

BALANOGLOSSITES-DOMINATED ICHNOFABRICS AND DIAGENETIC OVERPRINT IN THE EARLY EMSIAN LIMESTONE-DOMINATED SUCCESSION OF THE PRAGUE SYNFORM

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Abstract. The ichnofossil record of the early Emsian limestone-dominated succession in the Prague Synform, including the Bohemian Graptolite Event beds, was studied with a focus on ichnofabric development and its sedimentological and diagenetic implications. The studied interval yields a diverse ichnoassemblage comprising *Balanoglossites*, *Zoophycos*, *Planolites*, *Taenidium*, *Phycosiphon*, *Trichichnus*, *Polykeladichnus*, *Caulostrepsis*, and possibly *Trypanites*, along with indeterminate biodeformational structures. The trace fossil distribution and fabric arrangement indicate a combined depositional regime characterized by episodic turbiditic influx followed by periods of relative quiescence. Some ichnological features, such as the co-occurrence of *Zoophycos* and *Trichichnus*, are shared between the Bohemian Graptolite Event interval and the uppermost part of the Dvorce-Prokop Limestone, suggesting similar environmental conditions, likely influenced by reduced oxygenation. Notably, the slightly nodular (“knobby”) structure of the studied limestones is closely linked to the presence of a *Balanoglossites*-dominated ichnofabric. This ichnofabric also significantly influenced subsequent diagenetic pathways, including selective dolomitization and silicification.

INTRODUCTION

Research on the Pragian to early Emsian limestone-dominated succession of the Praha Formation (Prague Synform, Barrandian area, Czech Republic) dates back to the 19th century (e.g., Krejčí 1862; Katzer 1888; Kettner 1917). In recent decades, this formation has been intensively studied from multiple perspectives, including biostratigraphy, sedimentology,

sequence stratigraphy, elemental geochemistry, stable isotope analysis, gamma-ray spectrometry, and magnetic susceptibility (e.g., Hladil et al. 1996, 2010; Koptíková et al. 2010a, b; Hladil et al. 2011; Weinerová et al. 2017; Bábek et al. 2018a, b; Slavík & Hladil 2020; Weinerová et al. 2020; Šimíček et al. 2020). In contrast, ichnological data remain scarce.

As part of the Czech Science Foundation project GA21-21829S, several sections were studied in detail with the aim of searching for a candidate for the redefined basal Emsian Global Boundary Stratotype Section and Point (GSSP; Weinerová et al.

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2024; Slavík et al. 2025; Slavík et al. accepted). These sections expose slightly nodular calcisiltites of the Dvorce-Prokop Limestone Member representing a distal environment, and contain a key lithological marker, the Bohemian Graptolite Event (BGE) beds, which is correlated with the *atopus* Event in Morocco (Aboussalam et al. 2015). Detailed analysis of polished slabs, etched samples, and thin sections revealed a previously undocumented complex ichnofabric, with particular attention given to the trace fossil *Balanoglossites*. Although ichnofossils from this unit have been noted since the late 19th century, only a few studies have addressed them in detail. Weissenbach (1931) and Prantl (1944) focused on *Chondrites*-type burrows. Chlupáč (1990) discussed the palaeoenvironmental and sedimentological significance of *Zoophycos*, also noting *Chondrites* and *Monocraterion*-type burrows. Hladil et al. (1996) reported *Zoophycos*, *Chondrites*, *Skolithos*, decapod-like burrows and horn-shaped traces. Mikuláš & Hladil (2015) described a large, star-like trace fossil tentatively assigned to the ichnogenus *Capodistria*, and observed geometrically precise cylindrical *Trypanites* borings. Holcová et al. (2024) documented microborings within bioclasts.

Main objectives of this study are (1) to provide the first comprehensive description of the ichnoassemblages and ichnofabrics of the Dvorce-Prokop Limestone; (2) to contribute to the discussion on the sedimentary processes responsible for the formation of these limestones, where two prevailing models have been proposed—one favouring hemipelagic deposition and the other involving turbiditic input; (3) to assess whether, and how, the ichnological record reflects previously interpreted sea-level fluctuations and climatic changes; and (4) to describe the influence of ichnofabrics on sediment diagenesis.

GEOLOGICAL SETTING

The Prague Synform is an erosional relict of unmetamorphosed Ordovician to Middle Devonian sedimentary and volcanic rocks, which now forms an asymmetrical but almost elliptical structural depression that originated during the Late Devonian (Chlupáč et al. 1998; Melichar 2004; Knížek et al. 2010). During the Devonian, the Prague Synform was located in the peri-Gondwana realm, with affin-

ities to the Armorican Terrane Assemblage, approximately between 20° and 13° south of the equator (Tait 1999; Krs et al. 2001). Accordingly, the fauna show affinities to the Ibero-Maghrebian faunal province of the Rheic Ocean domain (Plusquellec & Hladil 2001). The Devonian sequences of the Prague Synform are subdivided into the Lochkov, Praha, Zlíchov, Daleje-Třebotov, Choteč, and Srbsko formations (Fig. 1B). The marine carbonate sedimentation dominated until the Givetian, when it was replaced by siliciclastic flyschoid sedimentation reflecting an Eovariscan phase of the Variscan orogeny (Chlupáč et al. 1998). Devonian sediments of the Prague Synform show a cyclicity of various orders (Bouček 1964; Chlupáč 2000). Bábek et al. (2018a) described the alternation of two modes in relation to climate-driven changes in organic production: colder episodes resulted in oligotrophic conditions, homoclinal ramp geometry and a good bottom water oxygenation (Praha and Daleje-Třebotov formations), whereas warmer episodes lead to mesotrophic conditions, carbonate platform/distally steepened ramp geometry and less oxic bottom conditions (Lochkov, Zlíchov, and Choteč formations).

Praha Formation

The Praha Formation originally corresponded to the Pragian Stage, which was defined on the basis of the entire thickness of the formation. However, due to the current issues with the basal Emsian GSSP defined in Uzbekistan (Yolkin et al. 1997), its middle and upper parts are now assigned to the Emsian (Carls et al. 2008). As summarized by Chlupáč et al. (1998), the Formation exhibits variable thickness ranging from 35 to 200 m, is composed of rocks of various colours, and shows considerable facies diversity. A general fining-upward trend is observed throughout its succession. Laterally, the facies distribution follows a recurring pattern established since the Upper Silurian, i.e., deeper-water facies prevailing on the SE flank of the basin and a growing proportion of shallow-water facies towards the NW and SW. The Formation is subdivided into several lithostratigraphic members reflecting a transition from shallow to deeper-water environments: Koněprusy Limestone Member (white to light grey, massive or indistinctly bedded, coarse-grained crinoidal limestones) represent shallow-water settings. Transitional environments are represented by Sliveneč and Vinařice Limestone members (pink to red,

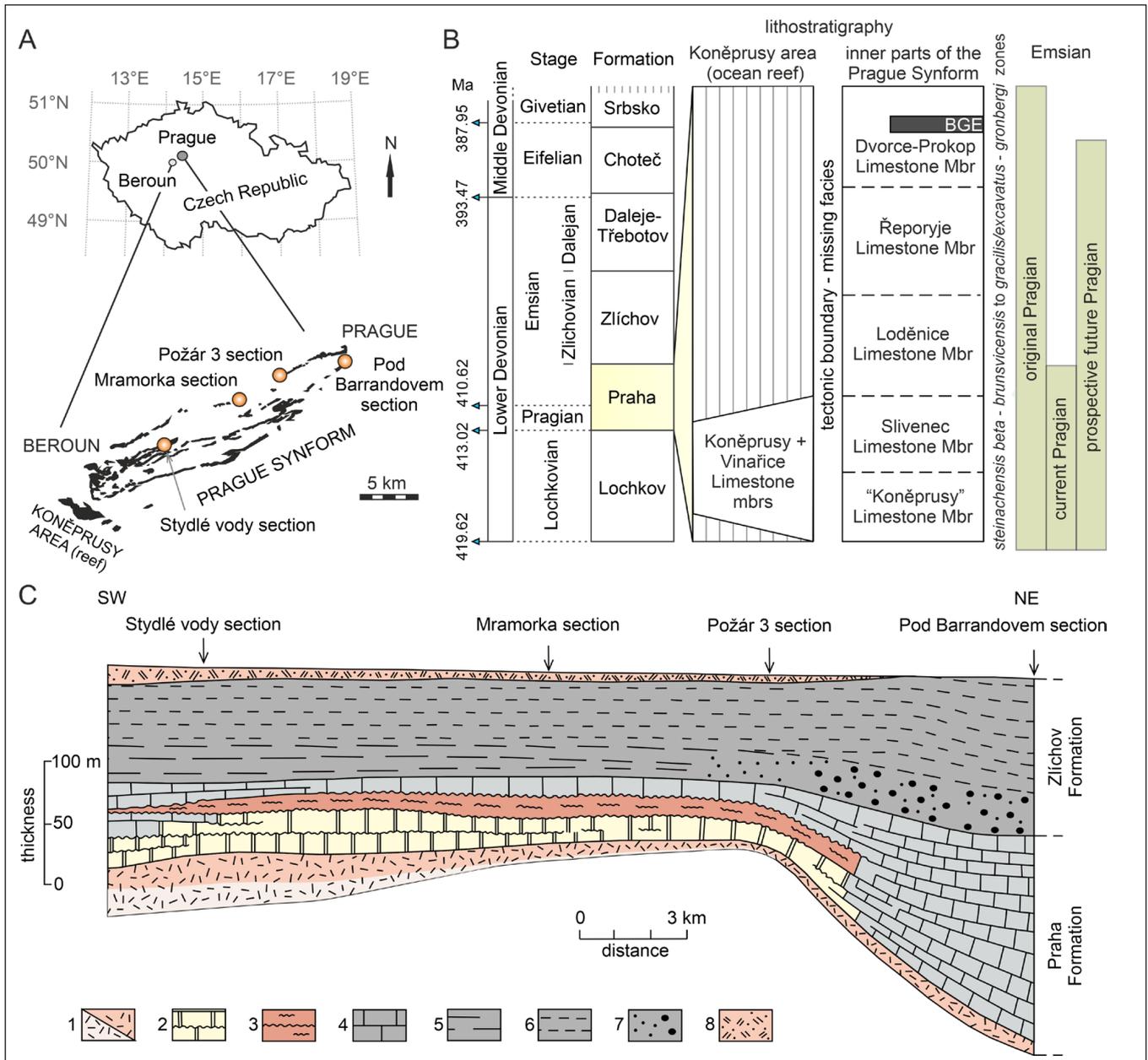


Fig. 1 - A) Distribution of the Praha Formation (Pragian to early Emsian) within the Prague Synform (Melichar & Hladil 1999, modified). B) Devonian lithostratigraphy of the Prague Synform (Bábek et al. 2018a; Slavík & Hladil 2020, modified). C) Facies development of the Praha and Zlíchov formations between the Stydlé vody and Pod Barrandovem sections (Chlupáč 1990, modified). Legend: BGE, Bohemian Graptolite Event; 1, bioclastic, crinoidal Koněprusy Limestone (white/light grey) and Slivenec Limestone (reddish); 2, variegated, platy/slightly nodular, mostly biomicritic Loděnice Limestone; 3, red, nodular, micritic Řeporyje Limestone; 4, grey, nodular and platy, micritic Dvorce-Prokop Limestone; 5, grey, platy, micritic limestones of the lower part of the Zlíchov Formation; 6, grey, thinner-bedded, knobby Zlíchov Limestone; 7, bioclastic and breccia layers of the Chapel Coral Horizon; 8, reddish, bioclastic Chýnice Limestone.

thick-bedded, coarse-grained crinoidal limestones), Loděnice Limestone Member (variegated, platy, fine-grained limestones) and Řeporyje Limestone Member (red, nodular, fine-grained micritic limestones), whereas the deepest environment is represented by the Dvorce-Prokop Limestone Member (grey, nodular to platy, fine-grained micritic limestones). The boundaries between the members are rather transitional, as facies shifted gradually across the ramp (Bábek et al. 2018a).

The depositional environments comprise reef settings, crinoidal meadows, and deeper-marine settings influenced by gravity flows and hemipelagic sedimentation (e.g., Hladil & Slavík 1997; Hladil et al. 1996; Vorel 2006; Weinerová et al. 2017; Bábek et al. 2018a).

A wide range of microfacies has been described from the Praha Formation (Velebilová & Šarf 1996; Čáp et al. 2003; Weinerová et al. 2017; Weinerová 2022). In proximal facies, bryozoans and

crinoids dominate (corals, algae, peloids, and corroids are also present). Towards more distal facies, bryozoans become rare and the abundance of ostracods, brachiopods, trilobites, dacryoconarids, molluscs, and globochaetids increases. In distal facies, dacryoconarids become the dominant group. The most distal facies also contain sponge spicules and radiolarians.

From a sequence stratigraphic perspective (Bábek et al. 2018a), the Praha Formation roughly corresponds to a 3rd-order sequence. The boundary between the Lochkov and Praha formations coincides with a sequence boundary. The basal coarse-grained crinoidal limestones (LST) of the Praha Formation gradually pass into micritic limestones representing the TST and HST, with the BGE interval likely corresponding to the maximum flooding. The overlying Chapel Coral Horizon (a limestone breccia near the base of the Zlíčov Formation) reflects the culmination of the FSST–LST with another sequence boundary. In the shallow water Koněprusy area, the Praha Formation is strongly reduced by hiatuses and contains reef structures (Hladil & Slavík 1997).

Studied sites

The four studied sections exhibit a distinct southwest-northeast proximal-to-distal gradient in both thickness and facies development within the Praha Formation, reflected in varying proportions of coarse-grained, crinoidal, shallower-water facies (Koněprusy and Slivenec Limestone) and deeper-water micritic facies (Loděnice, Řeporyje, and Dvorce-Prokop Limestone) (Fig. 1A, C; Table 1; Chlupáč 1957; Chlupáč & Lukeš 1999; Koptíková et al. 2010a, b): At the Stydlé vody Quarry (also known as Paraple Quarry), the Praha Formation reaches a total thickness of ~85 m, representing the most proximal setting among the studied localities. It shows a large proportion of coarse-grained, crinoidal, shallower-water facies (~40 m) compared to deeper-water micritic facies (~42–49 m). Further distal, the Mramorka Quarry and the Požár 3 section show substantially thinner successions of the Praha Formation (~44–56 m), with a reduced proportion of shallower-water facies (~9.5–12 m) and more prominently developed deeper-water facies (~33–44 m). The most distal expression of the Praha Formation is observed at the Pod Barrandovem section, where its exposed succession reaches ~173 m, to

which ~10 m missing at the base should be added (see Da Silva et al. 2016). Here, the shallower-water facies are considerably reduced (? up to ~20 m, including missing parts), while deeper-water facies dominate (~165 m). The unusually high total thickness at this site is attributed to enhanced subsidence (e.g., Bábek et al. 2018a). The base of the overlying Zlíčov Formation and the Zlíčovian Stage is also defined in this section (Chlupáč 1957, 1981). Just above this boundary lies a richly fossiliferous limestone breccia known as the Chapel Coral Horizon. These localities were subjected to many previous studies (e.g., Kettner 1917; Prantl 1939; Petránek 1951; Chlupáč 1955, 1957; Lukeš 1982; Chlupáč 1990, 1993; Chlupáč & Lukeš 1999; Hladil et al. 1996; Skoček & Kukul 1998; Chlupáč 2000; Slavík & Hladil 2000; Slavík 2004a, b; Buggish & Mann 2004; Koptíková et al. 2010a, b; Hladil et al. 2011; Da Silva et al. 2016; Slavík 2017; Slavík & Hladil 2020; Weinerová 2022; Vodrážková et al. 2022).

The stratigraphic interval covered in this study corresponds to the *celtibericus–gracilis/excavatus* to *gracilis/excavatus–gronbergi* conodont zones and includes the upper part of the Praha Formation (Dvorce-Prokop Limestone) and, in the Pod Barrandovem section, also the lowermost parts of the Zlíčov Formation. These sections were originally selected with the aim of studying and potentially redefining the base of the Emsian Stage (Weinerová et al. 2024; Slavík et al. 2025; Slavík et al. accepted), which might be located close below the BGE interval base on the *gracilis* Event.

The Bohemian Graptolite Event (BGE) beds represent a conspicuous lithological marker (usually less than 1 m thick set of limestone beds and black calcareous shale interbeds) within the Dvorce-Prokop Limestone on the northwestern flank of the Prague Synform (e.g., Hladil et al. 1996; Hladil & Kalvoda 1996, 1997; Weinerová et al. 2024). An equivalent in Morocco has alternatively been referred to as the “*atopus* Event” (Becker et al. 2012). The BGE is stratigraphically close to the base of the traditional Emsian, as defined in Germany (e.g., Slavík 2004b; Slavík et al. 2007; Carls et al. 2008). The Stydlé vody, Mramorka, and Požár 3 sections are situated on the northwestern limb of the Prague Synform, where the BGE interval is easily recognizable, whereas the Pod Barrandovem section lies in the northern part of the southeastern limb (see, e.g., Chlupáč et al. 1998). The Stydlé vody section

Tab. 1- Studied localities and material.

	Stydlé vody section	Mramorka section	Požár 3 section	Pod Barrandovem section
lithostratigraphy of the Praha Formation at the studied sites or their close surrounding	Chlupáč (1957)	Chlupáč (1957)	Koptíková et al. (2010a)	Chlupáč & Lukeš (1999), Da Silva et al. (2016)
	Praha Fm (~82-89 m): Koněprusy Lst (20 m) Slivenec Lst (20 m) Loděnice Lst (5-10 m) Dvor-Prok Lst (27-28 m) Řeporyje Lst (5 m) Dvor-Prok Lst (5-6 m)	Praha Fm (~47-56 m): Slivenec Lst (12 m) Loděnice Lst (10-15 m) Řeporyje Lst (17-20 m) Dvor-Prok Lst (8-9 m)	Praha Fm (~44 m): Koněprusy Lst (4.65 m) Slivenec Lst (4.75 m) Loděnice Lst (19 m) Řeporyje Lst (6 m) Dvor-Prok Lst (8.1 m)	Praha Fm (~10 m missing at the base + 173 m): Koněprusy Lst (?1 m) Slivenec Lst (79 m) Loděnice Lst (5 m) Dvor-Prok Lst (160 m)
therein studied part	thickness and lithostratigraphy	1.6 m (Dvorce-Prokop Lst)	5.5 m (Dvorce-Prokop Lst)	5 m (Dvorce-Prokop Lst)
	coordinates	49°58'19.25"N 14°8'47.96"E	50°0'13.64"N 14°16'11.072"E	50°1'38.423"N 14°19'40.574"E
	thin sections	12	17	9
	polished thin sections	0	2	0
	polished slabs	12	3	3
	etched samples	5	15	4
references	Lukeš (1982), Hladil et al. (1996)	Weinerová et al. (2024)	Slavík et al. (2025)	Slavík et al. (in review)

represents a classical locality of the BGE beds, as the description of the fauna from this interval originates from this site, and the youngest graptolites were found there (e.g., Bouček 1966; Bouček et al. 1966; Lukeš 1982; Chlupáč 1983; Havlíček & Vaněk 1998).

MATERIAL AND METHODS

The ichnofossil record was studied at four localities situated within the Prague Synform (see Fig. 1, Table 1). The Stydlé vody section is located in an abandoned quarry near Loděnice; the Mramorka section is also situated in an abandoned quarry near Chýnice; the Požár 3 section lies within an active quarry on the southwestern outskirts of Prague, while the Pod Barrandovem sections A and B correspond to an abandoned quarry and a road cut along Zbraslavská Street in Prague. For detailed information and photodocumentation of these sections, see Lukeš (1982), Hladil et al. (1996), Weinerová et al. (2024), Slavík et al. (2025), and Slavík et al. (accepted). Ichnofossil analysis was conducted both in the field and on laboratory-prepared samples, including polished slabs, thin sections, and etched specimens (Table 1; see Supplement 1 for the exact sampling locations within studied sedimentary sections). Sample preparation and imaging were performed at the laboratories of the Institute of Geology, Czech Academy of Sciences.

In total, 103 thin sections previously studied by Hladil et al. (1996; housed in the National Muse-

um collection), Weinerová et al. (2024), Slavík et al. (2025), and Slavík et al. (accepted) were re-examined for ichnofossil records. Photographs were taken using a SZX16 binocular microscope connected with a Canon EOS 1200D camera, Olympus BX51 polarizing microscope connected with an Olympus DP70 camera, and Keyence VHX-7000 digital microscope. Three polished thin sections were studied using scanning electron microscope TESCAN VEGA3XMU with energy dispersive X-ray spectrometer Oxford Instruments Ultim Max 65 (EDS). Polished slabs (14 samples in total) reach dimensions up to 15 × 25 cm. Etched samples were obtained in two ways. First, rock samples (averaging 3–5 kg each) were dissolved in 8–10% acetic or formic acid for conodont element extraction. These were repeatedly checked for ichnofossil records (44 samples in total), and some rock fragments were removed during the process and preserved to document the ichnofabric. Second, the other half of some samples, cut for polished slabs, were subjected to the same acid treatment (5 samples in total). Selected samples are housed in the Czech Geological Survey in Prague. Boxplots of U/Th ratios were generated in PAST 3 using the interpolation method for quartile calculation.

Abbreviations used: BGE – Bohemian Graptolite Event; STV – Stydlé vody section; MR – Mramorka section; PO – Požár 3 section; BARR – Pod Barrandovem section; gr X – Xth limestone bed within the BGE interval. E.g., BARR 136 – sample taken from the Pod Barrandovem section at height 136 m, STV bed no. 28 – bed no. 28 (numbering *sensu* Hladil et al. 1996) at the Stydlé vody section, MRgr 4 – the fourth limestone bed within the BGE interval at the Mramorka section.

RESULTS

Lithology and microfacies study

The ichnological study focused on the Bohemian Graptolite Event (BGE) beds, and the Dvorce-Prokop Limestone in its close surrounding at the Stydlé vody (1.6 m), Mramorka (5.5 m) and Požár 3 (5 m) sections, and the BGE beds along with a significant portion of the overlying Dvorce-Prokop Limestone up to the lower part of the Zlíčov Limestone at the Pod Barrandovem section (two separate subsections measuring about 25 m and 7 m, respectively), see Fig. 2. At the Mramorka and Požár 3 sections, the studied part of the sedimentary succession below the BGE consists of light-grey, locally pinkish or ochre, weakly nodular calcisiltites forming the first decimetre thick beds. At all four localities, the BGE interval (~1–2.5 m) comprises about seven grey to darker-grey platy calcisiltite beds intercalated with interbeds of dark-grey to black mudstone or calcareous shale. Above the BGE beds lie grey, weakly nodular calcisiltites forming the first decimetre thick beds. In the Pod Barrandovem section, from ~140 m, nodularity becomes less distinct and bedding more pronounced, whereas the uppermost part of the Dvorce-Prokop Limestone consists of darker grey, platy calcisiltites, often interlayered with mudstones or calcareous shales, and first interbeds of grey crinoidal calcarenites appear. Partial silicification (“incipient cherts” sensu previous authors) occurs. The transition into the lowermost beds of the Zlíčov Limestone is thus gradual, and is accompanied by the appearance of well-developed cherts. This is followed by a carbonate breccia, known as the “Chapel Coral Horizon”. For further details, see Weinerová et al. (2024), Slavík et al. (2025), and Slavík et al. (accepted). Please note that the base of the Zlíčov Limestone, the Zlíčov Formation, and the Zlíčovian Stage was defined at the Pod Barrandovem section at a level corresponding to 172.5 m in our numbering (see Chlupáč 1957, 1981). However, Slavík et al. (accepted) discuss the possibility that the upper part of the Praha Formation at this locality (approximately from 140 m) correlates with the lower part of the Zlíčov Limestone at localities such as the Požár 3 and Na Branžovech sections.

The microfacies in therein studied thin sections can be classified as packstones, wackestones, floatstones, and mudstones, with the groundmass composed of micrite, microsparite, and calcisiltite.

Nevertheless, these limestones differ in the relative abundance of dacryoconarids and other allochems.

Microfacies A. Floatstone with packstone to wackestone matrix, characterised by diverse bioclasts. Dacryoconarids are represented not only by styliolinids but also by larger nowakiids. Other allochems include crinoids, trilobites, molluscs (bivalves, gastropods, nautiloids), ostracods (commonly medium-thick-shelled and sculptured forms), globochaetids, brachiopods, and bryozoans. Bioclasts are found both well-preserved and fragmented. Bioerosion is common on trilobites, crinoids, and molluscs. Some dacryoconarid shells are interlocked with each other (“telescoping”). The groundmass often has a calcisiltite character. This microfacies was recorded at the base of some limestone beds (Figs 3A, E, 4A; Weinerová et al. 2024: fig. 3c) and also occurs within Microfacies B, rarely in well-defined bioturbation structures (Fig. 3C; Slavík et al. 2025: fig. 3b, e), but more commonly in poorly bounded patches (clusters of bioclasts, Fig. 3B, D; Weinerová et al. 2024: fig. 3A, F).

Microfacies B. Dacryoconarid-dominated wackestone or locally packstone is the most common microfacies (Figs 3B, C, D, E, F, G, 4B). Dacryoconarids are dominated by styliolinids, nowakiids are rare. The relative abundance of dacryoconarids compared to other bioclasts is higher than in Microfacies A. The composition of other bioclasts is similar to that in Microfacies A, but ostracods are dominated by thin-shelled forms. Bioclasts are generally smaller than in Microfacies A, but well-preserved shells and fragments, bioerosion, and occasional telescoping of dacryoconarid shells can still be observed. In some samples (especially from the Pod Barrandovem section), sponge spicules and radiolarians (commonly replaced by sparite or transformed into peloids) were recorded. The groundmass often has a calcisiltite character. A common feature is mottling, manifested by slight differences in the groundmass and the alignment of bioclasts.

Microfacies C. Mudstone to wackestone with dacryoconarids (prevalently styliolinids), molluscs, sponge spicules, and radiolarians, the latter commonly replaced by sparite or transformed into peloids. Other bioclasts are rare. The groundmass has a more micritic character compared to Microfacies A and B (Figs 3 H, 4J). This microfacies occurs in the highest part of the Praha Formation and in the Zlíčov Formation at the Pod Barrandovem section.

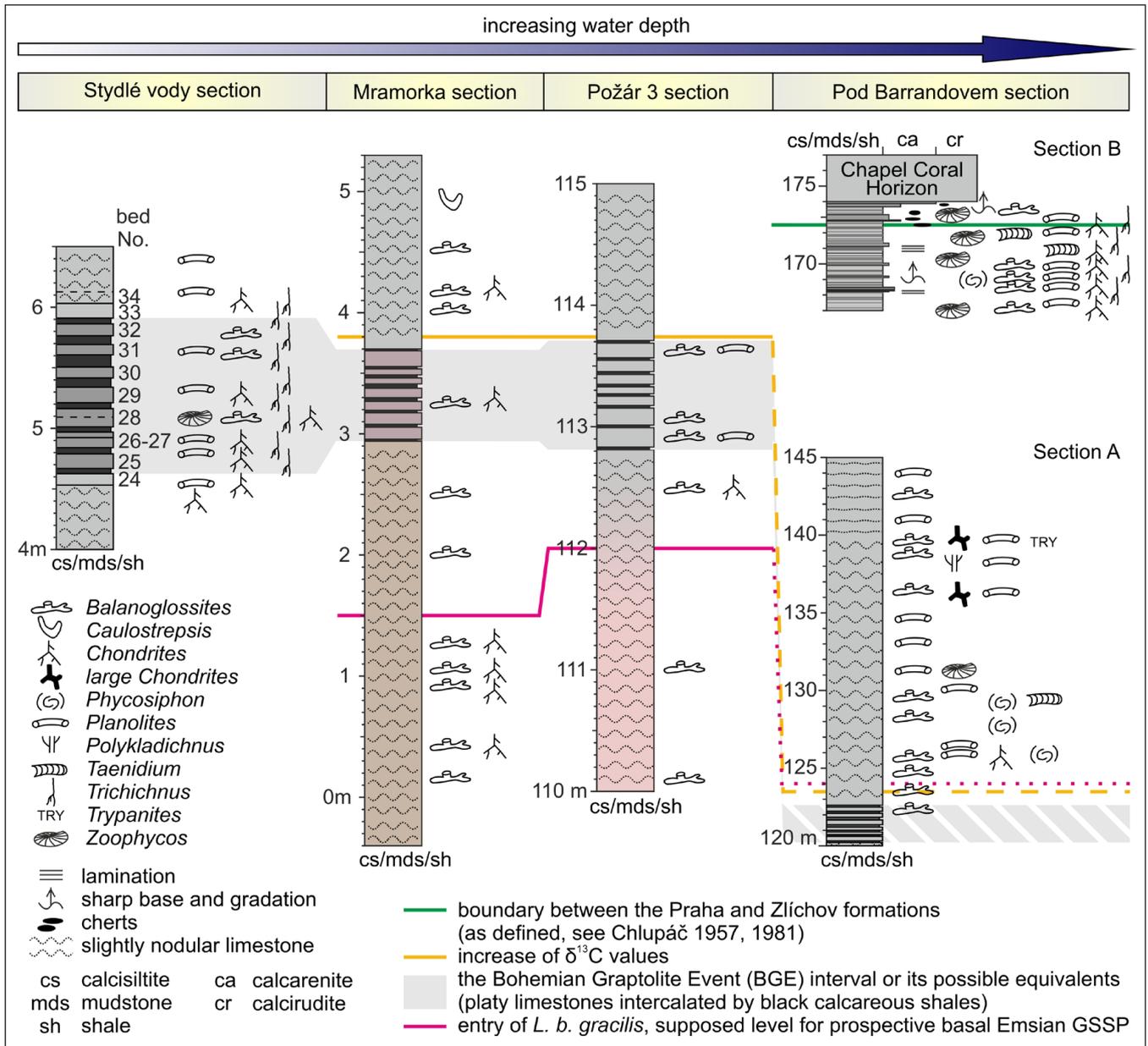


Fig. 2 - Four studied sections of the upper part of the Praha Formation comprising the Bohemian Graptolite Event (BGE) with indication of occurrence of trace fossils, rock colour and sedimentary structures. Trace fossils are arranged from left to right according to decreasing dominance in ichnofabric. Correlation of sections by $\delta^{13}\text{C}$ and conodont data follows Weinerová et al. (2024), Slavík et al. (2025), and Slavík et al. (accepted). In the Pod Barrandovem section, *L. b. gracilis* probably enters earlier than indicated by the current data.

Microfacies D. Dacryoconarid packstone to wackestone dominated by styliolinids. Other bioclasts are rare. The groundmass is prevalently sparitic (probably neomorphic sparite). This microfacies is associated with some trace fossils (e.g., *Planolites*, Fig. 4D) and probably represent Microfacies B modified by bioturbation-related differential diagenesis.

Microfacies E. Radiolarian, or rather peloidal, packstone to wackestone. Radiolarians are commonly replaced by sparite or more often transformed into peloids. Other bioclasts (e.g., styliolin-

ids) are rare. The groundmass is prevalently sparitic (probably neomorphic sparite). This microfacies is associated with some trace fossils (e.g., *Phycosiphon*, Fig. 4I) and probably represent Microfacies C modified by bioturbation-related differential diagenesis.

Microfacies F. Calcareous shale (Fig. 3I). The identification of bioclasts is somewhat complicated by significant fragmentation due to compaction, but dacryoconarids and, locally, sponge spicules dominate. *Chondrites* burrows probably contained a higher carbonate content and are therefore less com-

pacted. Transverse sections of partially compacted dacryoconarids within them resemble the shape of eyeglasses (Fig. 4G).

EDX elemental mapping. Three polished sections capturing the *Balanoglossites* burrows with various types of infill were subjected to elemental mapping. Sample MR 0.6 contains a *Balanoglossites* burrow that is stenomorphically filled by the ichnogenus *Chondrites*. The boundary between the *Balanoglossites* burrow and the surrounding sediment is indistinct. The infill of both ichnogenera is enriched in phyllosilicates and more strongly dolomitized compared to the surrounding sediment (Fig. 5A, D). A higher degree of dolomitization of the *Balanoglossites* infill compared to the host sediment is also observed in sample MR 4. However, in this case, a pressure-dissolution seam has developed at the boundary between the burrow and the surrounding rock, where phyllosilicates are concentrated (Fig. 5B, E). Sample BARR 169.5 captures a *Balanoglossites* burrow cross-cut by the ichnogenera *Phycosiphon* and *Planolites*. The boundary between *Balanoglossites* and the host rock is difficult to discern under plane-polarized light. The *Balanoglossites* infill is finely silicified (Fig. 5C, F, G). Fine pyrite is dispersed throughout the sample, with increased concentrations observed along the margins of *Planolites* (Fig. 5G).

SYSTEMATIC ICHNOLOGY

The ichnotaxa used (i.e., ichnogenera and ichnospecies) are listed in the following text according to a subjective criterion, namely the importance of the respective ichnotaxon for the understanding and interpretation of the entire ichnoassemblage in the context of the studied regional and stratigraphic unit. We find alphabetical ordering inappropriate given the composition of the ichnocommunity (e.g., *Bergaueria*, *Caulostrepsis*, *Zoophycos*...) and there is no substantial reason for sorting by ichnofamilies or broader informal units.

Ichnogenus *Balanoglossites* Mägdefrau, 1932

Diagnosis: Branched galleries with several openings and acorn-, bulb- or lance-shaped side-branches. Tunnels are elliptical or circular in cross-sections, margin is unlined and locally striated; tunnel size varies in the order of several magnitudes within a single gallery system (Knaust 2008).

Type ichnospecies: *Balanoglossites triadicus* Mägdefrau, 1932.

Ichnospecies *Balanoglossites triadicus* Mägdefrau, 1932

Figs 3D, 5A–E, G, 6A, B, 7A–C, 8A–C

Diagnosis: *Balanoglossites* with predominantly deep U- or Y-shaped tunnel elements (Knaust 2008).

Material: Hundreds of specimens observed in the field, 14 specimens collected to make polished samples, 16 specimens collected for etching in acids.

Description. Subhorizontal to slightly inclined tunnels with a variable diameter from 10 mm to 70 mm, showing a wavy surface with numerous bumps and protrusions. Determination of the minimum and maximum diameter on 2D sections is only approximate. Less than 20% of the area of *Balanoglossites* systems is represented by steeply inclined (angle of 50° and more) shafts of similarly variable diameter as horizontal to subhorizontal parts. It is not possible to determine the maximum length of (sub)horizontal tunnels, or rather it can be assumed that the passages formed a complex system in the respective tier with a total length of the order of metres or even tens of metres. The surface of the tunnels has more or less distinct bumps 1–3 mm high and usually 5–7 mm in diameter. Otherwise, the surface of the tunnels is smooth; no traces of mechanical scratching of the margins of the tunnels and shafts were found, as for example known from the ichnogenus *Spongeliomorpha*. The systems extend to a depth of up to 10 cm below the colonization surface. As a rule, one or two tiers (underground floors) are preserved on the samples, in one case a hint of a third tier was found.

Remarks. Compared to the material studied by Knaust (2008), there is a relatively small number

Fig. 3 - Vertical thin sections of the selected beds. A) Microfacies A (MR 1.6; Weinerová et al. 2024, modified). B) Microfacies B with poorly bounded patches of Microfacies A (MRgr 3). C) Microfacies B with Microfacies A in bioturbation (POgr 3; Slavík et al. 2025, modified). D) Microfacies B with poorly bounded patches of Microfacies A, and *Balanoglossites* filled with Microfacies D (PO 113.7; Slavík et al. 2025, modified). E) Microfacies A at the base of the bed, overlain by Microfacies B (BARR 139.55). F) Microfacies B (BARR 129.0). G) Microfacies B (BARR 140.4). H) Microfacies D (BARR 170.0). I) Microfacies F with *Chondrites* burrows (BARR 171.75). Abbreviations: *Bal*, *Balanoglossites*; *Ch*, *Chondrites*; *Ph*, *Phycosiphon*; *Pl*, *Planolites*; *Try*, *Trypanites*; white arrow, bio-erosion.

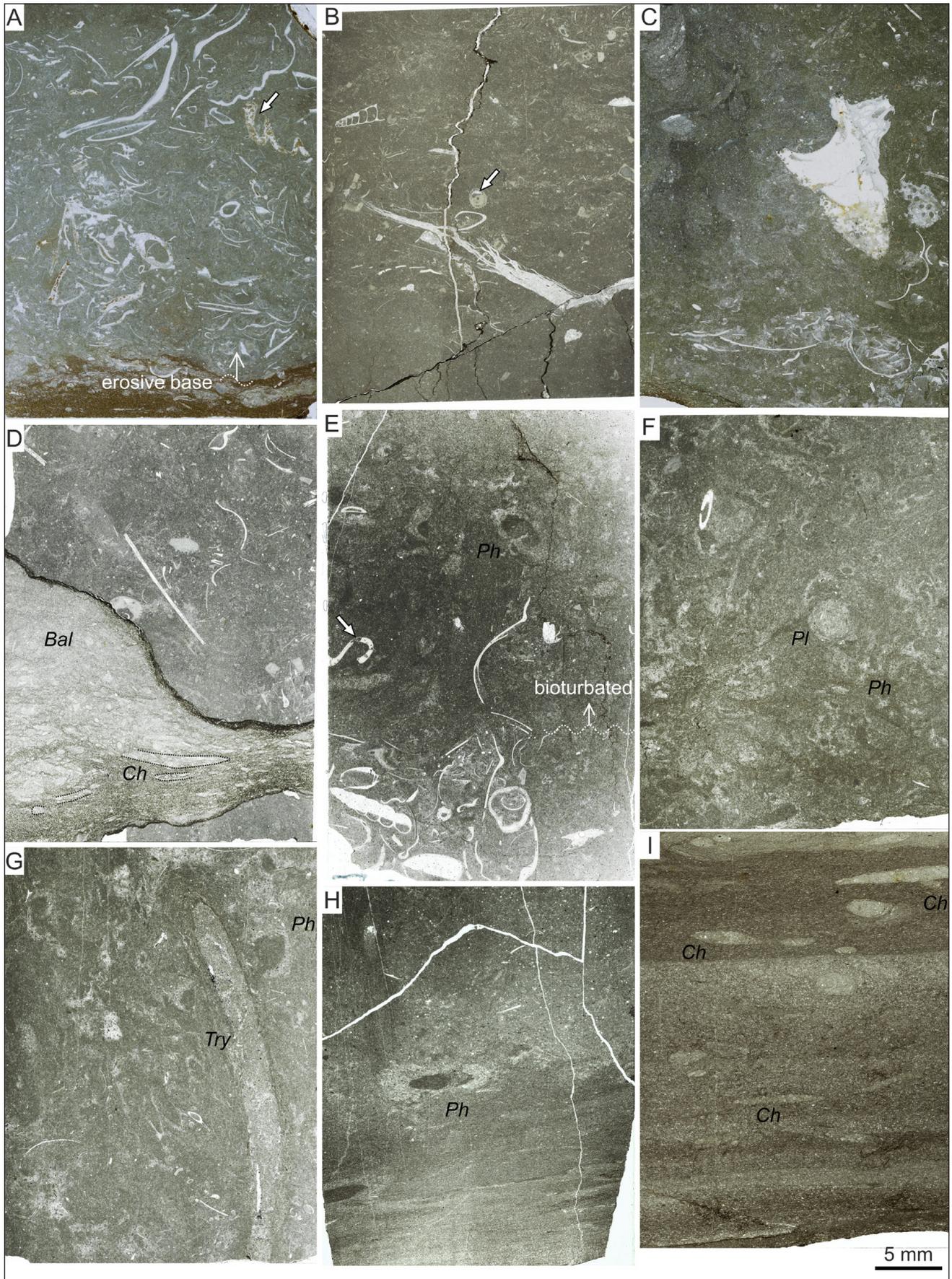


FIG. 3

of distinct hardgrounds in the investigated early Emsian limestones. This fact leads to a somewhat different taphonomic aspect compared to the Knaust's material. The material we describe is mostly fragmentary; in order to be classified, it requires a reconstruction of its original morphology. The rare occurrence of hardgrounds corresponding to the findings of Mikuláš & Hladil (2015), who studied ?*Capodistria* isp. and a larger number of cf. *Trypanites* isp. at the Branická skála locality, which geographically and stratigraphically is probably not far below the BGE (cf. black shale in the rocks above the transformer west of Branická skála). Processed samples usually do not have a large part of the layer surface exposed, nor is a horizontal section available. On the other hand, at least part of the found *Balanoglossites* can be obtained in 3D form by dissolving limestone in acid, while trace fillings dissolve much more slowly due to the greater proportion of dolomite or siliceous material.

In addition to the ichnogenus *Balanoglossites*, which dominates most of the above-described layers, a range of other ichnofossils have been found with varying frequency. This fact greatly expands the interpretative possibilities of ichnology. The relationships of mutual overlapping and intersection of traces are also significant.

Ichnogenus *Chondrites* Sternberg, 1833

Diagnosis: Regularly branching tunnel system consisting of a small number of sub-vertical master-shafts, connected to the ancient sediment-water interface, which branches at depth to form a dendritic network. Fill can be active or passive (Baucon et al. 2020).

Chondrites cf. *intricatus* (Brongniart, 1828)

Figs 3D, 6A

Diagnosis: Small *Chondrites* consisting of numerous, downward-radiating, mostly straight branches. The angle of branching is usually less than 45°. The branches are less than 1.0 mm wide (mostly about 0.5 mm). The burrow system is more than 20 mm wide (Uchman 1999).

Material: Five polished specimens and one thin section from the Stydlé vody section. Three etched specimens come from the Mramorka section, on which there are dozens of specimens densely occupying the *Balanoglossites* infill. Another five individuals of *C.* cf. *intricatus* from Mramorka section occur on large polished sections and thin sections, in the form of clusters on the cross-sections of the tunnels. At other localities, *C.* cf. *intricatus* recognizable on sections is considerably rarer. In the Stydlé vody section, cross-sections of tunnels are usually oval to circular in shape and their fill is darker than the surrounding rock. On the Pod Barrandovem section, small *Chondrites* are rather rare, with the exception of the 168–172 m interval. Finally, on the Požár 3 section, *C.* cf. *intricatus* was found in a single position, 112.5 m.

Description. Tunnels, mostly slightly bent, with a diameter of 0.8–1.0 mm, branching at intervals of usually 1 cm or less. They occur frequently; in the filling of *Balanoglossites*, they represent about 50% of the volume.

Remarks. *C. intricatus*, as described by, e.g., Uchman (1998), is characterized by usually straight tunnels, usually regularly, sometimes geometrically, branched. Between the end parts of the tunnels of the last order there is a certain minimum spacing, which represents more than twice the width of the tunnels (cf. Sternberg 1833; Mikuláš & Straková 1994; Uchman 1999). In our case, however, these criteria do not apply, or only partially. The reason is the stenomorphic character of *Chondrites*, which had to fit into the limited space of the *Balanoglossites* trace fill (see Bromley 1996 for stenomorphism of trace fossils). In cases not linked to the previous presence of the *Balanoglossites* trace-maker, the tunnels are noticeably further apart than at the Mramorka section.

C. cf. *targionii* (Brongniart, 1828)

Figs 6E, F, 7C, 8C

Diagnosis: Dendritic network with well-expressed primary successive branching. The angle of branching is usually acute (Uchman 1998).

Material: Two polished slabs from the Mramorka section. A shale slab with a dense network of subhorizontal tunnels of *C.* cf. *targionii* from the same locality. Several cross-sections of tunnels visible in samples from the Mramorka and Pod Barrandovem sections, for which affiliation to the ichnogenus *Chondrites* is probable.

Fig. 4 - A) Microfacies A, note the common geopetal structures and telescoping of the dactyloconarid shells, note the heavily bioeroded trilobite fragment in the lower right corner (MR 1.6). B) Microfacies B with *Caulostrepsis taeniola* geopetally infilled with Microfacies D (MR 5). C) Microfacies B with ?*Palaeophycus* (BARR 136.5). D) Microfacies B with ?*Planolites* filled by Microfacies D (BARR 134.95). E) *Palaeophycus* (BARR 140.05). F) *Phycosiphon* and *Planolites* in the *Balanoglossites* burrow, see also Fig. 5C (BARR 169.5). G) Calcareous shale with flattened *Chondrites* burrow, note deformed dactyloconarid shells inside the burrow (BARR 167.6). H) Microfacies B with *Zoophycos* and *Trichichnus* (BARR 171.5). I) ?*Phycosiphon* filled by microfacies D (BARR 130.55). J) Microfacies C with radiolarians (BARR 170.0). Abbreviations: bry, bryozoan; c, crinoid; d, dactyloconarid; m, mollusc; o, ostracod; p, peloid; r, radiolarian; s, sponge spicule; white arrow, telescoping of dactyloconarid shells; black arrow, geopetal structures; *Ph*, *Phycosiphon*; *Pl*, *Planolites*; *Trich*, *Trichichnus*; *Z*, *Zoophycos*.

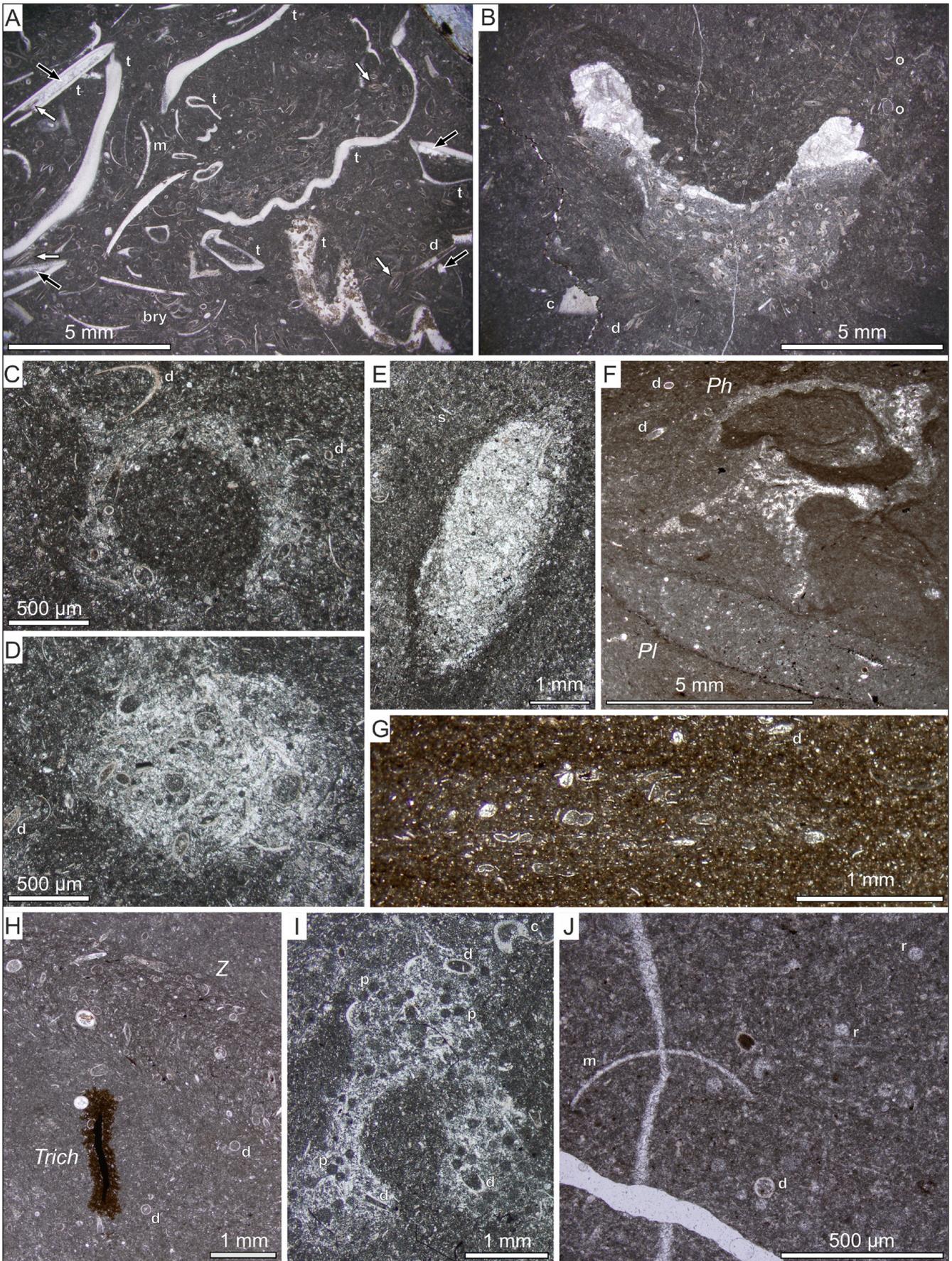


FIG. 4

Description. Subhorizontal to fully horizontal branching tunnels. Diameter of each branch is constant; from 1.7 to 2.0 mm. Intervals of branching are very variable, from 2.0 mm to 12.0 mm. They may occur frequently, forming the monotonous ichnofabric, or rarely.

Remarks. This ichnotaxon is relatively rare, occupying less than 1% of the studied substrates. In shales, *C. targionii* appears compressed, whereas in limestones (especially the darker beds from the Pod Barrandovem and Stydlé vody sections) it shows no signs of compaction; cf. Scharfenberg et al. (2025) for possibilities of more detailed morphological characteristics.

Ichnogenus *Zoophycos* Massalongo, 1855

Diagnosis: Complex burrow systems, the base of which is a thin plate curved like the blades of a propeller. The whole may be rather planar (horizontal to subhorizontal to bedding; only one thread) or helicoidal (corkscrew-like) with several threads. The helicoidal form features successive turns with varying radii, a marginal tube surrounding the perimeter, and a vertical shaft connecting the burrow to the surface. Spreiten structure occurs between the marginal tube and the corkscrew axis (compiled and edited from Kotake 1991, Zhang et al. 2015, and Monaco et al. 2017).

Zoophycos isp.

Figs. 4H, 6G

Description. Planar forms of *Zoophycos*. The thickness of the spreite varies from 2.2 mm to 3.0 mm and is almost constant within each specimen. The spreite laminae are fully horizontal. No specimen was found that ended on both sides with a marginal tunnel. The largest specimen observed has a width of 250 mm. The spreite lamina is smooth and clearly bordered on the upper surface, while on the lower surface the menisci of the spreiten-structure fade out in a blur. Thus, the entire vertical section of the trace resembles a fine saw blade, the teeth of which are approximately 0.2 mm apart; this value is not constant. In some layers there are more (2–3) of spreiten laminae one above the other; they are typically 25 mm apart. It cannot be excluded that these are marginal parts of one specimen (if it were a part close to the corkscrew shaft, the laminae could not be truly horizontal).

Ichnogenus *Phycosiphon* Fischer-Ooster, 1858

Diagnosis: Intricate, small, and often U-shaped burrows that typically have a central tube surrounded by a spreite (a series of

closely spaced, curved layers of sediment). The burrows are usually less than a centimetre in diameter and can be found in various orientations, including horizontal, vertical, and oblique (Arregui et al. 2023).

Phycosiphon isp.

Fig. 3F–H

Description. U-, C-, or S-shaped structures. They are detectable in thin sections, otherwise they cannot be detected due to the very low contrast between the trace filling and the surrounding substrate. The typical width of objects representing marginal tunnels or spreite is 1 mm. When measuring on sections, a greater length is usually found due to the fact that most sections are necessarily oblique. Structures interpreted as *Phycosiphon* sometimes cannot be safely distinguished from cross-sections of *Planolites* cf. *montanus*, i.e. simple unreinforced tunnels with a small diameter. Probably, both ichnofabrics can overlap in some cases. The best examples of the *Phycosiphon* ichnofabric come from the Pod Barrandovem section (BARR 120).

Ichnogenus *Taenidium* Heer, 1877

Diagnosis: Unlined or very thinly lined, unbranched, straight or sinuous cylindrical trace fossils containing a segmented fill articulated by meniscus-shaped partings (D'Alessandro & Bromley 1987; Bromley et al. 1999).

Taenidium isp.

Fig. 6H

Remarks. *Taenidium* is distinguished from other meniscate burrows, such as *Beaconites*, *Scyenia*, and *Anchorichnus*, by the absence of walls, wall striations, and a peripheral mantle (D'Alessandro & Bromley 1987).

Ichnogenus *Polykladichnus* Fürsich, 1981

Diagnosis: Vertical shafts that branches upward near the bedding surface into Y-shaped burrows. These burrows usually connect to the bedding surface and can have branching at several levels, including second-order branching. The tubes are circular in cross-section, with unornamented walls and no widened junctions at points of bifurcation (Uchman & Álvaro 2000).

Fig. 5 - Polished thin sections and EDX elemental maps. A) *Balanoglossites* (MR 0.6). B) *Balanoglossites* (MR 4). C) *Phycosiphon* and *Planolites* in *Balanoglossites* (BARR 169.5). D–G) elemental maps: D, detail of A; E, detail of B; F, detail of C; G, detail of C.

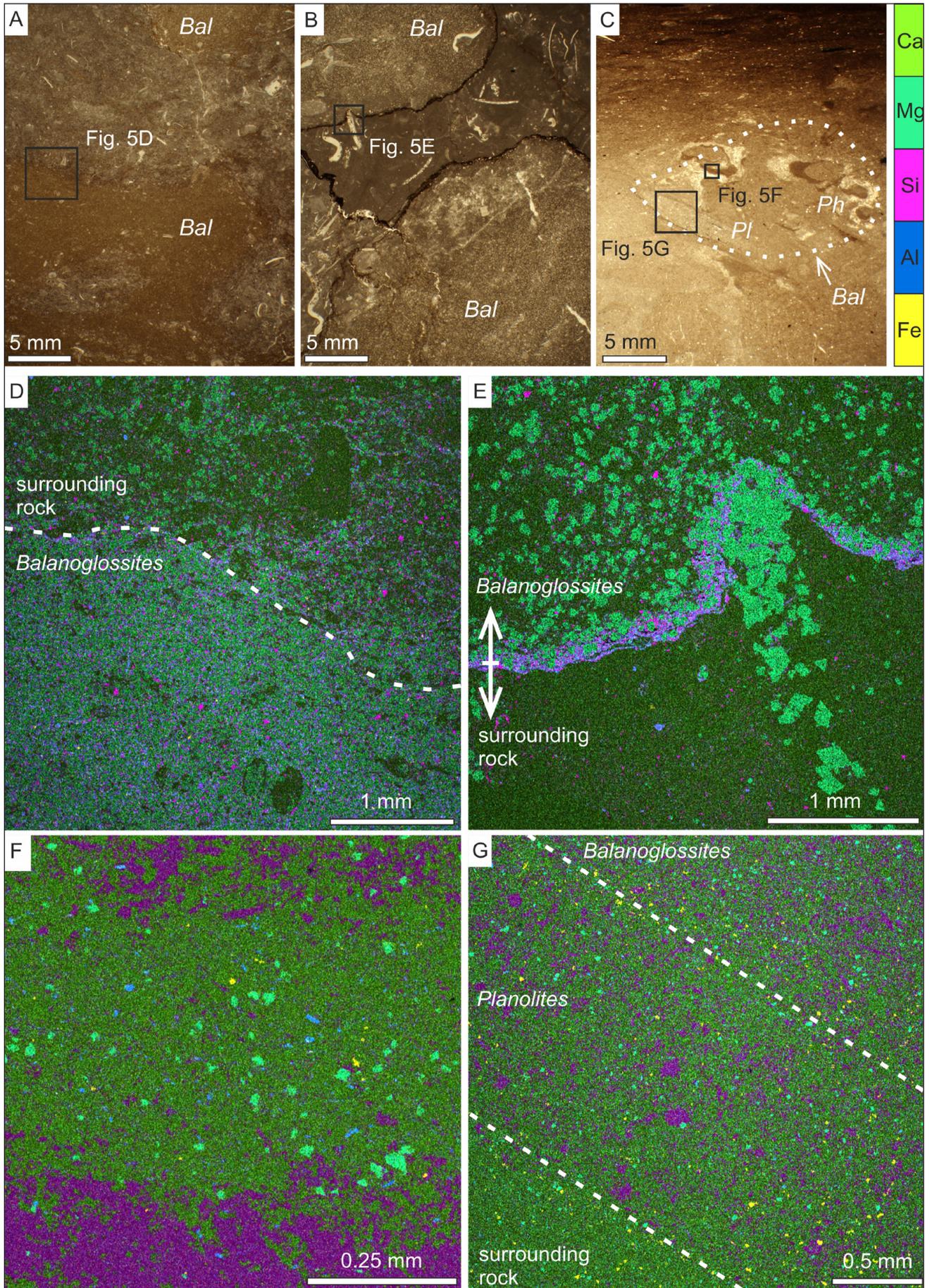


FIG. 5

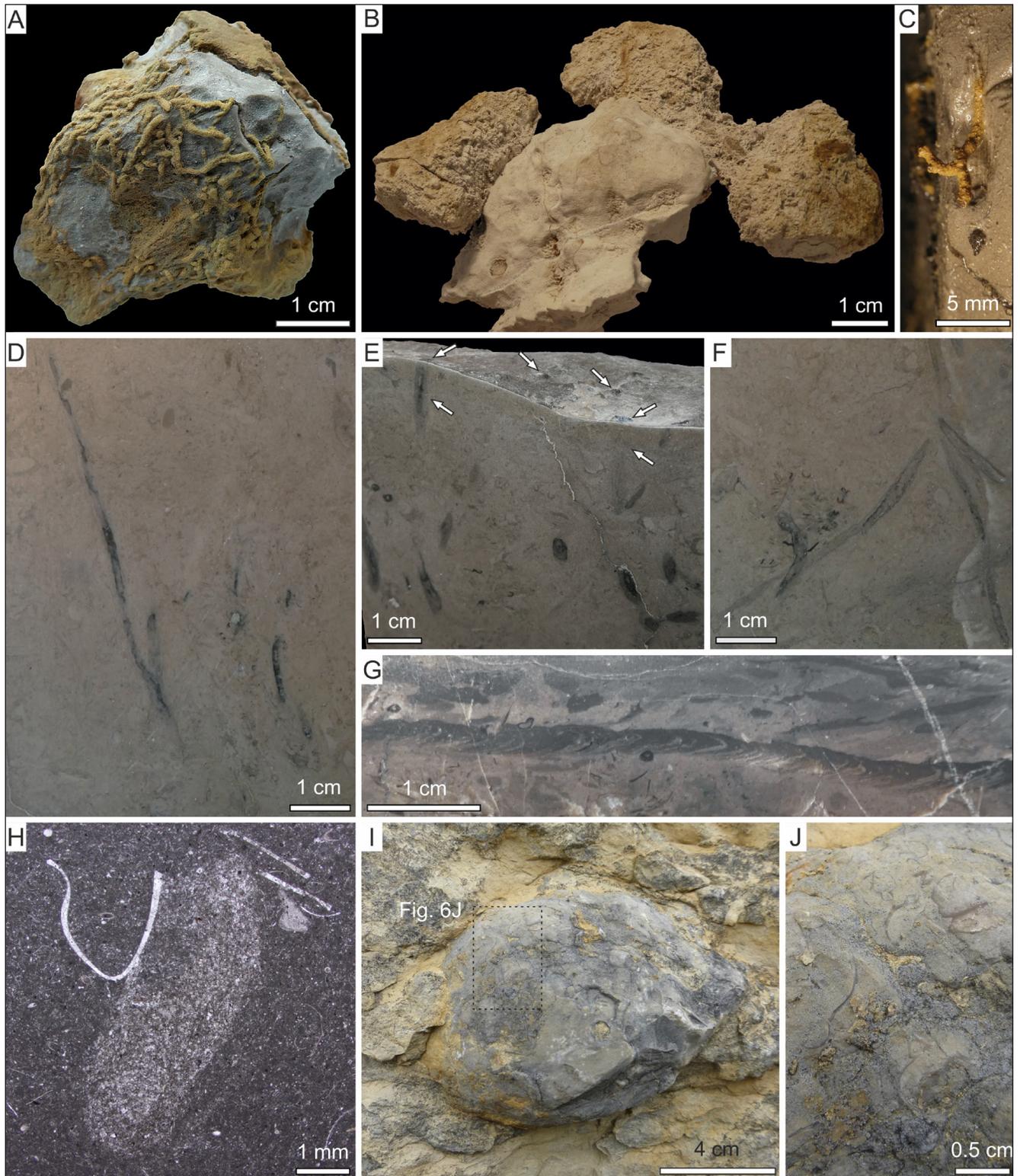


Fig. 6 - A) *Chondrites intricatus* filling selectively the passive infill of *Balanoglossites* burrow, *Chondrites* represents a typical stenomorphic burrow (etched sample, MR 0.2). B) silicified *Balanoglossites* burrow (etched sample, BARR 129). C) *Trichichnus* (etched sample, STV bed no. 28). D) *Polykladichnus* (polished slab, BARR 136.0). E) ?*Trypanites* (polished slab, BARR 140.4). F) *Chondrites targionii* (polished slab, BARR 135.4). G) *Zoophycos* (polished slab, STV bed no. 28). H) *Taenidium* (thin section, BARR 139.05). I) plug-shaped body found in the debris in the Mramorka Quarry. J) detail of I, a closer view on abundant trilobite remnants inside the trace fossil.

Polykladichnus aragonensis Uchman and Álvaro,
2000

Figs 6D, 8B

Description. Steeply inclined, upward branching burrows. The key specimen for the identification of the ichnospecies was a block of grey micritic limestone taken from the locality and layer BARR 136. On a polished section of the layer, *Polykladichnus* is observable 10.0 cm from the upper bedding plane. The only branching accurately reached by the rock section is at a depth of 6.4 cm from the bed top. The layers diverge at an angle of 15° after the branching. To the right of this branching burrow, three more branches, apparently of the same system of burrows, are reached; adjacent branches make an angle of less than 5°. This would imply that the common beginning of the burrows was at a depth greater than 15 cm, i.e. near the lower bedding plane. The diameter of the tubes is 1.4 mm.

Remarks. *Polykladichnus* has been reported from the Upper Jurassic to the Pleistocene. Although Palaeozoic records of the ichnogenus *Polykladichnus* have not yet been reported, the trace of *Polykladichnus* described by Mikuláš (1994) from the Praha Formation, facies of Slivenec Limestone, is an almost undoubted finding. For this reason, we consider the occurrence of the ichnogenus in the Praha Formation to be very probable.

Ichnogenus *Trichichnus* Frey, 1970

Diagnosis: Branched or unbranched, straight to winding, hair-like cylindrical structure, mostly 0.1–0.7 mm in diameter, oriented at various angles (mostly vertical) with respect to the bedding. The filling of the tubes is made up of pyrite or its decomposition products. (Emended by Kędzierski et al. 2015).

Trichichnus linearis Frey, 1970

Figs 4H, 6C

Material: Dozens of finds from the Stydlé vody sedimentary section, observable both on thin and polished sections, and much better on etched samples, where pyrite-filled rods remain free in space as 3D samples. The pyritized cross-section were occasionally found on fracture surfaces or polished sections in the Pod Barrandovem section.

Description. Branched or unbranched, straight to curved cylindrical structures, mostly 0.4–0.9 mm in diameter, oriented at various angles (mostly vertical) with respect to the bedding.

These thin, often up to 12 cm deep, mostly vertical or steeply inclined tubes may branch at irregular intervals (usually one individual has 2–4 observable branches). Near these branches, a part of the tube may be subhorizontal for a short section. The filling of the tubes is made up of pyrite or its decomposition products.

Ichnogenus *Trypanites* Mägdefrau, 1932

Diagnosis: Unbranched, cylindrical borings of approximately constant diameter with straight, winding, or spiralling course (Wisshak et al. 2019).

?*Trypanites* isp.

Figs 3G, 6E

Material: One specimen crossed by thin section, from the Pod Barrandovem section (BARR 140.4). A polished sample from the same level has more than ten (mostly long elliptical) cross-sections and on the upper bedding plane, 16 “scars” formed by interruption of the original substrate body are recognizable.

Description. The cross-section of the shaft attributable to *Trypanites* shows that the 3D biogenic structures had the character of cylindrical shafts with a diameter of approximately 3 mm. Inside these shafts, the filling is darker than the surrounding rock and also subvertical sections of the tubes have a darker filling. On the upper bedding plane, the scars are usually 1 cm apart. However, the decisive reason for assigning the biogenic texture from BARR 140.4 m to *Trypanites* is the thin section (Fig. 3G), which shows a constant trace diameter of 2.3 mm and geometric accuracy of the wall shaping.

Remarks. The current valid diagnosis includes several key features such as the dominance of deep borings, sharp walls, and vertical to subvertical cylindrical structures. The specimens found at location BARR 140.4 meet most of these criteria, but the consistency of the substrate at the time of the activity of tracemakers is not fully documented, for example by the cross-section of a shaft in a large bioclast. For this reason, we classify the found traces at the ichnogenetic level with doubt as ?*Trypanites* isp.

Ichnogenus *Planolites* Nicholson, 1873

Diagnosis: Relatively large, unlined, smooth-walled, horizontal to undulate, straight to sinuous cylindrical burrows; fills typically differ in colour from surrounding sediments (Pemberton & Frey 1982).

Planolites cf. *montanus* Richter, 1937

Fig. 3F

Material: Dozens of cross-sections observable in thin sections from the Pod Barrandovem section, more-or-less fully preserved, partly overlapping.

Description. Cross-section of cylindrical, horizontal to inclined cylindrical tunnels preserved as full-reliefs. Burrow width is 2–3 mm. Fill differs from the host rock.

Remarks. The described tunnel cross-sections are classified as being close to the ichnospecies *Planolites montanus* based on the work of Pemberton & Frey (1982), Orłowski & Żylińska (1996), Hofmann et al. (2012) and Knaust (2017). A new depiction of the holotype of *Planolites montanus* (Richter, 1937) was provided by Knaust (2017) in Figure 5.114 a-b. The holotype has, somewhat unusually, essentially a cleavage relief and a polished section of the same sample. Looking at the layered surface, it is clear that the straight or slightly curved sections of the tunnels are usually 8–10 mm and from the polished section a maximum diameter of 4–5 mm can be determined. Apart from the intensity of bioturbation (for the holotype, the BI is equal to 2–3; for our selectively assessed samples, i.e. only the frequency of occurrence of *P. montanus* is assessed, the BI is equal to 1–2), no difference can be found that would question the affiliation of our traces to *P. montanus*. Moreover, the density of bioturbation is not a recognizable ichnotaxobase (Bertling 2006).

Somewhat larger, isolated sections of subhorizontal tunnels from all the studied outcrops are elsewhere in the text referred as *Planolites* isp., as there is no useful clue to classify them at the ichnospecies level.

Ichnogenus *Bergaueria* Prantl, 1945*?Bergaueria* isp.

Fig. 6I, J

Remarks. This ichnotaxon is discussed briefly due to the finding of a single individual outside the studied sedimentary section; however, in our opinion, due to its unusualness, it is worth noting. A plug-shaped body found in debris of the Mramorka Quarry. Ichnologically it can be classified as *?Bergaueria* (Pemberton et al. 1988); the question is whether it also has the same ethological meaning,

i.e. a domichnion. Small plates formed by breaking trilobite shells could have been embedded in the wall of the ichnofossil as reinforcement. Possible organic residues that might have been present on the trilobite shell fragments could have served as “silage” intended for fermentation and microbial growth. However, the concentration of trilobite fragments at the bottom of the pit can only be the result of a mechanical process.

Ichnogenus *Caulostrepsis* Clarke, 1908

Diagnosis: Borings with one entrance or embedment structure, pouch-shaped, created by a U-shaped gallery. More complex structures can result from multiple lobes of similar structure (Gaaloul et al. 2023, emended).

Caulostrepsis taeniola Clarke, 1908

Fig. 4B

Description. Material attributable to the ichnospecies *Caulostrepsis taeniola* is recognized in only one find in the studied samples (vertical thin section shown in Fig. 4B; layer MR 5). This is a section of a subvertical U-shaped tube. The tube is sharply delimited from the surrounding substrate; the lower part is filled with a geopetal formation of micritic limestone, the upper part with sparite. This arrangement, regardless of the fragmentary preservation, shows the U-shaped base of the trace characteristic of the ichnogenus *Caulostrepsis*. The width of the preserved U-shape is 13 mm, but it was probably larger, because the ends of the U form an angle of 60°. The measured width of the tube is 2–4 mm. However, the measured value is affected by the inclination of the section, and therefore we conclude that the largest section width (4 mm) applied to the entire boring.

Taxonomically indeterminable bioturbational (biodeformational) structures

Figs 7A–C, 8A–C

The almost absence of primary sedimentary structures in all described sedimentary sections (except for relatively sharp, though not entirely abrupt, transitions between limestones and black shales) suggests intensive mixing of the sediment at the seafloor. In some layers, a mottled substrate has been preserved, most clearly visible in high-contrast photographs. The most common size of these

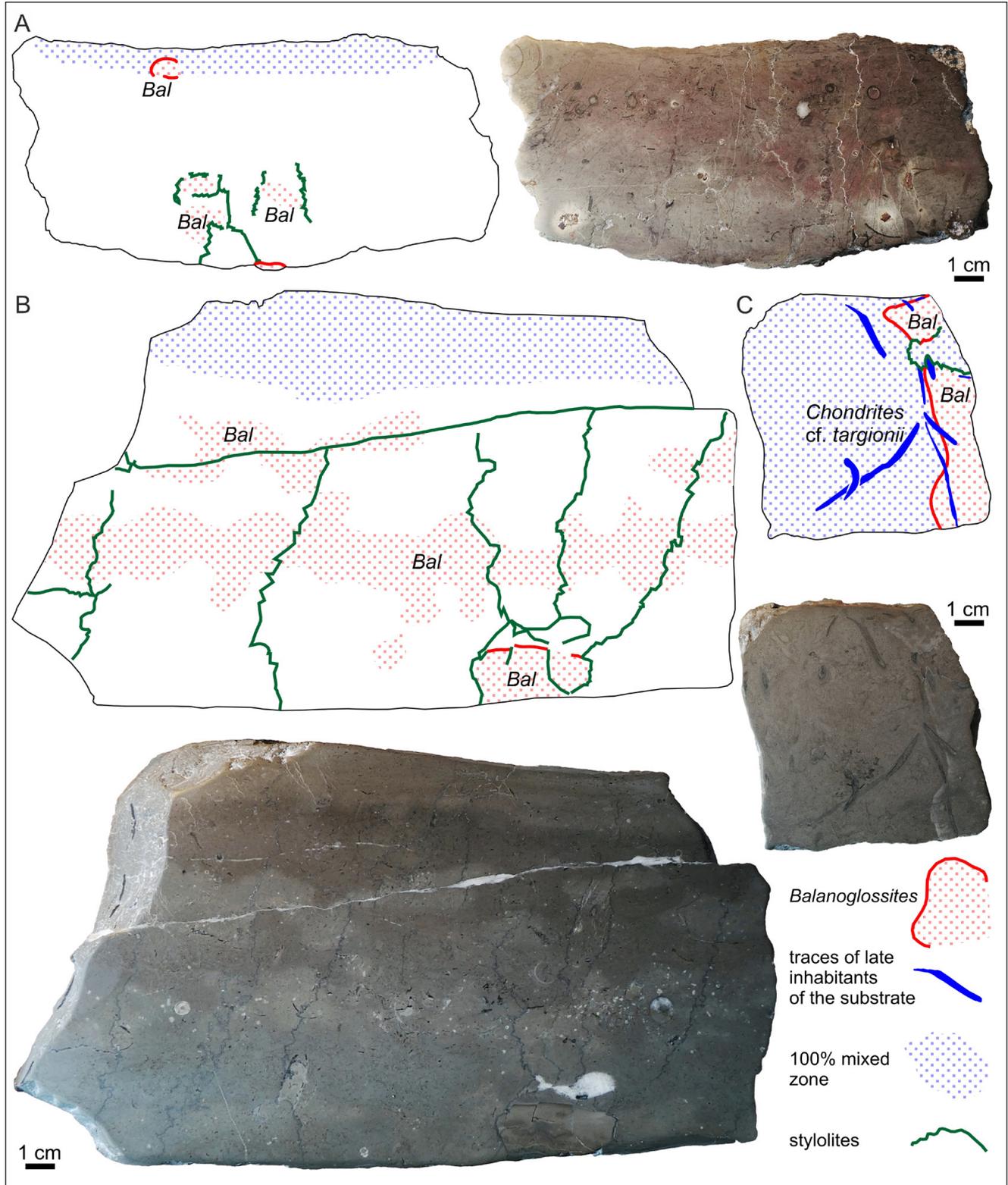


Fig. 7 - Interpretation of polished vertical sections of the selected beds: A) MRgr 4; B) POgr 2; C) BARR 135.4.

mottled spots “on the background” is 3–8 mm, although in some individual beds they exceed 10 mm. This structure can be understood as a fundamental component of the ichnofabric of the studied ear-

ly Emsian limestones. It cannot be confidently assigned within the framework of systematic ichnology, although some authors (e.g., Baucon et al. 2025) have identified similar structures as *Planolites* isp.

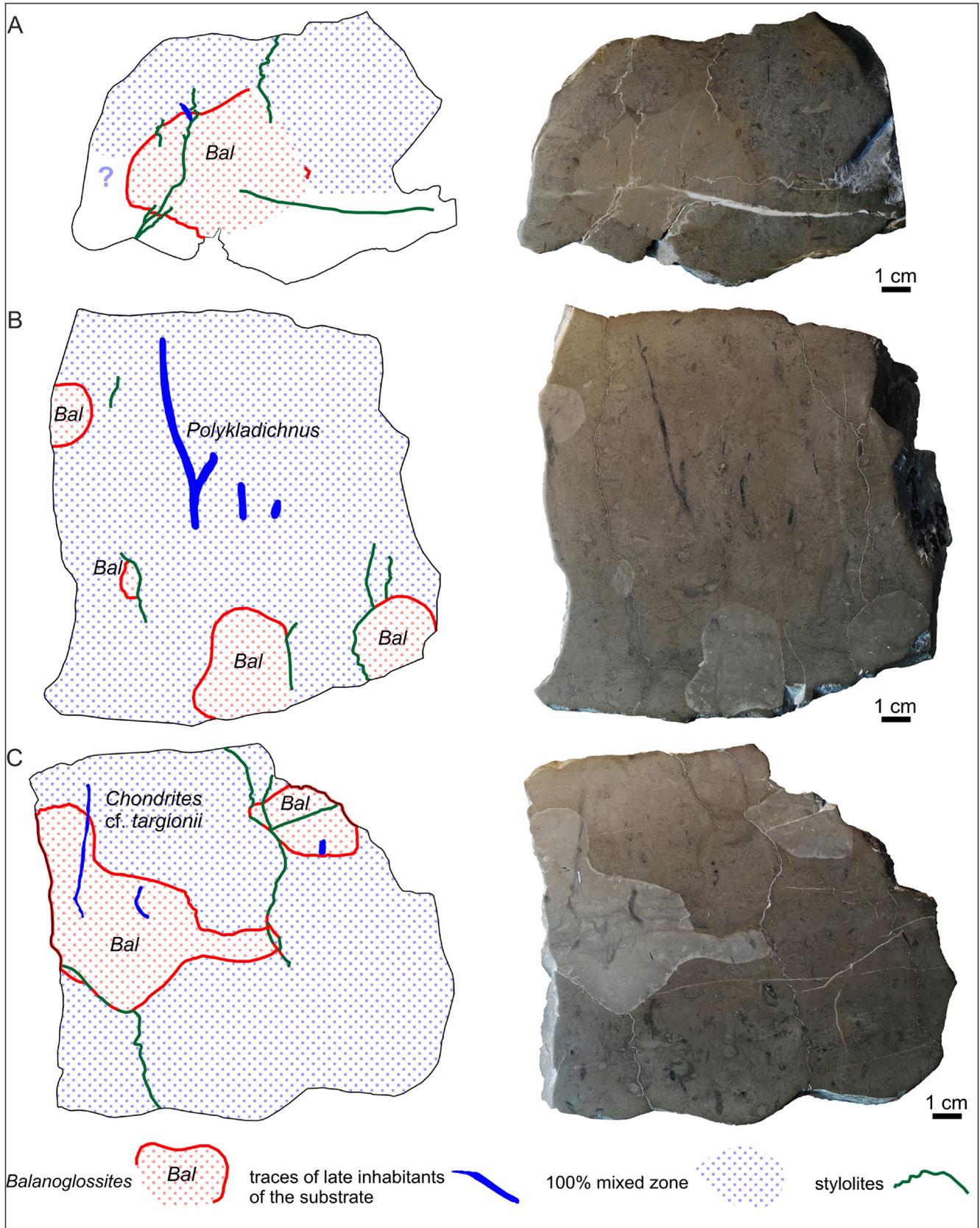
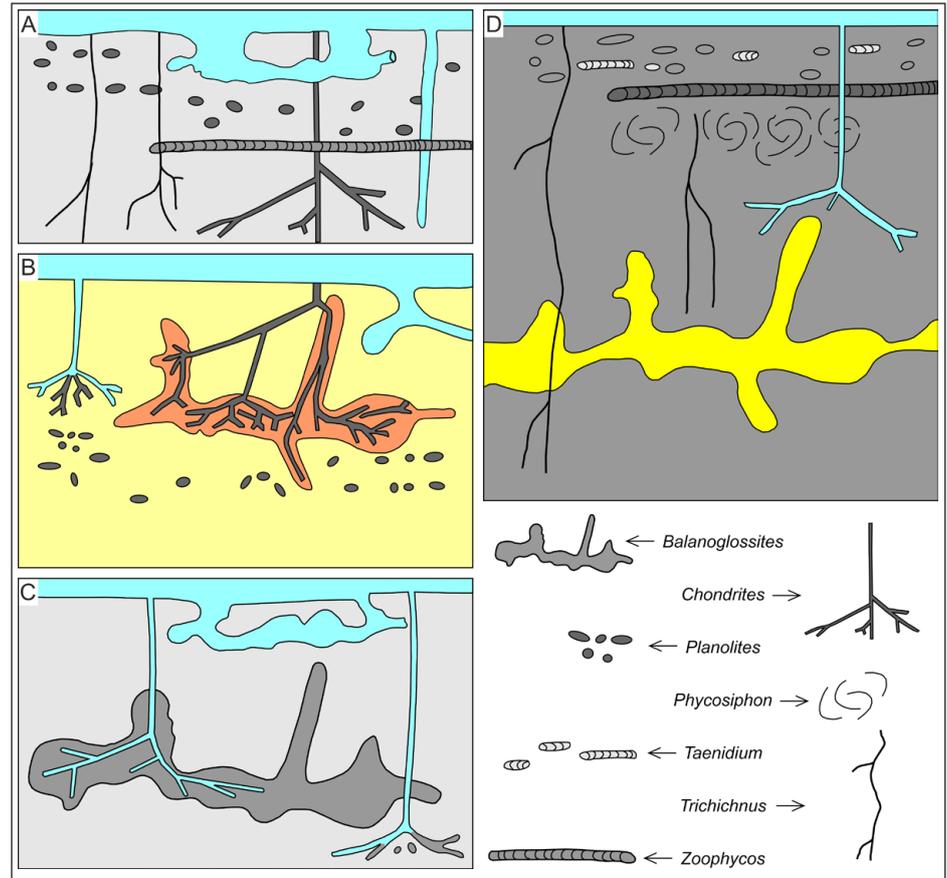


Fig. 8 - Interpretation of polished vertical sections of the selected beds: A) BARR 126.0; B) BARR 136.0; C) BARR 138.0.

Fig. 9 - Ichnofabric models for selected beds: A) Stydlé vody (STV bed no. 28); B) Mramorka (MR 1.3); C) Požár 3 (PO 112.6); D) Pod Barrandovem (BARR 172).



Distribution and temporal relationships of trace fossils

The Bohemian Graptolite Event (BGE) interval at the Stydlé vody section is particularly rich in the ichnogenera *Chondrites* (both “thin” and “thick” forms) and *Trichichnus*. *Balanoglossites* was recorded only in three limestone beds. *Planolites* was observed, while *Zoophycos* is rare, limited to a single bed (but appears frequently in debris derived from this locality). In the first strata directly overlying the BGE interval, only *Planolites*, *Chondrites*, and *Trichichnus* are abundant.

The Mramorka section shows a very abundant occurrence of *Balanoglossites* isp., stenomorphically filled by *Chondrites*, below the BGE beds. Within the BGE interval, *Balanoglossites*, *Chondrites* and a poorly represented *Planolites* were recognized in a single bed, although not all BGE beds were sampled for polished slabs. Above the BGE interval, *Balanoglossites* occurs with average frequency, while *Chondrites* is rare. *Caulostrepsis* was also observed in one sample.

The Požár 3 section is relatively weakly bioturbated. Within the BGE interval, *Planolites* was recorded in the oldest and youngest bed. *Balanoglos-*

sites is abundant in three out of seven beds. In the underlying limestone beds, both *Balanoglossites* with poor ichnofabric in the fill and *Balanoglossites* stenomorphically filled by *Chondrites* were recorded.

In the Pod Barrandovem section, a single horizon with *Balanoglossites* was found within the BGE interval, but not all beds were sampled for polished slabs. In the subsequent fifty metres, all recorded ichnotaxa are relatively abundant in at least some beds, including *Balanoglossites*, *Planolites*, *Taenidium*, *Phycosiphon*, *Polykadichnus*, ?*Trypanites*; and especially in the upper part, *Zoophycos* and *Trichichnus*.

The sequence of formation of the trace fossils is sometimes difficult to determine; however, by analysing multiple samples and using various preparation techniques, mutual cross-cutting relationships were established, and the relationships between the ichnotaxa can thus be inferred, see Fig. 9 and Supplement 2 for a detailed description of the ichnofabric in selected beds. It is evident that *Balanoglossites* was among the earliest structures to form, as it is often cross-cut and infilled by tunnels of the ichnogenus *Chondrites*, which in some cases extend beyond the original fill of *Balanoglossites* into the surrounding sediment (e.g., MR 1.3 and PO

112.6; Fig. 9B, C). One of the latest ichnofossils to appear was *Zoophycos*, which is only rarely intersected by other traces, e.g., *Trichichnus* and *Chondrites* (STV bed no. 28, BARR 172; Fig. 9A, D). Nevertheless, a *Zoophycos* intersecting the filled corridors of *C. targionii* is known from debris at the Stydlé vody section (collections of the Czech Geological Survey, Prague). Generally, the earlier ichnofossils likely include *Planolites*, *Balanoglossites*, and the rare *Taenidium*, followed by later ichnofossils such as *Zoophycos*, *Chondrites*, and *Trichichnus*.

DISCUSSION

Character of the ichnoassemblages

In the studied sedimentary sections, biodeformational structures were observed, along with the ichnogenera *Balanoglossites*, *Planolites*, *Taenidium*, *Phycosiphon*, *Trichichnus*, *Polykladichnus*, and *Zoophycos*, whereas the occurrence of *Trypanites* is considered uncertain. This ichnoassemblage, composed of post-depositional trace fossils (e.g., Madon 2021), provides valuable insights into the depositional and early diagenetic environment.

In modern environments, biodeformational structures typically form under well-oxygenated, nutrient-rich conditions (C_{org} content >2%) where endobenthic animals burrow without distinct behavioural specialization in soft to soupy sediment leaving bioturbations with no distinct outlines (Uchman & Wetzel 2011, and references therein).

Balanoglossites, *Planolites* and *Taenidium* belong to the suite of early trace fossils, representing different behavioural strategies and substrate preferences. *Balanoglossites* is a domichnion trace fossil known from a wide range of sedimentary environments, from supratidal and alluvial settings to deep marine deposits. Its tracemaker was capable of colonizing softgrounds, firmgrounds, and hardgrounds (Knaust 2021), but generally preferred shallow-water environments, particularly areas with carbonate sediments where the seafloor was partially lithified (Knaust 2008, 2021). Based on analogues from the Ordovician of Baltica (Knaust & Dronov 2013) and the Triassic of Germany (Knaust 2008), it is clear that the tracemaker of the ichnogenus *Balanoglossites* inhabited well-oxygenated environments on rapidly hardening carbonate substrates. In the studied area, such lithification likely corresponded only

to firmground conditions, as burrowing continued after the formation of *Balanoglossites*, producing traces such as *Zoophycos* and *Chondrites*. Moreover, some of the subsequent traces, usually recognizable only as mottles appeared in the soft mud fill of the firmground *Balanoglossites*.

Horizontal or subhorizontal *Planolites*, *Taenidium*, and *Phycosiphon* burrows are commonly interpreted as fodinichnia, produced by worm-like deposit feeders. *Planolites*, lacking internal structures, is generally regarded as a result of opportunistic, non-selective movement and feeding through the substrate. *Taenidium*, characterized by meniscate backfill structures, likely reflects non-selective deposit feeding, indicating systematic but undifferentiated sediment processing. In contrast, the producer of *Phycosiphon* is commonly interpreted as a selective deposit feeder that preferentially ingested fine-grained, organic-rich material. Its trace shows complex spreite morphology and compositionally distinct, fine-grained infill. The dark core of the structure likely represents faecal matter or metabolically processed sediment, while the surrounding spreite zones reflect successive movements of the tracemaker through the substrate. *Taenidium* is typically associated with well-oxygenated environments, although limited tolerance to slightly dysoxic conditions has been proposed. *Planolites* and *Phycosiphon* exhibit broader environmental tolerance. *Planolites* tends to occur in better-oxygenated substrates, while *Phycosiphon* is frequently reported from dysoxic, fine-grained distal marine environments (Bromley & Ekdale 1984; Uchman 1995; Wetzel & Bromley 1994). Thus, *Phycosiphon* likely belongs rather to the suite of later, stress-tolerant, traces, including *Trypanites*, *Polykladichnus*, *Chondrites*, *Zoophycos*, and *Trichichnus*. In studied sections, *Trypanites* was recorded very rarely. This ichnotaxon is commonly interpreted as domichnion, representing permanent domiciles of suspension-feeding organisms bored into lithified substrates (hardgrounds), rocks, and shells in well-oxygenated environments. Moreover, *Trypanites* is characteristic for assemblages of low to moderate ichnodiversity (e.g., Bromley & Asgaard 1993). The presence of this ichnotaxon suggests that, in some cases, the substrate may have lithified to a degree comparable to a hardground (see Mikuláš & Hladil 2015). *Polykladichnus* has been interpreted as both domichnion and fodinichnion associated with worm-like organisms, likely poly-

chaetes. The burrows likely served as both living spaces and feeding structures, allowing the organism to filter food particles from the surrounding sediment. This trace fossil is often associated with fine-grained sediments and occurs in a range of marine settings, from shallow to deeper environments. It typically appears in substrates with variable oxygenation, ranging from well-oxygenated to dysoxic conditions, reflecting the ecological adaptability of its tracemakers (Uchman & Álvaro 2000; Schlirf & Uchman 2005; Hanken et al. 2016).

Chondrites was recognized as a burrow produced by organisms highly tolerant of low-oxygen conditions, which searched for organic matter within the sediment (Bromley & Ekdale 1984). It is widely considered one of the most characteristic ichnogenera formed under dysoxic bottom waters and within an anoxic substrate, where chemosymbiotic relationships with bacteria could thrive (Bottjer & Droser 1991). In the studied sections, *Chondrites* is relatively abundant and represents the main, if not the only, agent of bioturbation within black shales. Two ichnospecies are present: the small and common *C. intricatus*, and the larger but much rarer *C. targionii*. The occurrence of an uncompact *C. targionii* in limestone beds suggests that it formed during a stage when limestone diagenesis was already relatively advanced. A noteworthy phenomenon is observed in the Mramorka and Požár 3 sections, where *C. intricatus* fills more than 80% of the volume within *Balanoglossites*-type burrows, while also sporadically penetrating the surrounding sediment (Fig. 6A, 9B). This provides strong evidence that *Chondrites* formed well after the abandonment of *Balanoglossites* burrows. Therefore, the ability to colonize a relatively firm substrate approaching firmground must have been within the ecological tolerance of both *Chondrites* ichnospecies.

The ethology of the *Zoophycos* tracemaker is still debated. It is unlikely that a single ethological principle can be found for such a stratigraphically and morphologically broad ichnogenus, or rather various but not recognized ichnotaxa (Zhang et al. 2015). However, for individual, homogeneous populations, more or less convincing hypotheses have been formulated about the origin of individual morphological elements and their function. One hypothesis suggests that *Zoophycos* represents gardening behaviour, similar to *Palaeodictyon*, where the organism cultivated microorganisms within the

burrow (Löwemark et al. 2007). Another possibility is that the burrows were used to cache food resources, as indicated by increased organic carbon concentrations within the burrows. Alternatively, *Zoophycos* may simply represent deposit-feeding traces, where the organism fed on organic particles within the sediment (e.g., Kotake 1991). The most convincing hypothesis joining the above-mentioned ones was formulated by Uchman & Wetzel (2016, 2024). They created a new ethological category for *Zoophycos* - sequestrichnia. The principle is that organic substances were deposited in the spreite and in times of food shortage, nutrients were obtained for the sustenance of the tracemaker with the help of external digestive juices. *Zoophycos* is typically associated with deep marine environments, often found in turbidite beds. It is known from both the fossil record and modern deep-sea sediment cores. *Zoophycos* can also occur in shallow-marine storm deposits and other environments with storm-supplied sediment input. It has a cosmopolitan distribution and has been found in sediments ranging from the Cambrian (Doucek & Mikuláš 2014) to the present. During the Devonian, *Zoophycos* predominantly inhabited nearshore to offshore environments, occurring in the shallow tier as a thin, planar spreite (Zhang et al. 2015).

Trichichnus is exceptional due to its very thin diameter and common pyritic filling. It has been interpreted as a remnant of a fossilized intra-sediment bacterial mat that is pyritized (Kędzierski et al. 2015). Thereby, *Trichichnus* forms dense filamentous fabric, which reflects that it is produced by modern large, mat-forming, sulfide-oxidizing bacteria, belonging mostly to *Thioploca*-related taxa. This fossil can be considered a “fossilized electric wire” due to its role in electron exchange between oxic and suboxic/anoxic layers in the sediment.

Trace fossils and sedimentary environment

Hemipelagites vs. calciturbidites: a brief introduction to the problem. The Dvorce-Prokop Limestone displays prominent high-frequency cycles, tens of centimeters thick, expressed either as alternations of more or less distinctly nodular limestones, or as platy limestones alternating with calcareous shale interbeds (Chlupáč 2000; Da Silva et al. 2016). Two main hypotheses have been proposed to explain the underlying sedimentary processes. Chlupáč (2000) considered Milanković-controlled hemipelagic sedimentation, with warmer periods associated with more intense car-

bonate deposition (see also Kukul 1960). He assumed the autochthoneity of fossil assemblages (Chlupáč 1983) and inferred different benthos-to-plankton/necton ratios between limestones and shales, although without detailed quantification for the interval studied here. He further argued that complex *Chondrites* are preserved in both components of the couplets, and *Zoophycos* burrows are filled with sediment derived from the overlying bed (Chlupáč 1990). While these ichnological features were interpreted in support of a hemipelagic origin, alternative explanations involving, e.g., combined hemipelagic–turbiditic processes cannot be excluded.

In contrast, Hladil et al. (1996) interpreted the limestone beds as resedimented hemipelagites, specifically muddy calciturbidites deposited by slurry or hyperconcentrated density flows. Their model suggests low-density turbidity currents travelled farther, reaching deeper basin areas. Supporting evidence includes sharp basal contacts, imbrication, graded and parallel bedding, micro-ripples, and the orientation and “telescoping” (cone-in-cone stacking) of dactyloconarid shells (see also Hladil et al. 2014; Mikuláš & Hladil 2015). Whether the small-scale cyclicity results from diagenetic overprinting (sensu Munnecke & Samtleben 1996; Nohl et al. 2019) remains insufficiently evaluated. To critically evaluate these contrasting interpretations, we examined microfacies characteristics and trace fossil distribution in our material.

Evidence from microfacies and trace fossil record. In the Dvorce-Prokop Limestone, sedimentary structures are scarce, which complicates sedimentological interpretation. However, ichnological evidence suggests that this is largely due to previously overlooked, very early bioturbation, which produced numerous biodeformational structures and gave the limestones their mottled appearance. A characteristic feature of many beds is the uneven distribution of bioclasts within individual layers. These often show diffuse patches with larger and more taxonomically diverse bioclasts (Microfacies A) embedded in sediment containing smaller bioclasts and a higher proportion of styliolinids (Microfacies B), all set in a micritic matrix rich in fine bioclastic silt. The presence of Microfacies A at the base of some beds (Fig. 3A, E) supports the interpretation of original grain-size sorting and a turbidite origin. We therefore infer that some beds were originally graded, with Microfacies

A (resembling the shallower-water Loděnice Limestone) at the base, and Microfacies B, with a higher proportion of the planktonic forms, in the upper part. Early bioturbation mixed these layers, obscuring primary sedimentary structures, although rare cases of lamination were observed in our material. Some turbidites may have been originally finer-grained and lack a coarse basal layer altogether. Micritic Microfacies C with allochem associations typical of deeper-water settings (styliolinids, radiolarians, sponge spicules, molluscs, thin-walled ostracods) most likely represents the uppermost part of turbidites grading into background sedimentation.

All *Balanoglossites* traces are interpreted as passively filled. Their infill is commonly fine-grained (Microfacies B), and in some cases even stratified (sample MR 4). However, exceptions exist where burrow infill contain relatively coarse bioclasts, including fragments of crinoids (e.g., samples POgr 1, POgr 2). Abandoned *Balanoglossites* burrows were likely filled either by coarser or finer portions of turbidity currents, or by hemipelagic sediments potentially influenced by bottom currents. These burrows may have acted as sediment traps, preserving otherwise lost sedimentary record (Wetzel 2015).

Tunnels of medium width, which we interpret as *Planolites*, have an infill very similar to the surrounding host rock. These traces were likely filled by a combination of biogenic activity and gravitational settling, almost immediately after the passage of the tracemaker. Subsequent neomorphic recrystallization of micritic portions of the burrowed sediment led to the development of Microfacies D (Fig. 4D). Cases have been found that *Planolites* isp. was crossed by a well-defined wall of *Balanoglossites*. The selectively feeding tracemaker of *Phycosiphon* produced structures with a dark, probably organically enriched core, and surrounding spreite zones, where neomorphic recrystallization of the micritic portions resulted in the formation of Microfacies D and E (Fig. 4C, E, F, I). Mild neomorphic recrystallization was also observed in *Taenidium* (Fig. 6H).

At polished slabs, some thin tunnels and shafts have a significantly darker filling than the surrounding rock (Fig. 6D–G). These traces were likely filled at a time when hemipelagic fine-grained sediment prevailed on the bottom surface. This filled the shafts either passively (*Polykladichnus*, partly *Chondrites*) or was actively transported by the tracemaker (*Zoophycos*). The darker appearance of these fills may be related

to factors such as a higher content of organic matter, differences in cementation or recrystallization, or in some cases, a higher content of “shaly” material.

Insights from the ichnofabric analysis. Differences between the ichnofabric of purely pelagic sequences and that of turbidite-bearing sequences have been described by, e.g., Uchman (2007) and Uchman & Wetzel (2011, 2012). Hemipelagic sediments exhibit a practically homogeneous ichnofabric, with sedimentary layers being uniformly and often completely bioturbated (Seilacher 1967). Usually, a maximum of three tiers is distinguished, with the tunnels and/or chambers being relatively small and only shallow (penetration 10–15 cm; Wetzel 1991). Trace fossil assemblages include ichnotaxa such as (alphabetically) *Asterosoma*, *Chondrites*, *Nereites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Teichichnus*, *Thalassinoides*, *Zoophycos*, with ichnospecies and ichnogenus diversity remaining moderate and stable (Buatois & Mángano 2011). Complete ichnofabric “spots” are formed only with an increased content of organic matter ($> 2\% C_{org}$). Otherwise, determinable burrows prevail. Spots of elite layers typical of pure turbidites are completely absent (Wetzel 1991; Buatois & Mángano 2011). In situations where layers of turbidites alternate with hemipelagic sedimentation on the seabed, a noticeable “spotty layer” is formed – a bioturbated distal part of the turbidites corresponding to the Td–Te stages according to Bouma (1962). Oval spots often appear in this zone, mainly planar burrows (*Planolites*, *Thalassinoides*), and their colour may be lighter or darker than the substrate depending on the current trophic level (Bromley & Frey 1974). Above this spotty layer lies the so-called “elite layer”, characterized by deeply penetrating traces as *Chondrites*, *Nereites*, *Phycosiphon* or *Scolicia*, which is indicative of sequential colonization and multilayer penetration into the sediment (MacEachern & Pemberton 1994). Traces of the so-called elite layer may occur due to the assumed (but sometimes difficult to prove) interplay between sedimentation and erosion (see Fig. 10). Bioturbation here shows significant crossing of traces between different generational phases and can lead to pseudolamination due to compaction deformations of biodeformational structures. Multilayered colonizers (e.g., *Chondrites*, *Ophiomorpha*) often penetrate the entire profile of turbidite layers, with higher trophicity mediating greater trace fossil diversity and deeper bioturbation compared to purely hemipelagic

sediments (Bouma 1962; MacEachern & Pemberton 1994).

Combined turbiditic-hemipelagic sequences can be distinguished from purely hemipelagic sequences by the following features: 1, presence of spotty layers and elite layers in turbidites (absent in hemipelagic sediments). 2, higher number of tiers and sequential colonization phases in turbidites versus stable, low number of tiers (< 3) in hemipelagite. 3, high diversity of trace fossil generation phases and cross-tracking in turbidites versus moderate, constant diversity in hemipelagite. 4, occurrence of pseudolamination and mixing of hemipelagite with turbidites versus absence of sharp contrasts and biodeformation layers without compaction deformations.

A model combining both sedimentation mechanisms (turbidites and hemipelagites) appears to best explain the complexity and mutual relationships of trace fossils in the Dvorce-Prokop Limestone. The observed succession (from early structures to later, less interrupted trace systems) suggests that impulsive turbidite deposition was followed by more stable hemipelagic sedimentation, possibly accompanied by bottom current activity. McIlroy (2004) explicitly linked analogous ichnofabric development to a two-phase depositional regime. Turbidite sedimentation is episodic and rapid. It typically leads to quick burial of the substrate, limiting the window for bioturbation to short, intermittent periods. This can result in partial overwriting or obliteration of earlier traces (Ponce et al. 2007). In contrast, hemipelagic sedimentation occurs under lower and more stable energy conditions. If bottom currents were present, they would allow for a longer-term horizontal transport of sediment along the seafloor (Stow & Smillie 2020). In the absence of high-energy depositional events, organisms have sufficient time to form more complex and continuous trace structures, gradually overprinting earlier ones (McIlroy 2004). For instance, the presence of well-preserved traces of the ichnogenus *Zoophycos*, which are rarely interrupted by other traces, suggests a period of long-term stability when the substrate did not change significantly (cf. Gong et al. 2007).

Vertical trace sequences. By studying the sequence of trace infill and analyzing the mutual relationships and intersections of biogenic structures, time-based models, referred to as time slices were constructed (Fig. 10). These models likely represent

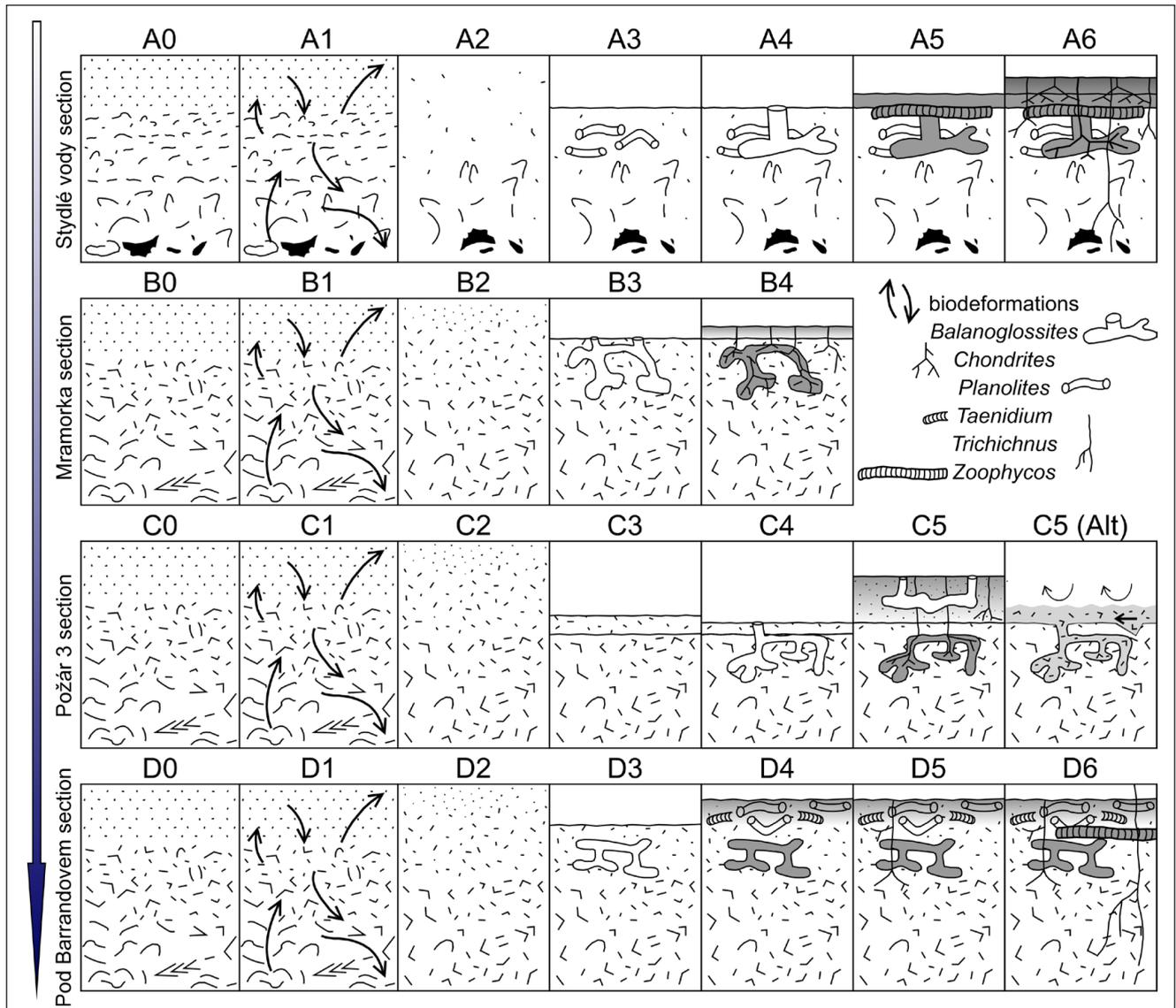


Fig. 10 - Ichnological, sedimentation/erosion and lithification history of the selected layers. A) Stydlé vody section (bed no. 28): A1, turbidite-graded bedding; A2, erosion of the upper part of the turbidite, hemipelagic/bottom current deposition, bioturbation-feeding burrows; A3, firmground colonisation by *Balanoglossites*; A4, *Balanoglossites* filled, hemipelagic sedimentation, dysoxia, *Zoophycos* supposedly filled with organic (detritus) material; A5, hemipelagic sedimentation, appearance of *Chondrites* and *Trichichnus*, dysoxia. B) Mramorka section (MR 1.3): B1, turbidite; B2, erosion, development of firmground, *Balanoglossites*; B3, hemipelagic sedimentation, *Balanoglossites* filled, selective colonisation by the *Chondrites* tracemaker. C) Požár 3 section (PO 112.6): C1, turbidite; C2, erosion and sedimentation of hemipelagic/bottom current deposits; C3, *Balanoglossites* first colonisation; C4, *Balanoglossites* in hemipelagic/bottom current deposits (second colonisation), *Chondrites*; C4 (Alternative), partial erosion, unstable bottom surface, *Balanoglossites* filled with sediment containing bioclasts sorted by sedimentary processes. D) Pod Barrandovem section (BARR 170.4): D1, turbidite; D2, hemipelagic/bottom current deposits, *Balanoglossites* colonisation; D3, firmground, dysoxia, hemipelagic sedimentation, *Balanoglossites* filled, *Planolites* and *Taenidium* appear; D4, dysoxia, *Chondrites*; D5, *Trichichnus* and *Zoophycos* colonized the firmground. The vertical arrow on the left indicates increasing water depth.

periods spanning decades, centuries, or even millennia of seabed development, beginning with a turbidity event and culminating in a state where the entire turbidity and post-turbidity sediment has become a historical layer in the sense of Bromley (1996). In general, three distinct phases can be identified.

Phase 1. (Fig. 10A0 to A2, B0 to B2, C0 to C2, D0 to D2) rapid, short-term turbidite pulse resulted

in initial sediment deposition, in some cases showing features such as sharp basal contacts, grain-size grading, and lamination. These freshly deposited turbiditic sediments probably contained relatively well-oxygenated pore water and a high amount of nutrients, which promoted intense non-specialized burrowing, obscuring primary sedimentary structures. Mixing of the material appears to have occurred very rap-

idly, and it is difficult to determine the exact style of bioturbation and its producer (trilobites or annelids are possible candidates). The substrate must have been of very soft or soupy consistency, as organisms moving through it mixed the sediment and left behind biodeformational structures with no distinct boundaries. Consequently, conditions favourable for the benthos may have changed for the worse very quickly.

Phase 2. (Fig. 10A3 to A4, B3, C3 to C5, D3 to D5) The appearance of trace fossils such as *Balanoglossites*, *Taenidium*, or *Planolites* may indicate the onset of colonization in a moderately energetic environment (Buatois & Mángano 2011). The sediment likely had the consistency of softground or firmground. Subsequently, overwriting and repeated reworking events may have occurred, as later organisms filled voids or even overprinted earlier structures—for example, *Chondrites* penetrating pre-existing sequences. The presence of *Chondrites* tunnels that not only occupy former *Balanoglossites* but also extend into the surrounding sediment may indicate reworking processes within the framework of turbidite cyclicity.

Phase 3. (Fig. 10A5 to A6, B4, D6) With the longer-term influence of hemipelagic sedimentation or possibly bottom currents, when deposition slowed down and stabilized, more sophisticated and persistent traces such as *Zoophycos* and *Trichichnus* may have formed. This stabilization protected the already-formed structures from further mechanical reworking. *Trichichnus* represents the final phase of macroscopic biogenic activity, and its pyrite-filled traces suggest that the sediment may already have been completely devoid of free oxygen.

The Dvorce-Prokop Limestone of the Prague Synform likely reflects multiple depositional environments and processes. Although mud mounds with autochthonous fauna are also known from this member (St. Prokop locality, see Chlupáč et al. 1998), a substantial portion of it was probably formed by turbidites.

Ichnoassemblages response to sea-level and climate changes

Only subtle ichnological changes are observed across the studied interval with the BGE, as the overall composition of the ichnological community remains stable throughout. Likewise, when assessing potential lateral variations in the trace fossil record, the taxonomic composition of the

ichnoassemblage (based on identified ichnotaxa) proves to be a limited indicator, as the principal ichnogenera remain consistent. In contrast, the detailed ichnofabric characteristics offer a more nuanced and informative basis for interpretation than the mere presence or absence of specific ichnotaxa. These data complement previous interpretations of sea-level and climatic changes (Bábek et al. 2018a, b; Šimíček et al. 2020).

Layers underlying the BGE beds at the Mramorka section have been interpreted as representing a late transgressive phase (Weinerová et al. 2024) and are characterized by a *Balanoglossites*–*Chondrites* ichnofabric. *Balanoglossites* burrows are so abundant that they significantly contribute to the weakly nodular, “knobby” appearance of the rock. In these layers, *Chondrites* occurs predominantly in a stenomorphic form within *Balanoglossites* burrows. It is plausible that the producer of *Balanoglossites* colonized soft to firm substrates, and its extensive burrow systems may have facilitated or accelerated further substrate hardening (see Knaust 2021). The bottom sediments were likely still relatively well oxygenated, in line with the generally oxic bottom-water conditions prevailing during the deposition of the Praha Formation (Koptíková et al. 2010a; Bábek et al. 2018a, b; Šimíček et al. 2020). *Balanoglossites* burrows may have been secondarily colonized by *Chondrites* for several reasons. The sediment within *Balanoglossites* burrows was likely softer and more easily penetrate. Additionally, Yan et al. (2025) recognized in Triassic material from China that the walls of *Balanoglossites* were impregnated with organic mucus, and this enrichment in organic matter promoted localized anoxic conditions. Therefore, *Balanoglossites* burrows may have represented microenvironments with lower oxygen concentrations and enriched organic content, which attracted the *Chondrites* trace-makers. Dacryoconarid-rich sediment within *Balanoglossites* burrows may correspond to the upper parts of a turbidite or to hemipelagic sedimentation (possibly influenced by bottom currents), which may have been eroded by a subsequent turbidite. *Balanoglossites* burrows infilled with *Chondrites* were also observed at a corresponding, more sparsely sampled stratigraphic level in the Požár 3 section.

The Bohemian Graptolite Event (BGE) has been interpreted as representing a maximum flooding episode, with elevated U/Th ratios indi-

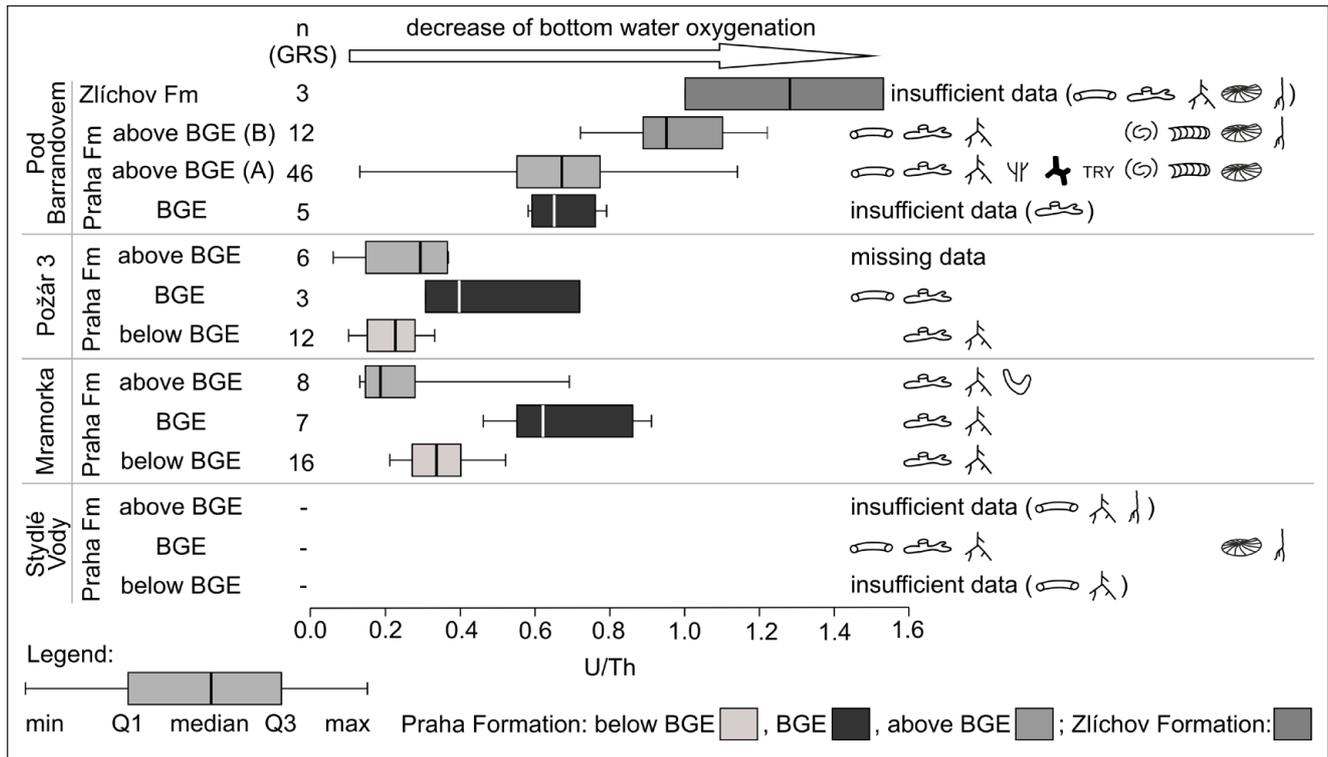


Fig. 11 - Comparison of U/Th values from the studied sections (data from Slavík & Hladil 2000; Weinerová et al. 2024 and Slavík et al. 2025), used here as a proxy for oxygenation, and the trace fossil record. Please note that part of U may be bound to detrital phases, which may slightly affect the redox signal. Abbreviations: n (GRS), number of gamma-ray spectrometry measurements; BGE, Bohemian Graptolite Event. The legend for the trace fossil symbols is given in Fig. 2.

cating a short-term decrease in bottom-water oxygenation (Bábek et al. 2018a, b; Weinerová et al. 2024; Slavík et al. 2025; Slavík et al. accepted). In the Mramorka and Požár 3 sections, U/Th values from the BGE interval are elevated compared to the adjacent underlying and overlying beds; however, they remain still lower than the values recorded in the uppermost part of the Praha Formation and in the Zlíchov Formation at the Pod Barrandovem section (see Fig. 11). Most ichnological data from the BGE interval come from the Stydlé vody section, where each limestone bed was sampled for a polished slab. A relatively diverse ichnoassemblage was documented, including *Planolites* and occasional *Balanoglossites*, as well as *Chondrites*, *Zoophycos*, and *Trichichnus*. It is worth noting that the latter two ichnotaxa have also been observed in the uppermost, oxygen-depleted beds of the Praha Formation at the Pod Barrandovem section. The presence of complex and continuous trace structures within the BGE interval suggests periods of stable conditions. The BGE interval is also characterized by dark calcareous shale interbeds containing *Chondrites*, which represent background hemipelagic sedimentation. The BGE limestone beds at other localities are gen-

erally poor in trace fossils. At the Mramorka section, *Balanoglossites* was recorded, but in much lower abundance than in the underlying strata. Another ichnotaxon, *Chondrites*, occurs independently, no longer preferentially filling *Balanoglossites* burrows. At the Požár 3 section, *Planolites* and *Balanoglossites* were documented. It can be speculated that the oxygenation decline during the BGE affected proximal settings more strongly, whereas in generally less-oxygenated distal environments (Pod Barrandovem section), the change was not as pronounced.

Layers overlying the BGE beds have been thoroughly studied in a distal development at the Pod Barrandovem section, extending into the lowermost part of the Zlíchov Formation. The ichnoassemblage is relatively diverse, including *Planolites*, *Balanoglossites*, *Taenidium*, *Phycosiphon*, *Chondrites*, *Polykladichnus*, *?Trypanites*, and, in the higher parts (Section B), also *Zoophycos* and *Trichichnus*. This relatively high ichnodiversity likely reflects a combination of ecological and taphonomic factors under more stable depositional conditions. Section A probably reflects highstand conditions, whereas Section B corresponds to the late highstand and sea-level fall (Slavík et al. accepted). In many respects, the

Dvorce-Prokop Limestone in Section B represents a transition into the overlying Zlíchov Formation. The bioclastic beds rich in crinoid debris appear, and *Zoophycos* becomes common (Chlupáč 1990; Weinerová 2022; Slavík et al. accepted). A decline in oxygenation is indicated by increased U/Th ratios (Slavík & Hladil 2000; Slavík et al. accepted), darker limestone colouration, and a sparse macrofossil record (Petránek 1951; Chlupáč & Lukeš 1999). The appearance of *Zoophycos* and *Trichichnus*, both associated with deeper-tier and more stress-tolerant behaviours, suggests that the benthic community adapted to low-oxygen but relatively stable substrates. The overall decline in benthos and its activity may have facilitated the preservation of these more complex trace fossils. According to Bábek et al. (2018a) and Šimíček et al. (2020), the transition from the Praha Formation to the Zlíchov Formation reflects a climatic warming and a shift from a well-oxygenated carbonate ramp to a more poorly oxygenated platform setting.

The influence of ichnofabric on sediment diagenesis

Ichnofabrics are well known to influence sediment diagenesis, as bioturbation modifies organic content, porosity and permeability, enhances fluid flow, and leads, e.g., to fabric-selective silicification and dolomitization (e.g., Bromley & Ekdale 1984; Gingras et al. 2004; Knaust 2021; Niu et al. 2022; Eltom et al. 2025). This effect is clearly demonstrated in the studied sedimentary sections. At the Mramorka and Požár 3 sections, *Balanoglossites*/stenomorphic *Chondrites* burrows are more intensively dolomitized in comparison to the host rock, whereas at the Pod Barrandovem section, *Balanoglossites* burrows are selectively silicified (see also Weinerová et al. 2024; Slavík et al. 2025; Slavík et al. accepted). These silicified *Balanoglossites* burrows at Pod Barrandovem likely represent the so-called “incipient cherts” described by earlier authors (Petránek 1951; Chlupáč 1957). Determining the origin of the silica is beyond the scope of this paper. However, for chert nodules, bands and other forms of silicification in the Devonian of the Prague Synform, a biogenic, terrigenous, and volcanic source of silica have been proposed (Petránek 1946; Bouček 1964; Kukul 1964; Čáp et al. 2003; Mergl 2010).

Among the studied sedimentary sections, Pod Barrandovem represents the deepest depositional

environment. This is evidenced, e.g., by a higher content of sponge spicules and radiolarians, with the upper part of the Dvorce-Prokop Limestone exhibiting the highest proportion of organisms with siliceous skeletons representing a potential source of silica (see Weinerová 2022: figs 27, 28).

Locally, the *Balanoglossites* ichnofabric contribute significantly to the slightly nodular (“knobby”) character of the limestone beds. This phenomenon is well documented from various stratigraphic levels worldwide (see Knaust et al. 2021; Yan et al. 2025 for references), but had not been recognized in the Prague Synform until study by Weinerová et al. (2024). In the studied sedimentary sections, the nodular appearance of limestones resulted largely from the abundance and shape of the *Balanoglossites* burrows, their relative susceptibility to pressure dissolution along the burrow–host rock boundaries, and the contrasting resistance of their infills (more intensely dolomitized, or silicified) compared to the host rock. The Devonian sediments of the Prague Synform exhibit a wide variety of nodular limestone types, ranging from those with a “knobby” surface to well-developed limestone nodules floating in a mudstone or calcareous shale matrix (e.g., Chlupáč et al. 1998). Although the mode of nodule formation is still under discussion (see Kukul 1964, 1975; Mikuláš 1994; Mikuláš & Hladil 2015), we demonstrate that ichnofabric is responsible for the weakly nodular appearance of some limestone beds. The identification of *Balanoglossites* at other stratigraphic levels remains a subject of further research. The situation is complicated by the fact that the *Balanoglossites* ichnofabric is often much more easily recognized after acid etching of samples than directly in the field.

CONCLUSIONS

Early Emsian limestone-dominated successions close around the Bohemian Graptolite Event beds (Praha Formation, Prague Synform, Czech Republic) were evaluated for their trace fossil record.

Biodeformational structures, along with trace fossils *Balanoglossites*, *Zoophycos*, *Planolites*, *Taenidium*, *Phycosiphon*, *Trichichnus*, *Polykladichnus*, *Caulostrepsis*, and possibly also *Trypanites*, were identified.

Although *Polykladichnus* is mainly known from the Upper Jurassic to the Pleistocene, this study confirms its earlier occurrence in Devonian limestones

of the Prague Synform, as previously noted by Mikuláš (1994).

The observed ichnoassemblage likely reflects a combined depositional regime, in which episodic turbidite input was followed by phases of more stable, hemipelagic sedimentation.

The Bohemian Graptolite Event interval and the uppermost part of the Dvorce-Prokop Limestone share several ichnological features, such as the occurrence of *Zoophycos* and *Trichichnus*. This suggests similar environmental stressors, particularly reduced oxygenation under otherwise relatively stable depositional conditions.

This study demonstrates that the slightly nodular (“knobby”) character of some Devonian limestones in the Prague Synform is related to the presence of a *Balanoglossites* ichnofabric.

Balanoglossites ichnofabric had a strong impact on diagenesis, including selective dolomitization and silicification.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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