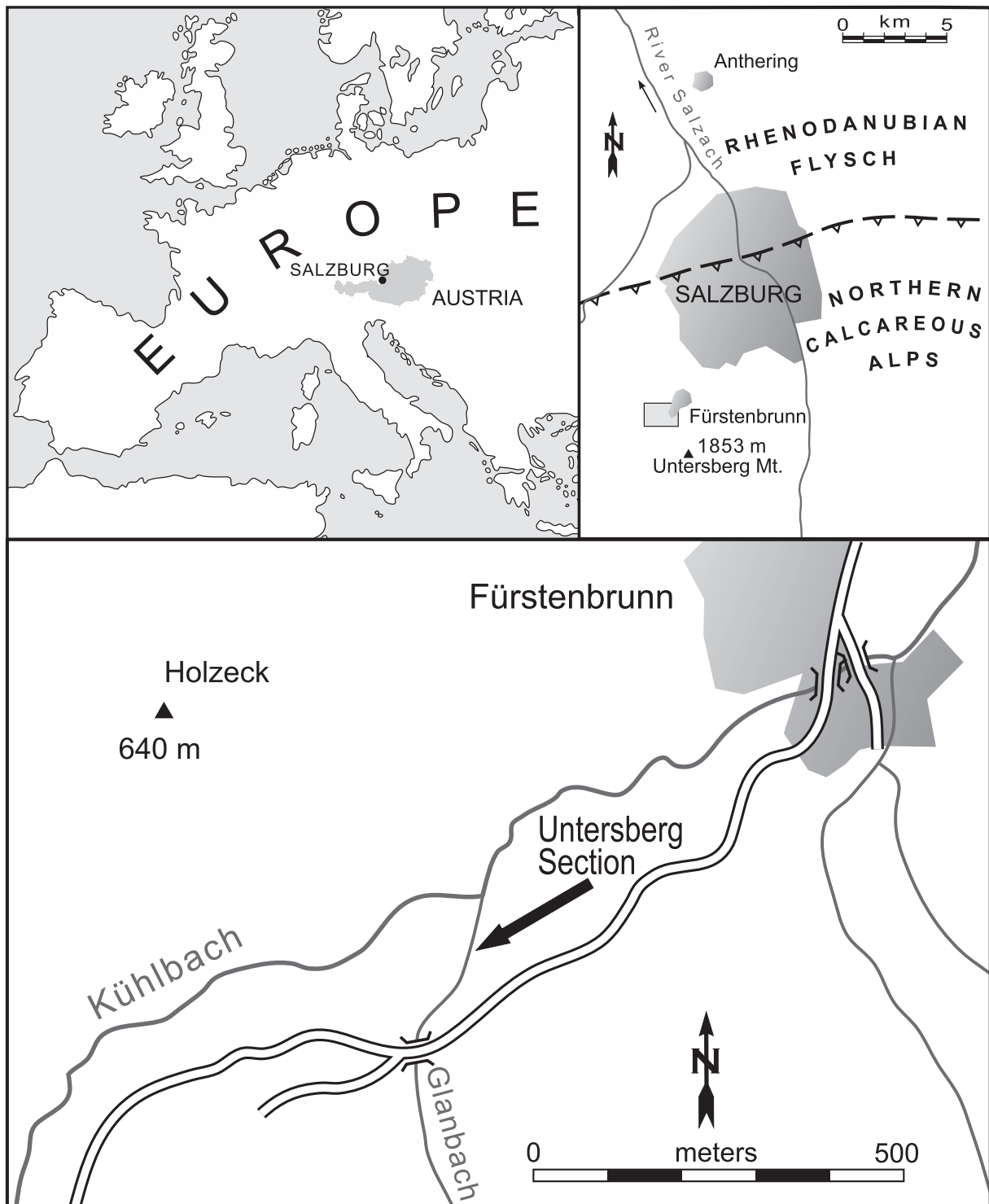

Fig. 1. Location of the Untersberg outcrop.

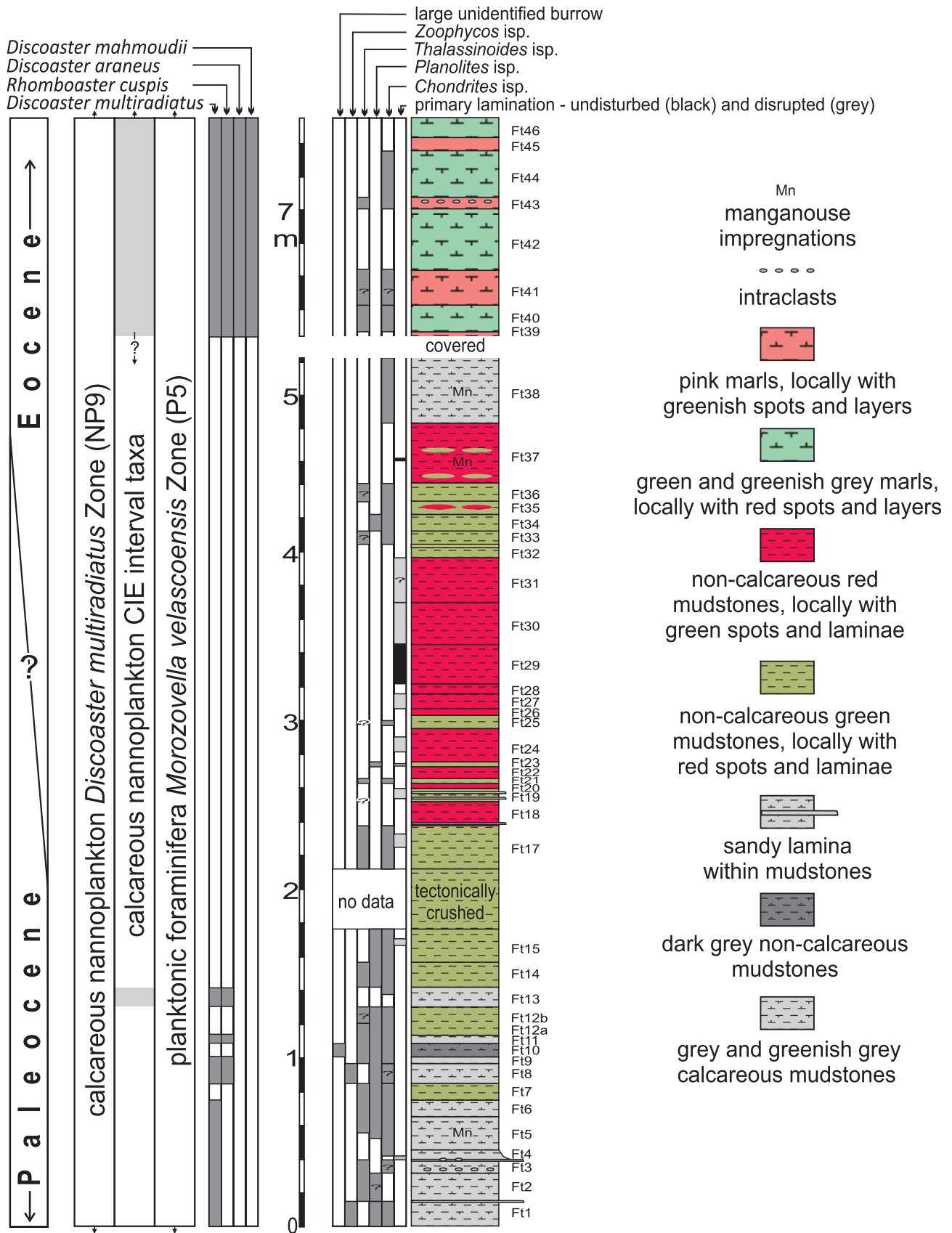UCHMAN, EGGER and RODRÍGUEZ-TOVAR

Fig. 2. Stratigraphic column of the Fürstenbrunn section with indication of sedimentary and biogenic structures, stratigraphically important calcareous nannoplankton taxa and biostratigraphic zonations.

Hanken 2003) invertebrates of unknown origin, which ingest organic detritus and accumulate fecal pellets in a subsurface structure (Löwemark et al. 2006). Recent studies can be found in Löwemark (2012, 2015), Kotake (2014), Zhang et al. (2015a,b), Dorador et al. (2016), and Monaco et al. (2016a).

A large unidentified burrow was observed in the field (level of sample Ft10) as an oval spot, 20–30 mm wide. Its ichnotaxonomic affinity remains unknown, but *Scolicia* (an irregular echinoid burrow) or a larger *Thalassinoides* can be assumed.

Trace fossil abundance and distribution

In modern oceans, bioturbated pelagic sediments show a subdivision into two parts: (1) the up to 10 cm thick, smooth near-surface mixed layer, where the majority of burrowing organisms occur (Boudreau 1998, 2004), and (2) the underlying more consolidated transitional layer, which is affected only by deep burrowing organisms (Ekdale & Berger 1978; Berger et al. 1979; Bromley 1990, 1996). The interpretation of trace fossil assemblages is mainly based on the preservation of burrows, the cross-cutting relationship and their tiering arrangement in the sediment. As a general rule, traces with sharp outlines were produced deeper, and later, in more compacted sediment than less distinct traces. Deeper traces cross cut more shallow traces.

The trace fossil distribution pattern at the Untersberg section shows a clear three-fold subdivision (Fig. 2). The highest abundance and diversity of trace fossils was recognized in the lower part of the section (0–2.40 m), where *Chondrites* isp., *Planolites* isp., *Thalassinoides* isp., *Zoophycos* isp., and large unidentified burrows occur. All ichnotaxa show a more or less consistent record, with the exception of *Zoophycos* and the undeterminable large burrows, which are restricted to a few horizons. These horizons indicate an episodic increase in nutrients on the sea-floor (Löwemark 2015). The major part of the deposits consists of grey and greenish grey mudstone with occasional presence of red coloured spots and layers. This mottled mudstone is attributed to near-surface mixed layer bioturbation. Local exclusive presence of disrupted primary lamination suggests that the uppermost part of the mixed layer was temporarily bioturbated.

The middle part of the section (2.40–4 m) consists of non-calcareous red coloured mudstone, which predominantly shows disrupted primary lamination indicating very shallow burrowing. *Chondrites* isp., *Planolites* isp., and *Thalassinoides* isp. are the only trace fossils, which are exceedingly rare in this interval. Around 3.10 m from the base, a 0.3 m thick layer does not possess any indicators of bioturbation and displays undisturbed sedimentary lamination.

In the upper part of the section (4–7.50 m) the same trace fossil genera occur as in the middle part but with a significant increase in abundance and stratigraphic persistence. *Chondrites* shows a more or less consistent record, and *Thalassinoides* is common, while *Planolites* occurs only sporadically. A 5 cm thick unbioturbated layer with primary lamination occurs at 4.60 m of the logged section and records another short hostile

episode negatively affecting bioturbation producing macrobenthos. In some intervals trace fossils are not recognized but unrecognizable bioturbation structures are there.

Discussion

Previous studies (Egger et al. 2005, 2017) revealed a number of environmental changes associated with the Paleocene–Eocene transition at the Untersberg section: (1) a shoaling of the calcite compensation depth by at least 1 km indicated by a lithological shift from marlstone to clayey mudstone, (2) an increase in bottom water oxygenation indicated by a shift from grey to red sediment colours, (3) enhanced continental run-off indicated by an almost 50 % increase in the input of terrigenous quartz and feldspar into the basin, (4) an increase in plankton productivity indicated by increased numbers of radiolarian casts, (5) acidification of surface waters indicated by the occurrences of irregularly shaped discoasterids (*D. araneus* Bukry, and *D. mahmoudii* Bown), and (6) a change to unfavourable ecological conditions at the sea-floor indicated by a depauperation of agglutinated foraminifera assemblages, which consist essentially of *Glomospira* spp. As we demonstrate above, hostile conditions on the sea-floor also affected macrobenthic communities.

The primary sedimentary lamination in the middle part of the Paleocene–Eocene transition at the Untersberg section reveals the absence of a bioturbating benthic macrofauna. A similar red laminated horizon is recorded at the Paleocene–Eocene interval at the Zumaia section at the Bay of Biscay, Spain (Rodríguez-Tovar et al. 2011a). In contrast to laminated horizons at other PETM sections (Dee Marl in Nicolo 2008; Nicolo et al. 2010) the Untersberg and Zumaia sections display red rock colours, which suggest oxic conditions on the sea-floor (Rodríguez-Tovar et al. 2011a; Wetzel & Uchman 2018 and references therein). Consequently, we assume that oxygenation of deep-sea waters was not the critical factor for the collapse of the benthic ecosystem there.

The red sediment colour indicates that all decomposable organic matter enclosed had been decomposed prior to burial and/or the input of organic matter was very low, thus minimizing the potential for oxygen consumption by decaying organic matter (in contrast to the interval before and after the PETM event). Such oligotrophic sediment will not attract burrowing organisms. However, low organic matter content in red mudstones does not necessarily reflect a low primary content of organic matter as shown for some of the so-called variegated shales in the Carpathians on the basis of ichnological analysis, where red turbiditic mudstones are deeply bioturbated and relatively higher primary organic matter content by oxidation and consumption by organisms (Wetzel & Uchman 2018). At many sites, variegated shales are intensively bioturbated (Leszczyński & Uchman 1993). Therefore, it is unlikely that oligotrophic conditions caused the disappearance of the benthic community at the Untersberg and Zumaia sections.
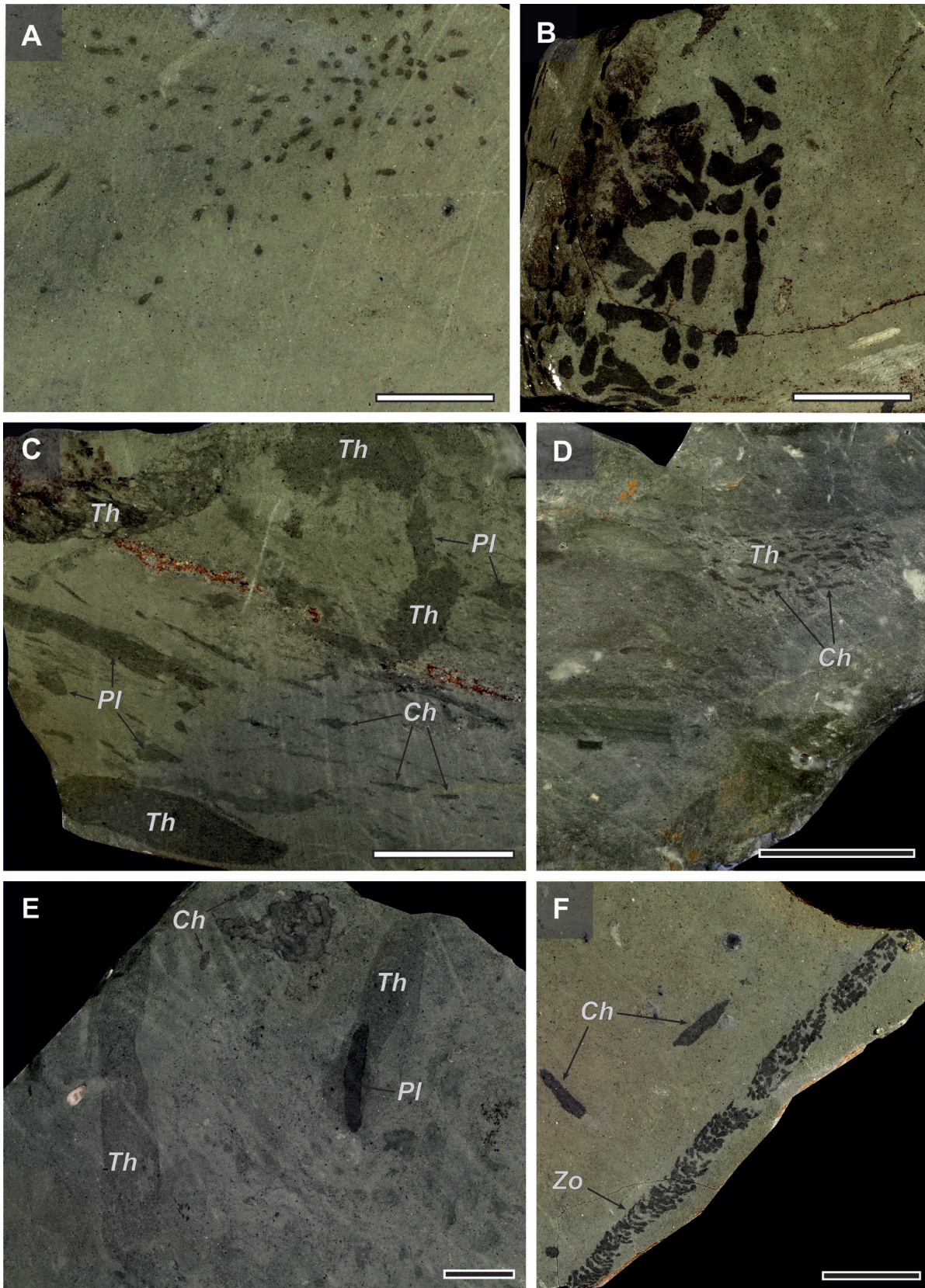
Fig. 3. Trace fossils from the Fürstenbrunn section: **A** — *Chondrites* isp., sample Ft12b; **B** — *Chondrites* isp., sample Ft5, horizontal section; **C** — *Chondrites* isp. (*Ch*), *Planolites* isp. (*Pl*), *Thalassinoides* isp. (*Th*), sample Ft9, vertical section; **D** — *Chondrites* isp. (*Ch*) in *Thalassinoides* isp. (*Th*), sample Ft17, vertical section; **E** — *Chondrites* isp. (*Ch*), *Planolites* isp. (*Pl*), *Thalassinoides* isp. (*Th*), sample Ft11, horizontal section; **F** — *Chondrites* isp. (*Ch*) and *Zoophycos* isp. (*Zo*), sample Ft1, horizontal section. Scale bar is 1 cm.
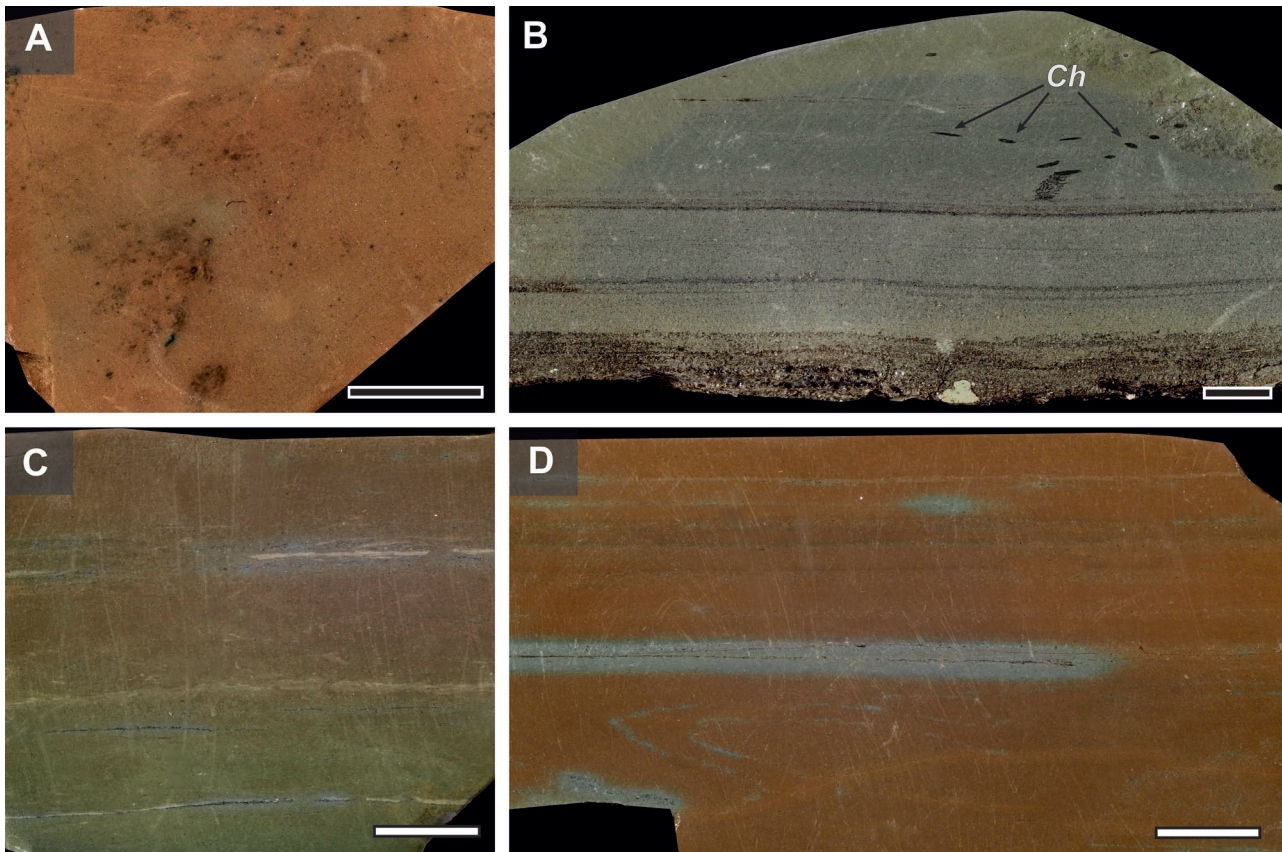
Fig. 4. Primary lamination and bioturbation structures from the Fürstenbrunn section: **A** — Bioturbation structures, sample Ft18, horizontal section; **B** — Horizontal lamination in the lower part of bed and with *Chondrites* isp. (*Ch*) in the upper part, sample Ft4, vertical section; **C** — Interrupted horizontal lamination, sample Ft25, vertical section; **D** — Horizontal lamination, sample Ft29, vertical section. Scale bar is 1 cm.

In the Untersberg section, abundant radiolarian casts suggest high surface water productivity, which was probably triggered by the enhanced terrigenous input into the ocean during the Paleocene–Eocene transition. This increased continental run-off is documented in many sections on a global scale and is attributed to hydrological changes and to a sea level fall at the Benthic Foraminiferal Extinction Event (see Pujalte et al. 2016). This seems to be contradictory to the notion of oligotrophic conditions on the sea-floor during that time. However, Ma et al. (2014) suggested that an increase in surface water productivity may not necessarily result in high carbon burial in the sediments if the sinking particulate matter is efficiently regenerated by increased bacterial activity and converted to dissolve inorganic and organic carbon. This process can be stimulated by high seawater temperatures. Climate model simulations indicate that mid- and high-latitude sea-surface temperatures (SST) met or exceeded modern tropical temperatures at the P–E boundary, and predict tropical SSTs higher than 35 °C (see Frieling et al. 2017, for a review).

The complex interaction of variable limiting factors

According to the above, other environmental changes than changes in oxygen concentration could have a major relevance during the Paleocene–Eocene transition at the Untersberg section. Thus, other reasons for the benthic crisis can be taken into consideration:

- As deep sea burrowing organisms are well adapted to a life below the CCD, the carbonate solution cannot be a factor influencing the distribution of trace fossils. However, the presence of calcium carbonate in sediments influences the shear strength and may positively influence the preservation of trace fossils (Ekdale et al. 1984). Nevertheless, any influence of this factor is not observed at the Untersberg section.

- A significant increase in deep-sea water temperature during the Paleocene–Eocene transition, even by 15 °C compared to the present, was postulated by Brass et al. (1982) and Shackleton (1986). Bowen et al. (2006) estimated an increase in the temperature in the deep sea by c. 4–5 °C and the ocean surface waters at all latitudes by c. 5–9 °C. Such warming could be responsible for a collapse of benthic ecosystems dominated by groups adapted to cold waters.

- Low sedimentation rates, which are important factors controlling the deposition of the oceanic red beds (Wang et al. 2005) negatively impact the burial of organic matter. Therefore, it is very probable that burial of particulate organic matter was very low in the red sediments of

the Untersberg section. For the Zumaia section, Rodríguez-Tovar et al. (2011a) suggested that food for burrowing organisms just concentrated in the shallowest sediment depths, with deeper depths being food-depleted. However, it is an open question whether this extreme situation, where the food is completely absent in most of the sediment, indeed leads to very limited bioturbation. There are no recent equivalents of such conditions.

- Some authors assumed (e.g., Brass et al. 1982) that hypersaline bottom-water changed ecological conditions at the floor of the deep-sea across the Paleocene–Eocene transition. This would have a severe effect on macrobenthic life, even if oxygen was available. However, no evidence of hypersalinity, such as evaporitic minerals, was found in the investigated section or elsewhere.

- Another scenario will be the presence of methane clathrates, which will be dissociated with increasing bottom water temperature. With increasing temperature, dissociation of oceanic methane caused the enormous increase in the light carbon isotopes characteristic for CIE and causing further warming (e.g., Dickens 2000). The methane can saturate pore waters and prevent functioning of burrowing macroorganisms.

Thus, a single and conclusive interpretation of lacking bioturbation structures during the PETM at the Unterberg section is difficult, and a complex scenario, with the interrelation of several factors, is possible.

Conclusion

Ichnological analysis conducted at the Paleocene–Eocene transition at the Untersberg section reveals a complex scenario of environmental changes negatively affecting the macrobenthic tracemaker community. The occurrence of laminated oceanic red beds suggests that the extinction of the macrobenthic tracemaker community in the earliest Eocene was not generated by dysoxic or suboxic bottom waters. The distinct change from grey to red sediment colours at the onset of the extinction event, rather indicates that bottom-water oxygen concentrations increased. This change is interpreted as the result of an efficient regeneration of organic matter by increased bacterial activity in the water column due to a significant increase in water temperature and/or reduced export of organic matter to sediment leading to low nutrient levels on the sea floor.

Regardless of the scenario behind the severe crisis in the burrowing activity, the occurrence of laminated red sediments confines the stratigraphic position of the PETM, with unprecedented precision.

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