

ENDOLITHIC MICROBORINGS IN CORALS FROM THE *ACANTHOPYGE* LIMESTONE (MIDDLE DEVONIAN, EIFELIAN; BARRANDIAN AREA; CZECH REPUBLIC)

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Abstract: Three types of microborings are described on corallites of aulopodid corals from the *Acanthopyge* Limestone, Choteč Formation, Middle Devonian (Eifelian) of Central Bohemia. Straight unbranched galleries and swellings of *Irhopalia* isp. are interpreted as being produced by a phototroph, likely a chlorophyte. Two other rare ichnospecies likely represent sponge borings (*Entobia*? isp., *Dendrina*? isp.). The microborings are preserved by the hydrated iron oxide mineral casts after pyrite fillings. The perfect three-dimensional preservation of the microborings represents an alternative for the resin casting method, which cannot be used in solid limestone, where the microborings are filled by precipitated calcium carbonate.

Keywords: Endolithic borings, chlorophyte, *Irhopalia*, *Entombia*, *Dendrina*, Eifelian, Koněprusy reef, Barrandian

INTRODUCTION

Modern methods of study of microborings use polymerizing resin for making three-dimensional casts inside carbonate substrates (Golubic *et al.* 1970, Tapanila 2008, Wisshak 2017). After the polymerization, the carbonate is removed by acid, and the resin-cast replicas are studied using a scanning electron microscope (SEM). This method is unusable where the microborings are in material embedded in hard limestone because bioerosional traces are often filled by calcium carbonate precipitates. The dissolution of the carbonate shell also removes the microborings and their natural infills. Micro-computed tomography enables virtual three-dimensional reconstruction of the specimen. It is intensively used for the study of recent and fossil bioerosional traces and internal structures (e.g., Schönberg & Shields 2008, Lee *et al.* 2017, Wisshak *et al.* 2017, Heřmanová *et al.* 2020, 2023, Kočová Veselská 2021) but has limitations related to the micro-CT image resolution and the chemical composition of examined materials (Schönberg & Shields 2008, Heřmanová *et al.* 2023).

The diagenetic processes provide natural alternatives, such as infills by fine mud or micritic limestone inside dissolved shells and other large

naturally dissolved bioclasts (Furlong & McRoberts 2014, Mergl 2020). Recently, hydrated iron oxide mineral fills of microborings have been observed in residues after the dissolving of limestone by acetic acid, originally conducted to extract conodonts and shells of organophosphatic brachiopods. These three-dimensional casts clearly replicate the complex system of microborings that shallowly penetrate into corallites of corals and probably to other but hardly identifiable carbonate substrates. Salomon *et al.* (2021) described similar ferruginous crusts and iron-filled microborings in corals from the Cenomanian of Germany. The natural pyrite fillings of microborings were described by Tapanila (2008), where pyrite casts provided sufficient permeability for resin infiltration.

MATERIAL AND METHODS

The limestone pieces (ca. 10 kg) were dissolved in 15% solution of acetic acid for 3–5 days. The residue was rinsed with water in Petri dishes, left unsieved, and air-dried. Loose small hydrated iron oxide mineral casts were picked from the residue under a stereomicroscope, mounted on SEM stubs,

coated with gold, and examined in Scanning Electron Microscope (JSM-7401F JEOL) at the Biology Centre of the Academy of Sciences of the Czech Republic at České Budějovice, South Bohemia. In a light photo, the whitening by ammonium chloride was used (Plate I, fig. 1).

The hydrated iron oxide casts take a form similar to fragile laminae or thin flakes. They represent mineralized coatings of the original calcium carbonate substrate. These hydrated iron oxides originated from diagenetically transformed pyrite. Some of the casts preserved iron hydroxide pseudo-

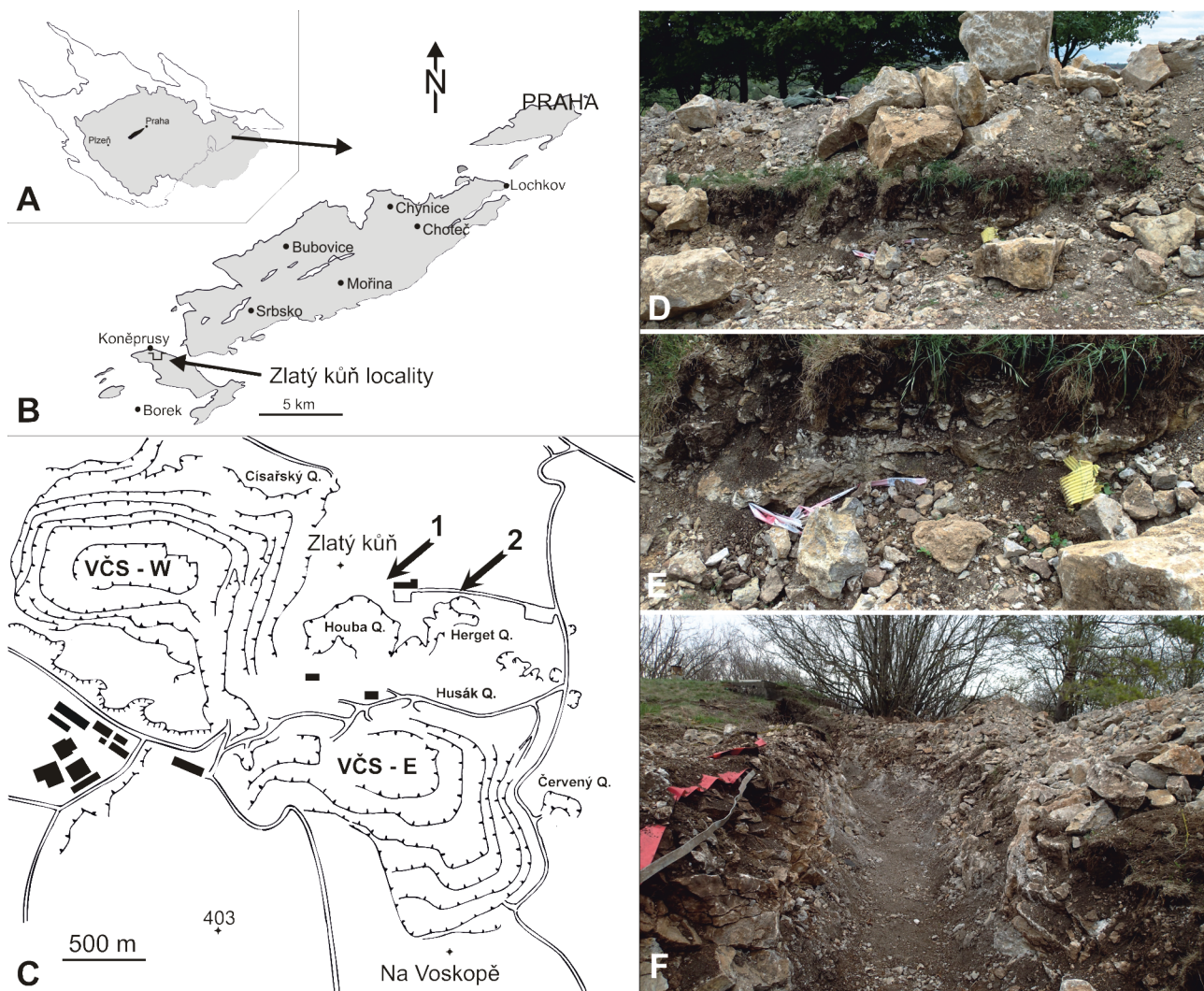


Figure 1. Sketch maps of the Czech Republic in the Bohemian Massif (A); the Devonian in the Barrandian (B) with position of the Koněprusy area; the Koněprusy area (C) with marked sampled localities (1, 2); the locality 2 (D), the road cut near asphalt road to the Zlatý Kůň hill and its detail (E) with beds of the tectonized and weathered Acanthopyge Limestone; the locality 1 (F), a temporary excavation (in June 2022) on the east slope of the Zlatý Kůň, with the outcropping Acanthopyge Limestone.

Plate I. *Irhopalía* isp.; *Acanthopyge* Limestone, Eifelian; Zlatý Kůň locality, Koněprusy, Central Bohemia.

1–6 – Cluster of aulopodid corallites (coated by ammonium chloride) and particular corallites (uncoated) with microborings, PCZCU 2876; number at arrows indicate figured corallites; note length and direct course of tunnels. 7 – Cast of corallite surface, showing original growth rings and fills of tunnels of *Irhopalía* isp., PCZCU 2877. 8, 9 – Cast showing growth rings of corallite surface and tunnels with two swellings, PCZCU 2878. Bar lengths in μm if not stated otherwise.

Plate I

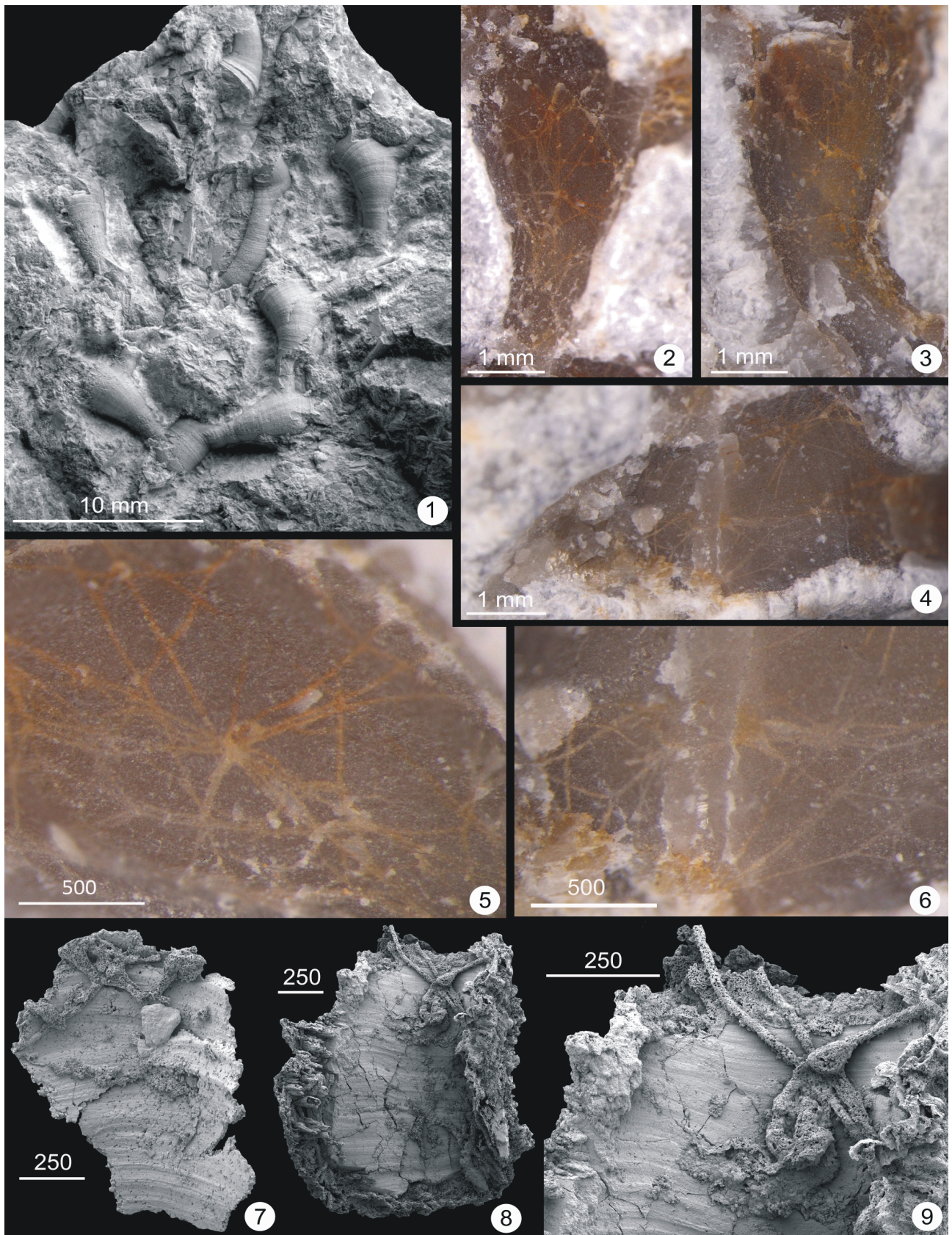
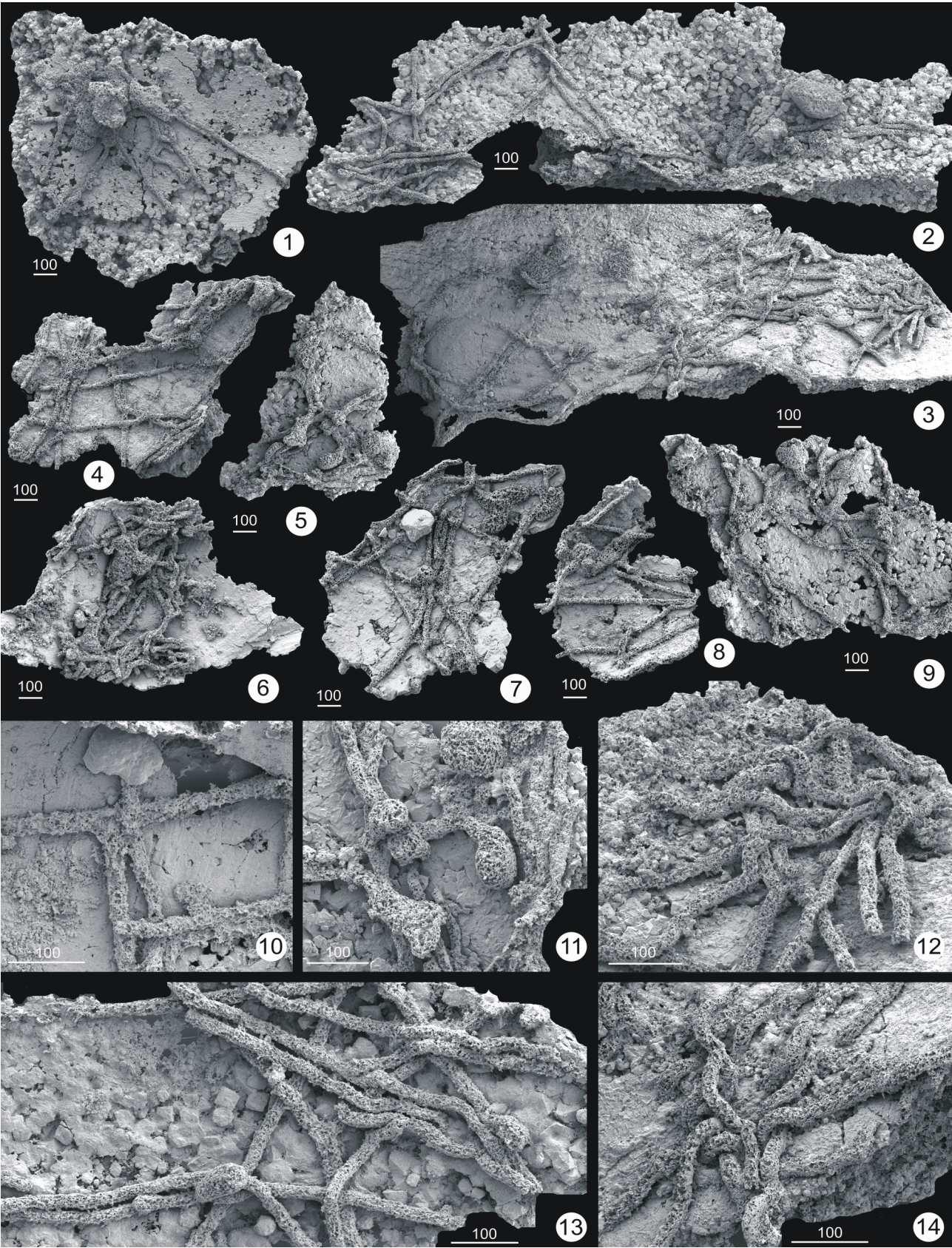


Plate II



morphs after cubic and octahedral pyrite crystals adjacent to the corallite surface (Plate II, figs 2, 13). The microborings inside the corallites are preserved as galleries filled with porous hydrated iron oxides, showing different textures from the surface mineralization. The growth rings of rugose corals are clearly preserved in some larger casts (Plate I, figs 7–9). The original taxonomic group of some substrates cannot be identified due to the small size of casts (Plate II, figs 1, 6, 7).

Probably the same microborings were observed in weakly recrystallized corallites of auloporid coral growth preserved in solid limestone (Plate I, fig. 1). The microborings form the intersected galleries with rusty infill (Plate I, figs 2–6).

The abundance of tunnel fills in the examined casts is amazing. Almost all examined large and medium-sized casts (19 specimens; small casts were not considered) bear the microboring traces, although casts covered only a small portion (one to three quadrate millimeters) of the host surface. The comparatively smaller microborings of cyanobacteria and fungi have not been identified in casts. Their absence is considered the original feature, but it cannot be excluded that pyrite was not able to form casts of significantly smaller tunnels.

All figured specimens are stored in the collections of the Center of Biology, Earth and Environmental Sciences of the University of West Bohemia at Plzeň, Czech Republic (PCZCU 2876 to PCZCU 2890).

GEOGRAPHICAL AND GEOLOGICAL SETTING

The *Acanthopyge* Limestone is a local member of the Choteč Formation, representing Middle Devonian shallow-marine, peri-reef deposits atop the Koněprusy submarine elevation in the Prague

Basin. The member consists of crinoidal grainstones/rudstones, and bahamites (Havlíček & Kukal 1990, Galle & Hladil 1991). The Eifelian age of the *Acanthopyge* Limestone is well-documented by goniatites (Chlupáč & Turek 1983), conodonts (Zikmundová & Kalvoda 1991, Berkyová 2009, Vodrážková & Suttner 2022), and other invertebrates (Chlupáč 1983, Havlíček & Kukal 1990). The Eifelian/Givetian age of the interval above the dark interval (“upper dark interval” *sensu* Hladil *et al.* 1992) of the *Acanthopyge* Limestone has been established by index tabulatophylloids and stromatoporoids (Hladil 1993).

All specimens come from the upper part of the *Acanthopyge* Limestone, from the interval that was informally referred to as “*Amplexus* limestone” (Svoboda & Prantl 1949). The limestone beds were temporarily exposed in 2022 in a shallow excavation along the asphalt road approximately 350 m eastward from the summit of Zlatý Kůň hill (Figures 1C, D, E) and in a trench about 140 m east of the summit of Zlatý Kůň hill (Figures 1C, F). The studied interval consists of poorly bedded, bioclastic limestone, dominated by crinoids and corals, with a grey micritic matrix between corallites, crinoid ossicles, and other skeletal remains. The fossils are characteristic of the *Acanthopyge* Limestone, with abundant trilobites (proetids, *Phacops hoseri*, *Acanthopyge haueri*; see Chlupáč 1983), smooth-shelled spire-bearing brachiopods (e. g. *Karbous hassiacus*, *Trigonatrypa baucis*, *Quasidavidsonia mediocarinata*, *Eoreticularia fraterna*, *Cingulodermis columbina*; see Havlíček & Kukal, 1990), and diverse rugose and auloporid corals (see Galle 1994). Other fauna is less common. The rare occurrence of *Tortodus* sp. conodont elements indicates the upper Eifelian (*Tortodus australis* Zone or *T. kockelianus* Zone).

Plate II, *Irhopalina* isp.; *Acanthopyge* Limestone, Eifelian; Zlatý Kůň locality, Koněprusy, Central Bohemia.

1 – Cast with radiating tunnels and complex swelling, PCZCU 2879. **2, 13** – Large cast with tunnels and large swelling, and detail of crossing tunnels, note pyrite crystals pseudomorphs; note one incipient swelling and one small swelling in left low corner, PCZCU 2880. **3, 12, 14** – Large cast with two crossings of tunnels and their details, PCZCU 2881. **4** – Cast with crossing of direct tunnels, PCZCU 2883. **5, 11** – Cast with several swellings, and its detail, PCZCU 2885. **6** – Cast with clusters of meandering tunnels and a swelling, PCZCU 2884. **7** – Cast with parallel straight tunnels, PCZCU 2888. **8** – Cast with straight tunnels and one elongate swelling, PCZCU 2886. **9** – Cast with meandering tunnels and a swelling, PCZCU 2882. **10** – Cast with branching (?) tunnel, PCZCU 2887. Bar lengths in μm .

SYSTEMATIC ICHNOLOGY

Ichnofamily Ichnoreticuliniidae Wisshak, Knaust & Berling, 2019

Ichnogenus *Irhopalia* Wisshak, Knaust & Berling, 2019

Diagnosis: See Radtke (1991).

Type ichnospecies: *R. catenata* Radtke, 1991 comb. nov. by Radtke (1991).

Irhopalia isp.

Plates I, II

Material: Twelve casts with numerous microborings (PCZCU 2876 to PCZCU 2887).

Description: The preserved casts represent a complicated system (Plate II, figs 1–9) of principally unbranched direct tunnels, with scattered swellings of uneven size (Plate II, fig. 13). The tunnels are circular in a cross-section, having very uniform, 22 to 25 μm diameters ($n = 30$). The lengths of tunnels are up to 1 mm (Plate I, figs 5, 6). The tunnels lack any constrictions or inflations along their length. The tunnels are principally straight (Plate II, fig. 2). This form of a tunnel is well developed in weakly bored parts of a host substrate. There the tunnels run immediately below a surface of corallite, likely leaving a thin sheet of material above a roof of the tunnel (Plate II, fig. 12). This is apparent from rounded profiles of the tunnel infill that is only loosely attached to the planar surface of a cast. The tunnel crossing the earlier generation of tunnels immediately returns to the intact surface of a corallite. Some infills could represent a real blind end of a tunnel (Plate II, figs 3, 10, 12). Only one perpendicular branching of tunnels has been observed (Plate II, fig. 10).

The elongate, blind sac-like smooth swellings locally extend from tunnels (Plate I, figs 7–9; Plate II, figs 1, 2, 5, 9). The swellings are inconspicuous (Plate II, fig. 13), but likely expanded with time. Their final size (up to 150 to 170 μm) several times exceeds the diameter of tunnels. The swellings are always hollowed inwards from a parent tunnel (Plate II, figs 1, 11, 13). One complex system of unevenly sized swellings was observed (Plate II, fig. 1). It seems likely that the radiating system of evenly sized tunnels extend from this swelling

cluster (Plate II, fig. 1). The radiating systems and the intersections of direct microborings are clearly seen also in the corallites of the aulopodid colony (Plate II, figs 5, 6).

Remarks: The spacing of individual tunnels indicates up to seven tunnels arising in a tie sequence. The earliest tunnel run is always immediately below the surface of the corallite. The subsequent tunnels were dug up below the earlier existing tunnels. As soon as possible, the tracemaker of the subsequent tunnels returned immediately below the surface of the corallite. A plausible interpretation is that the tracemaker was light dependent. When considering the spatial distribution of tunnels and their diameter, a chlorophyte origin of galleries is suggested. However, the size and arrangement of tunnels and swellings are also similar to C-type microborings observed on shells of the Pliocene bivalves (Mayoral 1988) that likely originated by fungi.

Ichnofamily Entobiaidae Wisshak, Knaust & Berling, 2019

Ichnogenus *Entobia* Bronn, 1837

Diagnosis: See Wisshak (2008).

Type ichnospecies: *Entobia cretacea* Portlock, 1843 by subsequent designation of Häntzschel (1962).

***Entobia*?** sp.

Pl. III, figs 1, 4

Material: One natural cast (PCZCU 2889).

Description: The cast of microboring shows the aggregation of simple, externally semi-opened, irregularly shaped sac-like hollows. The hollows have 50 to 120 μm diameters and smooth surfaces. They are interconnected by about 50 μm wide and more than 500 μm long tunnel which split into several thinner and shallowly excavated tunnels at one end (Plate III, fig. 4, left end). Short cylindrical excavations penetrate into a floor of the tunnel (Plate III, fig. 4).

The X-like crossing of the thinner tunnel near the surface of the host substrate and the wider and more deeply hollowed tunnel is discernible. The roofs of tunnels are not preserved.

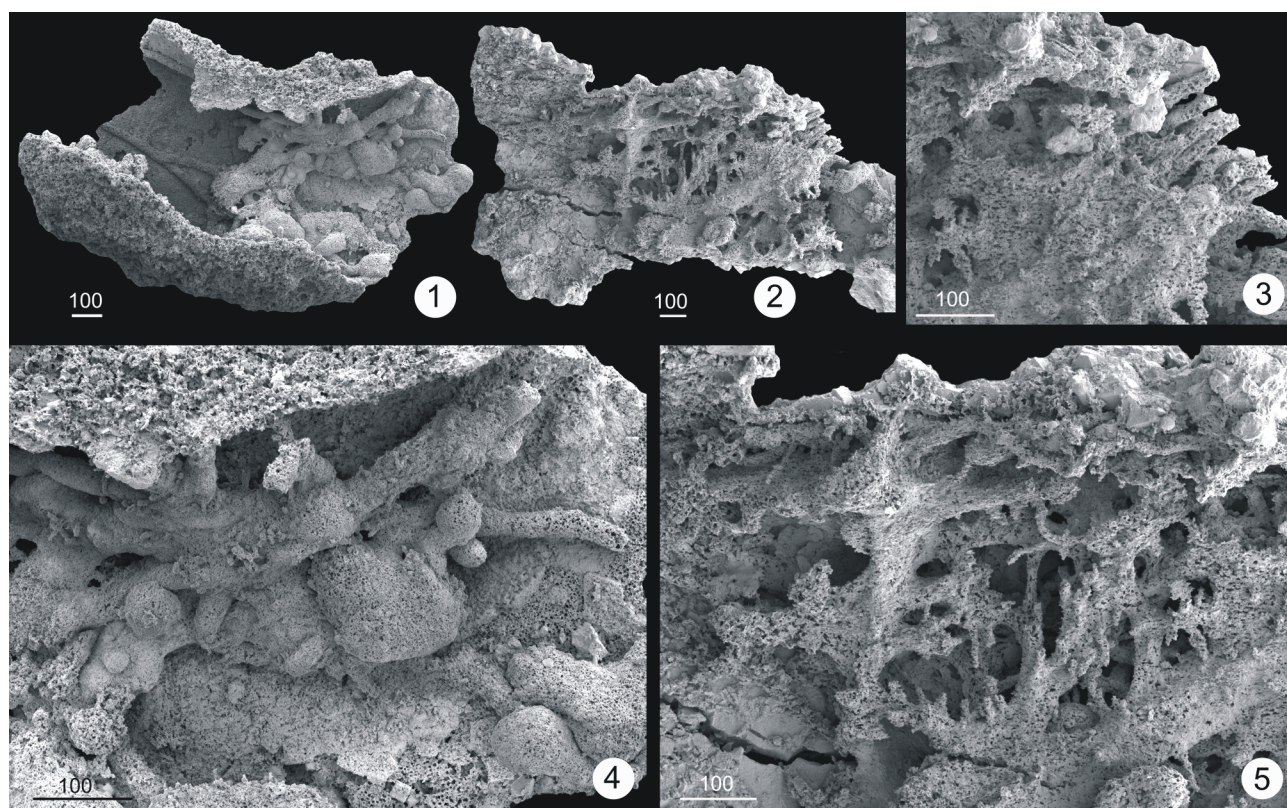


Plate III, 1, 4 – *Entobia?* isp.; *Acanthopyge* Limestone, Eifelian; Zlatý Kůň locality, Koněprusy, Central Bohemia; cast with cluster of swellings and wide tunnels, and its detail; compare slender straight tunnel of *Irhopalia* isp. in left, PCZCU 2889. **2, 3, 5** – *Dendrina?* isp.; *Acanthopyge* Limestone, Eifelian; Zlatý Kůň locality, Koněprusy, Central Bohemia; cast with broad excavations and short lateral galleries, and its detail; note several parallel infills of *Irhopalia* isp. in the upper right corner of Figure 3, PCZCU 2890. Bar lengths in μm .

Remarks: The only observed irregular cluster of hollows is clearly larger than the associated galleries of *Irhopalia* isp. The sac-like hollows are to some extent similar to sponge boring traces, which are known from the Devonian to the Recent (e.g. Radtke 1991, Wilson 2009). The sac-like hollows are conspicuously small to *Entobia* ichnogenus. The prevalent extent of *Entobia* systems is in a magnitude of a few centimetres to more than a decimetre (Wisshak 2008). However, the same author described small forms *Entobia mikra* Wisshak, 2008 and *E. nana* Wisshak, 2008 from the Pleistocene deposits of Rhodes with a size of only a fraction of a millimetre. The borings are cca 60 to 760 μm sized, potato-sack-shaped with botryoidal surface microsculpture. The boring sponges are most likely the tracemakers of these dwarf entobias (Wisshak 2008). The sponge tracemaker

of herein-described *Entobia?* isp. is rather problematic because a botryoidal microsculpture is not developed on the surface of the cast, hollows are rather irregular and fused to root-like cylindrical tunnels. Therefore, the open taxonomy is preferred. The finer vermiform structures distinct in a floor of a larger tunnel and adjacent large chamber (Plate III, fig. 4, centre) likely have a different tracemaker.

Mikuláš (1994) described similar chamber-like structures from the Devonian of Moravia (Czech Republic). He compared these excavations observed in stromatoporoids and tabulate corals with *Entobia magna* Bromley & D'Alessandro, 1989, which was described from the Pliocene and the Pleistocene of Italy.

Ichnofamily Dendrinidae Bromley, Wisshak, Glaub & Botquelen, 2007

Ichnogenus *Dendrina* Quenstedt, 1849

Diagnosis: See Wisshak (2017).

Type species: *Talpina dendrina* Morris, 1851, by subsequent designation of Häntzschel (1962).

***Dendrina?* isp.**

Plate III, figs 2, 3, 5

Material: One natural cast (PCZCU 2890).

Description: The infill shows an irregular anastomosing system of deeply penetrating tapering tunnels with a spinose structure (Plate III, fig. 2). The secondary, short, side tunnels extend from the proximal tunnels at diverse, usually acute angles. They have irregular spacing. The diameter of proximal tunnels attains up to 100 μm , and their lengths attain 400 to 500 μm . The secondary tunnels are less than 50 μm long, rapidly taper, and pointed; some also curve toward their ends. Their bases are about 10 μm wide (Plate III, fig. 5).

Remarks: The only observed and likely incomplete boring has a similar structure and branching as some dendritic borings summarised by Wisshak (2017). However, the boring lacks a distinct stellate arrangement, which is characteristic for dendritic borings. A sponge origin of the boring is suggested, but the open taxonomy is preferred.

DISCUSSION

The tunnel-like microborings in mineralized skeletons of Recent as well as ancient marine organisms of different but fairly constant diameters are produced by fungal hyphae, filamentous cyanobacteria and thalli of eukaryotic algae (Golubic *et al.* 2005, Tribollet 2008). Both phototrophs and heterotrophs maintain contact with the substrate surface and often spread parallel to it. However, the marked differences between the boring behaviour of phototrophs and heterotrophs exist. Fungi proliferate within organic lamellae and often crisscross the bored shell. Endolithic algae and cyanobacteria proliferate in a mineral portion of the skeleton, immediately below the surface of the skeleton and are apparently unable to digest and penetrate the surrounding organic lamellae (Golubic *et al.* 2005, Tribollet 2008).

The observed system of tunnels and swellings represents the traces of a very common, likely dominant endolithic tracemaker which preferably infested the corallites of auloporid corals. The tunnels are clearly concentrated immediately below a surface of the corallite where the highest light intensity was. The direct measurements of light intensity reaching the layer of phototrophic endoliths in the skeleton of the Recent corals for different water depths are scarce (Tribollet 2008, Glaub *et al.* 2009). Their data can be directly applied to the Devonian corals. However, it makes sense that the galleries in the auloporid corallites were excavated by light-dependent autotroph, probably a chlorophyte. It is unclear whether the alga occupied the live coral and was mutualistic similarly to recent algae in the corals in the Recent coral reefs (Fine & Loya 2002, Verbruggen & Tribollet 2011). Because the dense clusters of *Irhopalina* isp. occur only in small spots (Plate II, i figs 12, 14) and the tunnels are remotest from each other, the impact of infestation, both positive or negative, to coral growth was likely insignificant.

The tubular, straight, unbranched shapes of galleries produced by cyanobacteria are similar, but the diameter of their tunnels (ichnogenes *Hyella*, *Eurygonum* and *Scolecia*) is clearly smaller. It is usually only a few μm (Vogel *et al.* 2000, Wisshak *et al.* 2008, Gektidis *et al.* 2007, Radtke & Golubic 2011). The diameter of tunnels in examined casts substantially exceeds the diameter of tunnels produced by cyanobacteria but fits well with a suggested size of eukaryotic cells of chlorophyte thalli.

The galleries of fungi usually penetrate much deeper into the host substrate and often follow the organic layers or thalli of phototrophs (Golubic *et al.* 2005). The ichnotaxa *Eurygonum*, *Orthogonum* and *Saccomorpha* are rather similar by straight and perpendicularly branching galleries, but the diameter of their tunnels is strikingly smaller, only 1 to 3 μm (Radtke 1991, Golubic *et al.* 1996, Glaub *et al.* 2009). The swellings extending from hyphae have nearly constant size and shape (Glaub *et al.* 2009). In contrast, the swellings of described *Irhopalina* isp. have uneven sizes and shapes.

Judging from the frequency of other endoliths (Plate II, figs 1, 2), the tracemaker of *Irhopalina* isp. was a dominant microbial euendolith in the shallow photic zone in the Koněprusy area in the upper Eifelian. Considering the observed abun-

dance of microborings in corallites present in the *Acanthopyge* Limestone regardless of the biological group of the tracemaker, it significantly contributed to the micritization of bioclasts on the seafloor of the Koněprusy reef.

CONCLUSION

The hydrated iron oxide mineral casts covering the corallites of auloporid corals from the *Acanthopyge* Limestone (Choteč Formation, Eifelian) provided significant information about the microboring diversity and activity in a marine shallow water environment of the Koněprusy reef. The suggested phototrophic organism, likely a eukaryotic chlorophyte or rhodophyte was the dominant tracemaker of the microborings in corallites. The sponges contribute to the bioerosion of corallites in a lesser extent.

Abundance and spatial distribution of the suggested phototrophic tracemaker document the euphotic zone. The shallow euphotic zone is very rich in cyanobacteria boring traces (Gektidis *et al.* 2007, Radtke & Golubic 2011). The cast from *Acanthopyge* Limestone does not have any microborings similar to *Eurygonum*, *Fascichnus*, *Hyella*, and *Scolecia*. When considering that their absence is primary, it indicates only an insignificant presence of cyanobacteria in the local environment. The absence of fungal microborings in casts indirectly supports the euphotic zone. The fungi generally prefer the shaded and deeper environments below the euphotic zone (Vogel *et al.* 2000, Gektidis *et al.* 2007).

The plausible model suggests that phototrophic tracemaker of *Irhopalina* isp. occupied predominantly coral substrates in the sea floor with good light conditions. Therefore, it seems likely that dominant coral *Amplexus floescens* and associated auloporid corals grew in depth 5 to 20 meters. This is consistent with modern observations on light penetration in the recent coral reefs (Gektidis *et al.* 2007).

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