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THE TRACE FOSSIL *CHONDRITES* IN UPPERMOST JURASSIC–LOWER CRETACEOUS DEEP CAVITY FILLS FROM THE WESTERN CARPATHIANS (CZECH REPUBLIC)

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Abstract: The common marine trace fossil *Chondrites* occurs in thin layers in laminated micrites which fill deep submarine cavities in peri-reefal biocalcarenites and calcirudites of the Tithonian-Berriasian Stramberg Limestone. The cavity fills display several generations which originated during long periods of time. Periodic colonization of this very stressful environment by the *Chondrites* trace maker was possible probably owing to episodic deposition of more oxygenated and more nutritious sediment at a certain stage of development of the cavities related to increased tectonic activity during the Berriasian. In more bioturbated laminae ?*Palaeophycus* also occurs. The occurrence of *Chondrites* in fillings of deep cavities represents new evidence for adaptation of its trace maker to stressful environments.

Key words: Jurassic, Cretaceous, Western Carpathians, Czech Republic, peri-reefal cavities, cryptobionts, trace fossils, *Chondrites*, *Palaeophycus*.

Introduction

Chondrites Sternberg, 1833, is one of the commonest invertebrate trace fossils in Phanerozoic marine deposits. It occurs in a wide spectrum of environments from nearshore to the deep-sea, including occurrence in different high-stress environments. It is widely known from organic-rich, oxygen-deficient environments, where it occurs commonly as the first trace fossil in the transition from anaerobic to dysaerobic deposits (e.g., Bromley & Ekdale 1984; Savrda & Bottjer 1994). In flysch deposits, *Chondrites* represents the last, deep colonization of turbidites under conditions of decreased food and oxygen content in sediments (Wetzel & Uchman 2001). *Chondrites* is also common within a low-diverse trace fossil assemblage in well-oxygenated, organics-poor, deep-sea variegated shales, where it is related to strong oligotrophy (Leszczyński & Uchman 1993). It also occurs in brackish (Wightman et al. 1987; Pemberton & Wightman 1992) and hypersaline deposits (Gibert & Ekdale 1999).

Surprisingly, *Chondrites* occurs in fillings of deep cavities in the Stramberg Limestone of the Kotouč quarry in Štramberk (Moravia, Czech Republic) (Fig. 1). *Chondrites* appears here in distinct horizons providing a new insight into the problem of filling of the cavities. The aim of the present contribution is to describe and interpret the occurrence of *Chondrites* in this environment, which is uncommon in the fossil record, that is in the fill of submarine cavities within peri-reefal limestones.

Geological setting

Several huge limestone bodies composed mostly of Tithonian to Berriasian limestones and locally of accompanying Lower Cretaceous carbonate and siliciclastic rocks occur at Štramberk in northern Moravia in the Czech Republic (e.g., Houša 1975, 1990) (Fig. 1). There are four main bodies, from several hundred metres up to 1 km long, and dozens of smaller bodies (tens of metres across) in their close neighbourhood. All the bodies are isolated from the strata originally underlying them, but they are partly accompanied by their original sedimentary cover of flysch deposits of the Silesian Nappe of the Carpathians.

The Stramberg Limestone is dominated by Tithonian-lower Berriasian biocalcarenites and calcirudites with local blocks of true biohermal limestones. They represent peri-reefal accumulations; bioherms preserved *in situ* have not been recognized. They were deposited on the so-called Baška Elevation. The peri-reefal sedimentation persisted till the calpionellid C. ferasini Subzone (Early Berriasian). The following C. elliptica Subzone is not reliably documented. Probably, at the time interval of this zone, the Baška Elevation was partially emerged, and reef and peri-reefal sedimentation was terminated. The emergence corresponds to the global Early Berriasian eustatic sea level fall (Houša 1990). It was followed by a new sedimentation cycle represented by argillaceous limestones (Olivetská hora Member), which contain calpionellids of the C. simplex Subzone. As the successive C. oblonga Subzone was not ascertained, it presumably represents the time interval of the next phase of emergence of the Baška Elevation. Sedimentation took place in the late Valanginian again. Deposits of the Gloriet Formation, which contains pelites, conglomerates and blocks of the Stramberg and Olivetská hora Limestones, accumulated at that time. Sedimentation continued till the Hauterivian, represented by the deposits of the Plaňava Formation, which is dominated by black pelites with blocks of the Stramberg and Olivetská hora Limestones. Barremian, Albian, and early Aptian sediments are not documented in the

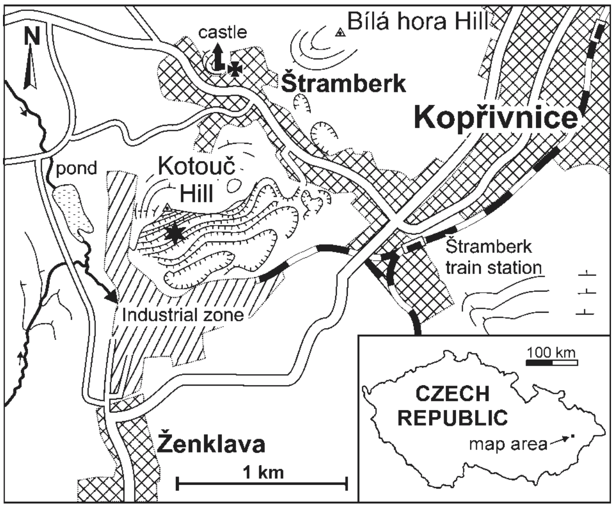

Fig. 1. Location map. The occurrence of the cavities described in the Stramberg Limestone is marked by asterisk.

area. During this period, we presume a long-lasting break in sedimentation of the Stramberg Limestone and its karstification. The karst cavities of that age are filled with poorly sorted conglomerates (Chlebovice Formation), which contain pebbles mostly from the Stramberg Limestone, and less commonly from all the above-mentioned Early Cretaceous formations (Houša 1990).

To summarize, Early Cretaceous sedimentation was interrupted by three main emergence episodes corresponding to eustatic sea-level falls. Probably, it was also influenced by local tectonic activity, which was responsible for formation of deep and narrow fissures in the Stramberg Limestone. The fissures are filled with upper Lower Cretaceous deposits (Houša 1965) and represent places of unique epifaunas on their walls (Houša 1974) and interesting bioerosion (Mikuláš 1992).

Cavities in the Stramberg Limestone

Contemporaneously with sedimentation of the Stramberg Limestone, various cavities, several decimetres to more than 1 m across, formed in the rising body (Houša 1964). They were partly formed by falls of huge limestone blocks; some of them, however, are found in calcarenites and thus they might have originated at places within bodies that were capable of decay, leading to a cavity (e.g., wood, algal masses). The roof and side walls of the cavities are usually covered with stromatolitic crusts. The fill of the cavities is complex. Several generations of mainly marly micritic limestones can be observed. The succession corresponds to the order of sedimentation on the Baška Elevation during the Late Jurassic and Early Cretaceous. However, each cavity shows its own peculiar features.

Houša (1964) distinguished the following generations of the filling of the primary cavities in a stratigraphic order (Fig. 2): (Ia) (the author's original acronym) finely laminated micritic limestone of the same lithology as the Stramberg Limestone, covering the uneven floor of the cavity. Certain laminae contain numerous ooids and pseudo-ooids; (Ib) micritic limestone with convolute-structure; (Ic) rhythmically stratified light to dark yellowish-green argillaceous limestone with "burrows". Its lithology is very similar to the Olivetská hora Limestone; (Id) thicker layer of yellowish-green argillaceous limestone identical to Ic; and (II) yellowish-green calcareous claystone to argillaceous limestone identical to a terminal generation of the fill of the "fissures", that is greenish-yellow argillaceous limestones (Houša 1965). Some of the generations may be missing in some cavities. The filling material of the cavities, especially the generations Ib to II, contrasts lithologically with the surrounding rock, which is composed mostly of biocalcarenites, biocalcirudites and biolitites. The "burrows" from generation Ic and Id are referred to as *Chondrites* in this paper.

According to Houša (1964), generation Ia is contemporaneous with the reef sedimentation and therefore it is Tithonian to earliest Berriasian in age. In the beginning, the cavities were connected to the sea floor only by pores in the detrital substrate. Later, as the reef body was tectonically elevated, thin fissures appeared, connecting the cavities with the sea floor. Contemporaneously, large and deep fissures appeared. They were called "fissures of the Štramberk generation" by Houša (1964). Generation Ib probably corresponds to termination of sedimentation of the Stramberg Limestone and the related short hiatus. Generations Ic and Id originated presumably contemporaneously with the Olivetská hora Limestone (late Berriasian). Generation II, richest in clay minerals, originated very probably contemporaneously with the terminal phase of fill of the "fissures of the Olivetská hora generation" (Houša 1964). These argillaceous limestones have no analogue among the adjacent Cretaceous formations, and do not contain any fossils. They probably belong to the late Valanginian.

We presume that nearly all cavities were only connected with the sea floor through thin fissures which were always formed together with widening of large fissures during the above-mentioned uplift phases of the Baška Elevation. As new

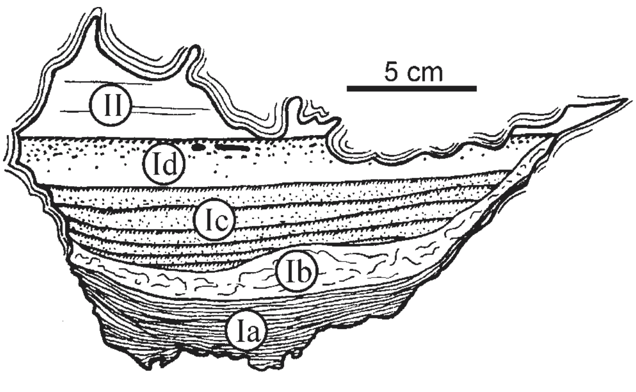

Fig. 2. Schematized section of a cavity in the Stramberg Limestone and its fill. Drawn according to Houša (1964) and collected samples of fill of cavities. **Ia–Id**, **II** are generations of the fill as described in more detail in the text. The ceiling and roof of the cavity is covered with a stromatolitic growth which occur typically on cavity roofs, but may also cover walls and bottoms. For details of Ic–Id generations see photographs on Figs. 3C and 4A.

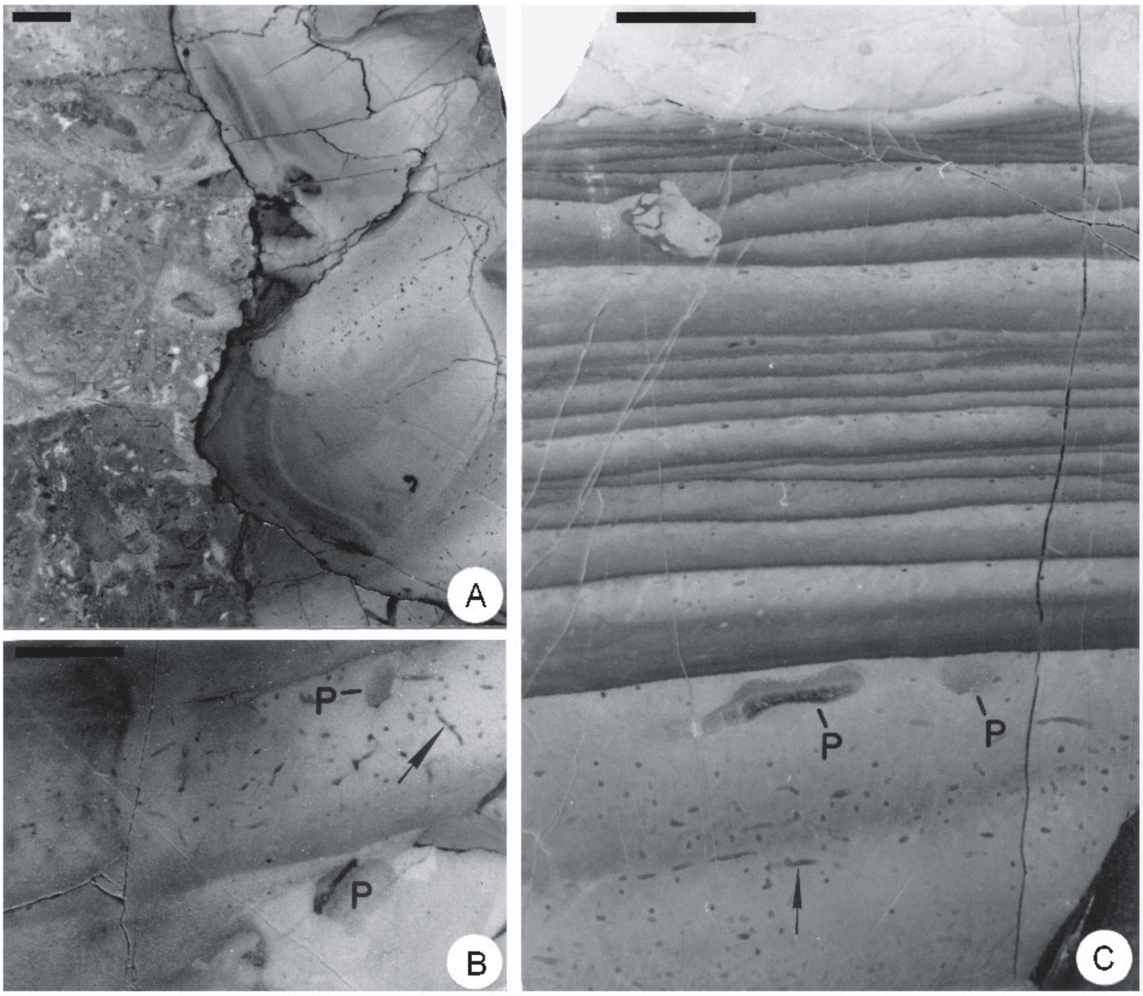

Fig. 3. Filling of the cavities from the Stramberg Limestone. Scale bars = 1 cm. **A** — Contact of the filling (to the right) with calcarenites of the Stramberg Limestone (to the left); **B** — fragment of the filling with *Chondrites* (an example indicated by the arrow) and ?*Palaeophycus* (P); **C** — fragment of filling of "cavity 1964", floor No. 4 of the Kotouč quarry (after Houša 1964: pl. I, fig. 2). Bioturbated laminae of the Ic (in the middle and lower upper part) and Id generations (in the lower part) with *Chondrites* (arrow) and ?*Palaeophycus* (P).

space within large fissures became filled and thin fissures were stopped up, sedimentation in cavities became extremely slow or halted.

Up to now, several dozens of cavities have been observed in walls of the Kotouč quarry. Numerous samples of their fill are stored in the Institute of Geology, AS CR, Praha, and in the Jagiellonian University, Kraków. The Institute of Geology also owns a photographic documentation of the former quarry walls. In spring of 2000, dozens of filled cavities were observable in the quarry walls of floors Nos. 5 and 6 of the Kotouč quarry, but only one cavity having generation Ic containing *Chondrites* was easily available at floor No. 6 (Fig. 1).

Chondrites and its host deposits

The cavity filling containing *Chondrites* was classified by Houša (1964) as generations Ic and Id. Both generations are composed of laminated micrite. In generation Ic (Figs. 2, 3C, 4, 5) the laminae are parallel, 5–12 mm thick. The limestone displays different colour zonation from light-grey, grey to yellow-grey. Boundaries of the laminae are sharp or slightly diffuse at a distance of about 1 mm. There are also a few centimetre-thick bundles of hummocky laminae between the parallel laminae (Figs. 3C, 4B). They are uneven, with smooth, irregularly wavy boundaries. Individual laminae display swellings and narrowings. They are at most 4 mm thick in the swellings.

In generation Id (Fig. 2), the micrite is light-grey, grey, dark-grey and yellow-grey in colour. The lamination is indistinct and is marked by the occurrence of *Chondrites*. The filling is cross-cut by dark stylolites (Fig. 3A). Locally, stylolites occur at the boundary of this lithology. In the filling, irregular patches of very fine, stromatolitic-like lamination are present (Fig. 4A).

Chondrites has been observed in vertical and horizontal sections in polished slabs and in thin-sections. It occurs as groups of small dots and single or branched straight bars (Figs. 3B–C, 4, 5, 6), which are cross-sections of slightly curved tunnels branched in a dendroid manner, similarly to other occurrences

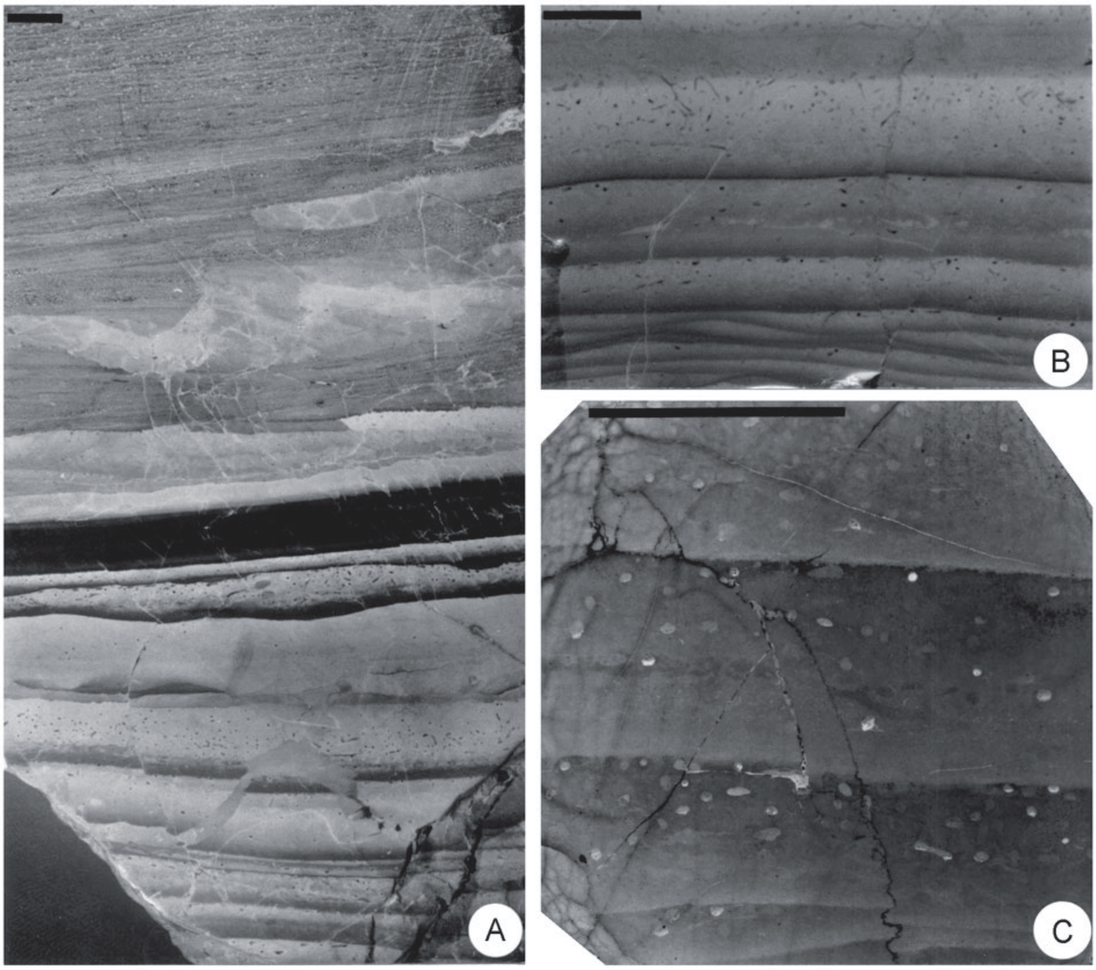

Fig. 4. Other examples of filling of the cavities from the Stramberg Limestone. Scale bars = 1 cm. **A** — Fragment of filling of the "cavity 1981", floor No. 4 of the Kotouč quarry. The bioturbated Ic generation (lower part) with *Chondrites* (close view in Fig. 5) and the overlying generation II (middle and upper part); **B** — the generation Ic with *Chondrites*. The hummocky lamination in the lower part; **C** — detail of B in a thin section. Some *Chondrites* tunnels exhibit geopetal filling.

(e.g., Werner & Wetzel 1981; Ekdale & Bromley 1991; Wetzel & Uchman 1998). The tunnels are 0.3 to 0.5 mm wide and differently oriented to the bedding. The tunnels are usually filled with slightly darker and coarser material than the host rock or with blocky calcite cement. Combinations of these two types are also present, where the blocky cement occurs as geopetal structures (Fig. 4C). The tunnels filled with micritic limestone are often surrounded by a diagenetic "halo" up to 1 mm thick (Fig. 3C).

The small size and simple morphological elements suggest that the analysed form is a small *Chondrites intricatus* (Brongniart, 1823). This ichnospecies was discussed, for instance, by Fu (1991) and Uchman (1999). As the individual tunnels are rarely branching and we cannot observe a radial structure of the system, they resemble the ichnogenus *Pilichnus* Uchman (1999), but the latter displays long, exclusively horizontal tunnels.

In generation Ic, *Chondrites* occurs in the upper part of the parallel laminae up to 8 mm from their top. In some laminae, the zone with *Chondrites* is only 1–3 mm thick, and in other laminae it does not occur at all. Some of the laminae devoid of

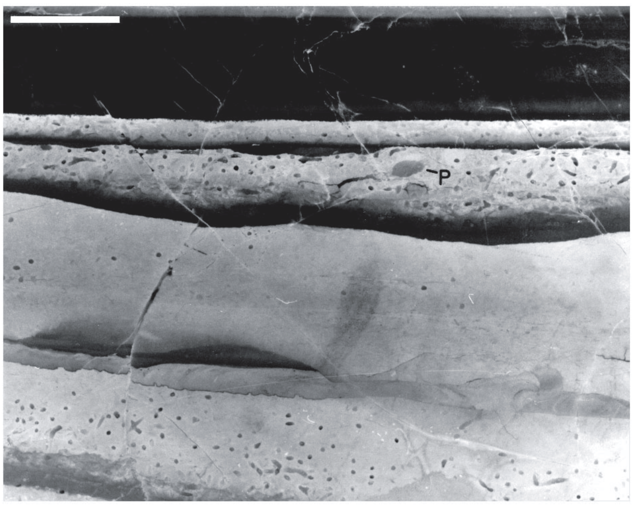

Fig. 5. Detail of Fig. 4A. Dark non-bioturbated laminae in the upper part. *Chondrites* and ?*Palaeophycus* (P) in other laminae. Scale bar = 1 cm.

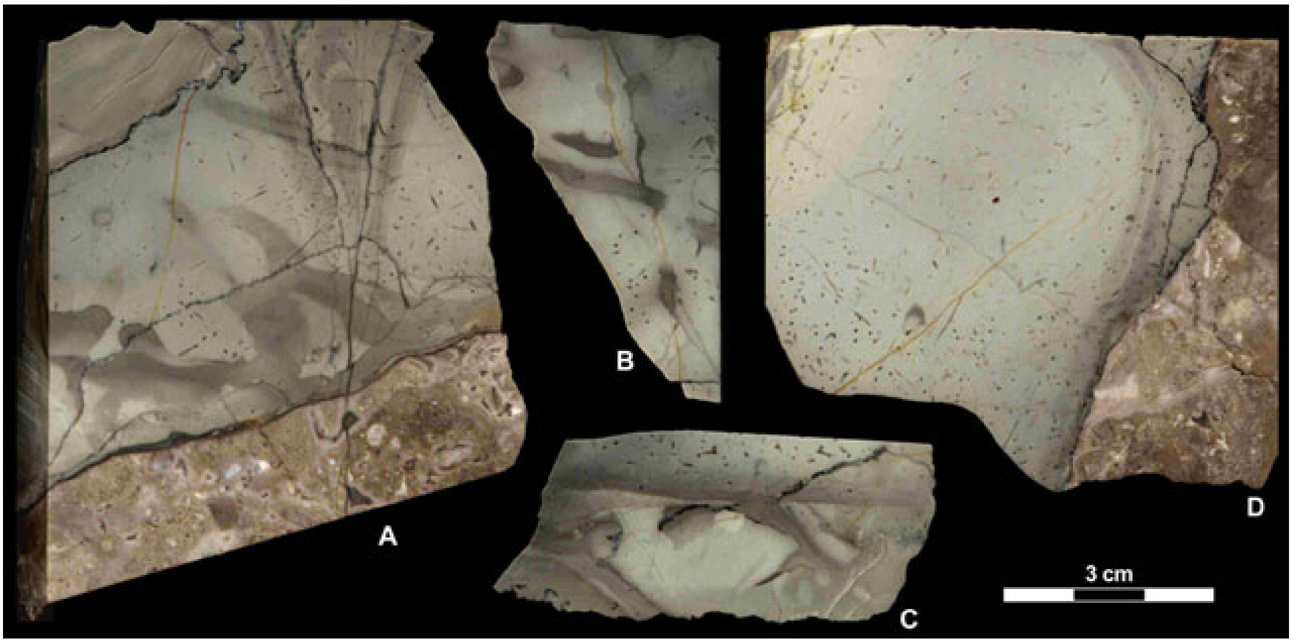

Fig. 6. Horizontal cross-sections of the described trace fossils. **A, D** — *Chondrites intricatus* (Brongniart, 1823). Contact of the filling with calcarenites of the Stramberg Limestone clearly visible. **B, C** — *Chondrites intricatus* (Brongniart, 1823) and ?*Palaeophycus* isp. Scale bar = 3 cm.

Chondrites are dark (Figs. 4A, 5). No *Chondrites* cross-cuts the laminae boundaries. It is the only trace fossil in most of the laminae examined. However, two of the laminae of the Ic generations, from two different cavities, also contain sections of a tubular, subhorizontal, slightly curved trace fossil, 2.0–2.5 mm in diameter, lacking discernible or having indistinct wall lining but apparently uncollapsed (Figs. 3A–B, 5). It may be classified as *Palaeophycus tubularis* Hall, 1847 (Pemberton & Frey 1982; Keighley & Pickerill 1995) if we presume that the wall is not a diagenetic effect. Provided the tunnels were originally unlined, they might be better referred to as *Planolites* Nicholson, 1873 (Pemberton & Frey 1982). Regardless of these doubts, it is very probably that all the described 2.0–2.5 mm thick tunnels represent the same ichnotaxon. As we cannot solve the problem under the present material, we leave the ichnotaxon in the open nomenclature as ?*Palaeophycus* isp.

In generation Id, *Chondrites* occurs in 8–25 mm thick zones (Fig. 3C). The thickest zone also contains sections of a tubular trace fossil, about 2 mm in diameter, with a thin wall, which is probably ?*Palaeophycus* isp.

Discussion

Trace fossils in cavities

Fauna exclusively inhabiting cavities (also called cryptic fauna, cryptos, cryptobionts, or coelobites) is known mostly from reef environments (see summary by Kobluk 1988b, who also reviewed pre-Cenozoic reef organisms; Kobluk 1988a). Most of animal cryptobionts are represented by sessile or vagile epibenthos. Infaunal soft-substrate cryptobionts are less known. Among them, trace fossils are the most obvious record of infaunal activity in cavities, but literature on the topic is very scarce. James & Kobluk (1978); Kobluk & James (1979) and Pemberton et al. (1979) mentioned trace fossils in filling of cavities in the Lower Cambrian reefs of Labrador in Canada, which include *Palaeophycus*, ?*Teichichnus*, *Torrowangea*, and three other unidentified forms (Kobluk 1988a). Most published data on trace fossils in cavities concern borings in hard substrates (e.g., Palmer & Fürsich 1974; Bromley & Asgaard 1993; Wilson 1998).

The case of Chondrites

We may presume that the cavities occurred several metres to several tens of metres below the sea floor when the generation Ia was formed. The stromatolitic crust on the cavity walls, produced probably by microbes, indicates that the cavities have been at least partially empty for long periods. The cavities were accessible only for very fine clay and micritic material, which could be strained through pores in the biodetritic substrate. Subsequently, as the bottom became more distant from the cavities, influx of the clay and micrite became weaker and the sedimentation of generation Ia stopped. It was, however, several times restarted, presumably when new thin fissures formed during phases of tectonic uplift of the Baška Elevation. Besides these processes, weak exchange of water enabled growth of stromatolitic ?microbial communities.

Further rejuvenation of tectonic activity was probably contemporaneous with the sedimentation of the Olivetská hora Member. Generations Ic and Id of the cavity fill correspond to this period. Lamination of the fill and concentration of *Chondrites* at the top of individual laminae suggest that the cavities have been filled incidentally. Deposition of individual laminae was rapid. It was followed by colonization of the *Chondrites* trace maker, and of the ?*Palaeophycus* producer for some laminae. The filling of some *Chondrites* is composed of blocky calcite cement, which probably originated in the early stages of diagenesis. This indicates cessation of sedimentation between deposition of laminae and that the sediment was undisturbed by other burrowers.

Penetration of *Chondrites* in the sediment is very shallow, especially in generation Ic. The diameter of the *Chondrites* tunnels is very small here in comparison to the diameters of *Chondrites intricatus* from the Rhenodanubian Flysch of the Alps (Uchman 1999, p. 92). Those facts and the fact that *Chondrites* occurs alone in most of the laminae, and that there is no evidence of intensive bioturbation, suggest an extremely stressful environment. The environment, however, differed in various cavities and changed according to the degree of communication of the cavities to the sea floor. One sample (Fig. 3C) shows a relatively intensive bioturbation (up to 40 % of the substrate volume) and occurrence of ?*Palaeophycus* in one of the first laminae of generation Id. In other cavities, bioturbation is generally weak. Approximately 90 % of the cavities do not display bioturbational structures in their fill.

The stress factors in deep cavities can be variable and related mainly to limited food, and oxygenation, and lack of light. The last factor is not important in the case of *Chondrites*, which occurs in the completely dark deep-sea environments. Low oxygenation in the limited, mostly stagnant environment of deep cavities is very probable. Black laminae (Figs. 4A, 5) are not colonized. The oxygenation may have improved during episodes of deposition, when influx of oxygenated waters, which enabled the colonization, took place. It is difficult to estimate the amount and role of food. Certainly, the cavities are isolated from the fertile plankton rain. *Chondrites* is a stationary structure that is relatively inefficient for deposit-feeding. According to Seilacher (1990) and Fu (1991), the tracemaker of *Chondrites* may have been able to live at the aerobic/anoxic interface as a chemosymbiotic organism, which pumps methane and hydrogen sulphide from the sediments. Deep submarine cavities or fissures can be conduits for these gases, which might be exploited by the *Chondrites* trace maker not only from sediment, but also directly from the water.

Another interesting problem is the occurrence of ?*Palaeophycus* in some laminae, which may indicate improvement of oxygenation. ?*Palaeophycus* occurs in laminae where the zone occupied by *Chondrites* is relatively thick or the intensity of bioturbation is relatively high. *Palaeophycus* is interpreted as a trace of a vagile ?carnivorous organism (Pemberton & Frey 1982) but, in the described case, ?*Palaeophycus* may rather represent a dwelling burrow of a stationary detritus-feeder. There is no evidence of other macroorganisms in the cavities.

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