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**Tracing Microendolithic Ichnocenoses: A paleoecological and
taphonomic approach over the Phanerozoic**

Disertační práce

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V Praze, 07. 2. 2024

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"Endless forms, most beautiful and most wonderful have been and are being evolved."

Charles Darwin, *On the Origin of Species*.

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Preface

This Ph.D thesis is written in the format of an introductory essay that accompanies scientific publications and is divided into 2 sections. The first section contains the state of art summarizing the current knowledge about the paleoecology and taphonomy of microbial endolithic structures, from marine hard substrates.

The second part of this thesis, Chapter 4 and on, is a compilation of the researched questions, and the solving methods applied in this doctoral study. A summary of the main achieved results from the three studied cases is also provided. Finally, individual publications, stemming from Ph.D Thesis, are attached.

The thesis examines the occurrence of microbial endolithic traces in tests of benthic foraminifera and other marine biofragments. Investigated samples are from the Early Mid-Paleozoic of the Prague Basin, Lower Maastrichtian of the Boreal Realm, and Oligocene-Miocene interval of Western Carpathians. This thesis aimed to investigate and provide a paleoecological picture of the aforementioned traces, as well as their contribution to paleobathymetric and taphonomic knowledge, as well as their environmental interactions and byproducts.

Abstract

The microbial endoliths study from the Western Carpathians region was a semi-quantitative survey that included six sampling localities. Samples, ranging from Upper Oligocene to Miocene (Serravalian), came from three localities in Czechia (Mikulov, LOM-1 and Hevlín), two in Slovakia (DNV and LKŠ) and one place in Hungary (Tard Clays, Rozalia Quarry). The main goal of this project was to verify how different levels of hypoxia, established for studied intervals, would affect the microendolithic assemblages present in tests of benthic foraminifera. Additionally, microbial activity and byproducts, and the overall interplay between bioerosion and bioprecipitation are also analysed. The degree of hypoxia was established using ratio of oxic/dysoxic and hypoxic foraminifera, defined as Benthic Foraminifera Oxygen Index (BFOi). Sampled index shows a predominance of dysoxic indicators, with rare oxic elements. Secondary electron elemental analysis (EDX) reveals a significant enrichment of sulphur, phosphorus and iron in biofilm samples from DNV and Hevlín, when compared to the rock matrix surrounding it. Resin casts reveal a predominance of Dysphotic to Deep Euphotic zones ichnocoenosis, with a predominance of Chlorophyte, Rhodophyte and heterotroph burrows. Few representatives of Cyanobacteria traces, such as *Euygonum nodosum* and *Scolecia filosa* are present on tests transported from well-oxygenated photic zones, in DNV. Framboidal pyrite from all samples, except for Mikulov, have an isotopic trace ($\delta^{34}\text{S}$) compatible to a biogenic deposition, while the vestiges of biofilms surrounding grains of framboidal pyrite is another evidence of their bacterial origin. Raman spectrometry of the biofilms have shown similarities with bacterial pigments. In summary, multiproxy analysis showed changes of microbial activity in relation to decreasing oxygen content, and allowed to identify allochthonous foraminiferal tests, transported from a shallower environment in this case.

Euendolithic assemblages in benthic foraminifera from Sassnitz, Lower Maastrichtian, were investigated in order to broaden the knowledge of a classical region for the ichnological studies. Ichnocoenosis shows a typical composition of Deep Euphotic paleobathymetrical zone, including the index elements: *Rhoupala catenata*, *Ichnoreticulina elegans* and *Conchocelis*, a developmental stage of the Rhodophycean algae *Porphyra*. In this work a new ichnospecies of Saccomorpha is described, a sign that more ichnological studies are still applicable to the Boreal Realm.

The study on microboring from Barrandian area, was a survey over 792 thin sections, clasts and shells from Ordovician to Middle Devonian of Prague Basin. The aim of the study was to verify the effects of paleoenvironmental and taphonomic factors affecting the distribution of microboring during this interval. The first register of microbial activity is a micrite envelope around brachiopod shells, from Letná Formation (Upper Ordovician). From the Ordovician to the lowermost Devonian, only rare microbioerosion, produced by bacteria and/or microfungi, were recorded. For the Upper Silurian Kopanina Formation (Ludlow) the first evidence of microendolithic activity are organodendritic structures evidenced by thin sections. Devonian representatives are found in crinoid columns, shells and bioclasts and are more abundant in petrographic slides. Results showed an increase of microboring abundance, and a change in the boring tendency from the surface of clasts to the interior of substrates. It may be explained by global trends of microbial evolution in the Early Paleozoic, in synergy with local factors. By local factor it can be cited the drift of Prague Basin to subtropical latitudes (Silurian) and finally tropical zones (Devonian), the increase of oxygen content on the seafloor, and a gradual decreasing of available nutrients, from Lockovian to Emsian.

Abstrakt

Fosilní záznam mikrobiální aktivity, zvláště endolitických organismů, byl studován na šesti lokalitách z oblasti Západních Karpat v rozsahu od svrchního oligocénu po miocén (serraval). Tři lokality jsou z České republiky (Mikulov, LOM-1 a Hevlín), dvě ze Slovenska (DNV a LKŠ) a jeden vzorek je z Maďarska (tardské jíly z lomu Rozalia). Hlavním cílem projektu bylo ověřit, jak snížený obsah kyslíku ovlivnil mikroendolitická společenstva a celkovou mikrobiální aktivitu zaznamenanou ve schránkách bentických foraminifer. Stupeň hypoxie byl vyjádřen pomocí „Benthic Foraminifera Oxygen Index“ definovaným jako poměr oxických/dysoxických a hypoxických foraminifer, který poukázal na převahu dysoxických taxonů ve společenstvech se vzácnými oxickými prvky. Dalším typem mikrobiální aktivity jsou biofilmy. Rentgenová spektroskopie (EDX) ukázala významné obohacení sírou, fosforem a železem ve vzorcích z biofilmů ve srovnání s okolní horninou. Metoda pryskyřičných odlitků umožnila identifikovat ichnocenózy indikující dysfotickou až hlubokou eufotickou zónu s převahou mikrovrtb produkovaných zástupci skupin Chlorophyta, Rhodophyta a heterotrofními organismy. Mikrovrtby produkované sinicemi *Euygonum nodosum* a *Scolecia filosa* byly zjištěny na několika schránkách z lokality DNV, které musely být transportované z mělké fotické zóny. Framboidální pyrit přítomný ve všech vzorcích s výjimkou Mikulova má izotopické složení síry ($\delta^{34}\text{S}$) odpovídající biogennímu původu. Biofilmy obklopující zrna framboidálního pyritu jsou dalším dokladem jejich bakteriálního původu. Ramanova spektrometrie biofilmů poukázala na podobnost s bakteriálními pigmenty. Souhrnně lze konstatovat, že komplexní geochemicko-paleontologická analýza prokázala změny bakteriální aktivity při snižujícím se obsahu kyslíku v prostředí. Umožnila také identifikovat alochtonní schránky, které musely být transportovány z odlišného prostředí.

Euendolitické společenstvo ve schránkách bentických foraminifer ze Sassnitzu (spodní maastricht boreální oblasti) bylo zkoumáno za účelem rozšíření znalostí o mikrovrtbách v klasické oblasti ichnologických studií. Ichnocenóza vykazuje typické složení hlubinné eufotické paleobathymetrické zóny, včetně indexových taxonů: *Rhoupala catenata*, *Ichnoreticulina elegans* a *Conchocelis*, což je vývojové stadium rhodophytních řas rodu *Porphyra*. V práci je popsán nový ichnodruh rodu *Saccomorpha*, tato skutečnost poukazuje na potřebu dalšího studia mikrovrtb z boreálního křídového moře.

Studie mikrovrteb z oblasti Barrandienu byla založena na analýze 792 petrografických výbrusů a bioklastů ze vzorků z ordoviku až středního devonu. Cílem studie bylo ověřit vliv paleoenvironmentálních a tafonomických faktorů ovlivňujících distribuci mikrovrteb v tomto intervalu. Nejběžnějším projevem mikrobiální aktivity je mikritová obálka, která se objevila již kolem schránek ramenonožců z letenského souvrství (svrchní ordovik). Od ordoviku do báze devonu byly zaznamenány jen vzácné mikrovrtby produkované bakteriemi a mikroskopickými houbami. Celkově ve studovaném intervalu ordovik-střední devon mikrobioeroze jednak ukazují trend zvyšování jejich hojnosti a dále posun aktivity endolitických organismů z povrchu klastů do nitra substrátů. Tyto skutečnosti lze vysvětlit dopady globální evoluce mikroorganismů ve spodním paleozoiku ve spojení s působením lokálních faktorů, jakými jsou posun pražské pánve do subtropických šířek (silur) a nakonec tropických pásem (devon), zvýšení obsahu kyslíku na mořském dně a postupný úbytek dostupných živin od lochkovu do emsu.

1 AN OVERVIEW OF MICROBIAL ENDOLITHIC STRUCTURES

1.1 What is a microboring?

Microbial endoliths or microborings are the traces left from the activity of microorganisms inside hard substrates. They are conventionally defined as structures with a diameter up to 100 μm , and metazoans such as sponges, protists and bacteria must be considered as producers of openings, dots, and tunnels fitting the microboring definition (Golubic et al., 1975). Their register occurs in a wide variety of environments, and in marine hardgrounds they range from the intertidal and wave spray zones to the abyssal depths (Zeff and Perkins, 1979, Wisshak, 2012). They are found on both fossil and modern hard substrates, exhibiting various patterns including simple spherical holes, cluster-like and ramified networks and dendritic arrangements (Glaub and Vogel, 2004). Microbial activity, and especially euendolithic type along the photic zone, contribute largely to the bioerosion of the carbonate substrates they live in, acting as a significant element of weathering of these substrates and their recycling on the nature (Tribollet, & Golubic, 2011; Garcia-Pichel, 2006; Neumann, 1966). A specific type of hard substrate is represented by tests of planktonic and benthic foraminifera which, the latter, is the main substrate considered in this thesis (Golubic et al. 1984).

Boring microorganisms (Fig. 1) have been studied in a variety of carbonate substrates, including the shells and skeletons of living organisms or their fragmented remains, and within coastal limestones (Glaub et al., 2007; Golubic et al., 1975). Their activity within carbonate

substrates produces characteristic boring patterns, which permit taxonomic identification and suggest some reliable ecological and paleoecological indicators (Golubic et al., 1975).

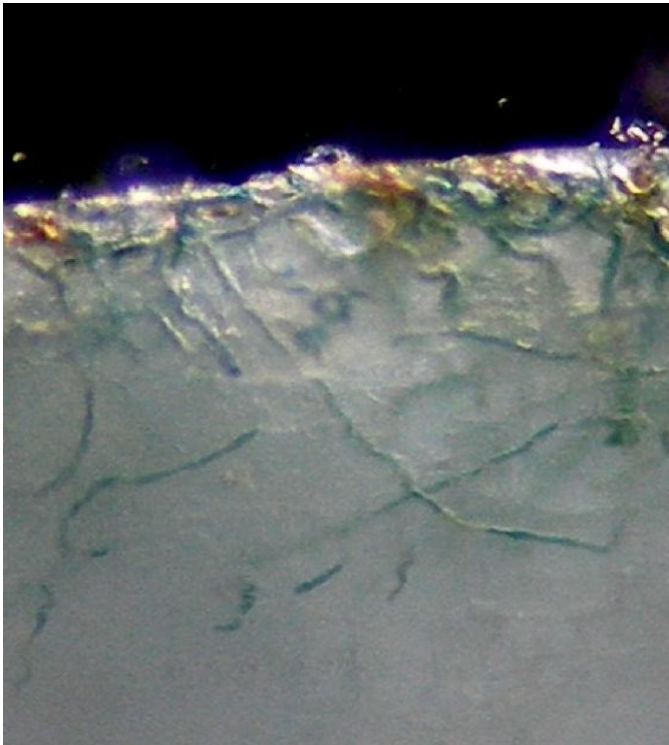


Figure 1 - Chip of crystalline calcite bored by filaments of cyanobacteria. Modified after Garcia-Pichel et al (2010). Credits to Edgardo Ramírez-Reinat

Although the existence of microendolithic traces and producers has been known since the mid-nineteenth century, necessary techniques for preparation and comprehensive analyze of this material, have developed only during the mid-seventies with pioneering efforts of Stěpko Golubič and collaborators (Golubic, 1984; Golubic et al., 1975). The communities of

microendolithic organisms could be used as an indicator of conditions at the sediment-water interface such as paleobathymetry, paleosalinity, environmental stress among other factors (Wisshak, 2012; Golubic, 1984; Golubic et al., 1975). During the past decades, thanks to the use of extensive long-term experiments, our understanding about the producers and their ecological impact has improved largely (Lloyd Newman et al., 2023; Carreiro-Silva & McClanahan, 2012; Wisshak et al., 2005).

1.2 Historical overview on the research of endolithic and microendolithic traces

The history of research of microboring structures can be traced back to the mid-nineteenth century. Initially considered as part of the rock or its natural weathering process but took as part of the initial substrate development (Carpenter, 1845). Lately it has been discovered to be

part of the living process and activities of microorganisms, such as algae and fungi, became known as "endoliths" (*sensu* Dievart et al., 2022; Carpenter, 1845). Endolith (Fig. 2) or lithobiont (Golubic, et al., 1975) refers to organisms that are capable of chemically (less commonly physically) drill and bore hard substrates as a mechanism of defense or seeking for nutrients. Wedl (1859) was the first to propose an organic origin to these structures, initially considered these borings to be algal reminiscent. Duncan (1876) compared recent and fossil endoliths in corals and gave the name *Palaeochlya perforans* to the fossil forms, while Roux (1887) provided the name *Mycelites ossifragus* for microbial borings found within vertebrate bones. The taxonomic affinities of both *taxa*, whether algal or fungal, have never been clarified, and subsequently they have been used as ichnotaxa without specifying the origin of the borings (Golubic et al., 1975).

In 1886, Lagerheim taxonomically described the first boring algae, *Mastigocoleus tatarum*, followed by Bornet and Flahault (1888) with additional algal descriptions and the first boring fungi. Nadson (1902, 1927) recognized the depth distribution and biogeochemical significance of boring algae, although many of his taxonomic identifications were unreliable. Ercegovic (1932) described an array of new intertidal boring cyanophyte species and studied their community structure and zonal distribution. Frémy (1945) reported the characteristics of algal and fungal borings from various environments.

In 1937, Pia reviewed the extensive literature on recent and fossil boring microorganisms and microborings, including those that indirectly contribute to substrate disintegration but do not leave recognizable boring patterns. Hessland (1949) reported on fossil microborings from the Ordovician of Sweden, opposing the use of ichnofossil names for microborings and recommended a classification according to size. Bathurst (1966) proposed that the widely distributed micrite envelopes commonly found on fossil skeletal fragments were initiated by

the activity of boring microorganisms. Research on microborings encompasses a wide, interdisciplinary field of study, significantly aided by modern instrumentation, since the work as such of Alexandersson (1972). In this work, he examined the diagnostic alteration of recent and subrecent borings in relation to environmental chemistry. In recent decades, results from diverse fields have contributed to an interdisciplinary source of knowledge around microendolithic traces. Their ability to adapt to a wide range of environments, from deserts to the deep depths of the oceans, saline lagoons, basaltic to carbonate substrates, are a few indicatives of their range of occurrence and the possibility to leave traces. Interdisciplinary fields as geochemistry, molecular analyses of recognized producers, and even analyses producing proxies for prospective samples from other planets, all demonstrate the potential contribution that the research over these traces can provide, from past and recent environments (Casero et al., 2020; Wisshak et al., 2011; Mason et al., 2007; McLoughlin et al., 2007; Rose et al., 2006; Pantazidou et al., 2006).

1.3 Dynamics of the microendolithic producers

The style of colonization may vary during the life cycle of boring organisms, and many adopt this habit only at some stage in their life cycle. This is the case of some species of red algae from genera *Porphyra* C. Agardh (1824) and *Bangia* Lyngbye (1819), that have an endolithic strategy during early stages of development, the so called "Conchocelis stage" and adopt different set of habits in their adult life (Dievart et al., 2022).

The endolithic strategy can be adopted in several ways. Among them (Fig. 2), a selection of niches was listed here, according to Dievart et al. (2022):

- Epiliths are those that live on the surface of the substrate.
- Chasmoliths adhere to the surface of fissures and cracks in the substrate,

- Cryptoendoliths that adhere to the surface of pre-existing cavities within porous rocks, with no dissolution action,
- Euendoliths comprising the group of organisms that actively penetrate hard substrates and reside partially or completely inside cavities of their own making.

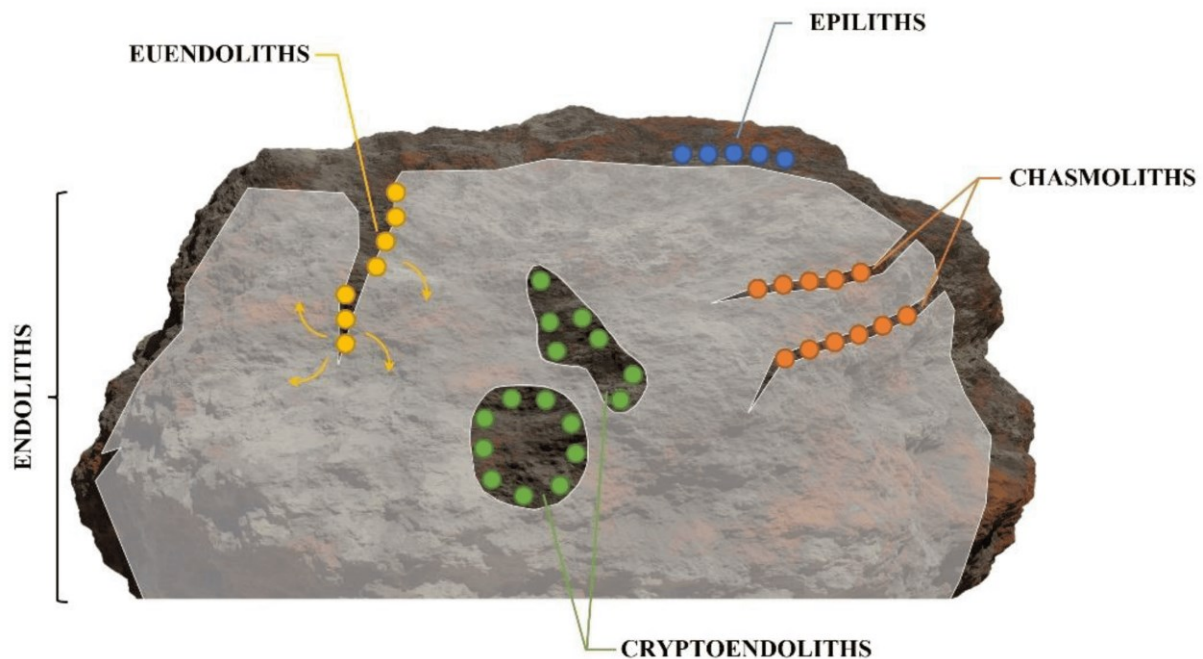


Figure 2 - Endolithic classification of organisms according to their position and life strategy on hard substrate. After Amarelle et al., 2019.

For the nature of microbial endoliths, as an indirect register of the activity of an organism, it is not always possible to be assigned to a specific producer. For that reason, it is adopted a classification based on their behavior (Vallon et al., 2016). Ethology is the classification of animal behavior into categories according to the trace they produce on and in the substrate, an important tool for paleoecological and stratigraphical inferences (Seilacher, 1964 and 1953). Under this classification, trace fossils are taken into ichnoform at genera and species levels, based on the implied behavior of their producers. Microbial endoliths are a category of bioerosion and, according to the system initially proposed by Seilacher (1953), and at the light of recent revisions (Vallon et al, 2016; Buatois et al., 2017; Buatois & Mángano, 2012; Ekdale et

al., 1984; Bromley, 1990, 1981, Seilacher, 1964 and 1953), they can be placed into the ethological category of **Dominichnia** and **Praedichnia**. In their original proposition by Seilacher (1953) and Ekdale (1985), these two categories were designated for traces produced in both hard and soft substrates. Dominichnia comprises dwelling traces, occupied by tracemaker, created as a permanent shelter or domicile (Bromley, 1996; Seilacher 1964, 1953). The ecological function of the structure is to provide protection from predators, and to buffer temporary changes in the local environment (Rindsberg, 2012). In present time, microborings are frequently found inhabited by their producer. The prevalence of microborings hosting resident euendoliths was found to be most prominent in the supratidal and upper intertidal zones, and it decreases in frequency towards the lower intertidal and subtidal regions (Golubic et al., 2016). Praedinichnia refers to traces of predation behavior so, it shows the interaction among a predator and its prey (Ekdale, 1985). Often the hard parts of the preyed organism carry the marks of this interaction, most commonly appearing in the form of drillholes, and characterized as the ichnological trace "Oichnos". Other characteristic marks are chipped margins in shells, scratching and biting traces (Ekdale, 1985). These marks are therefore, bioerosional structures (Bromley, 1981).

1.4 Producers and long-term connection with hard substrate

Endolithic microorganisms represent a heterogeneous group whose common characteristic is their capability of chemically perforate hard substrates in order to obtain protection and/or nutrients (*sensu* Whittaker, see Margulis, 1974 and Campbell, 1982). Around 133 ichnospecies of microborings are formally described, according to the last revision from 2019 (Wisshak et al., 2019) that includes a range of cyanobacteria, green and red algae, fungi, and foraminifers and even small invertebrates (Fig. 3).

Their activity within carbonate substrates produces characteristic boring patterns, which permit taxonomic identification and suggest some paleoecological indicators. For doing so, this relation between microorganisms and their substrate must be suitable for paleoecological inferences (Golubic et al., 1975, Radtke et al., 2016). They colonize hard substrates such as shells, skeletons, stromatolites, ooids, and hard grounds. Although less frequently they can be found in siliceous or phosphatic substrates, garnet crystals, volcanic glass and basalts (Königshof & Glaub, 2004; Staudigel et al., 2008 Ivarsson et al., 2018 Cockell et al., 2010).

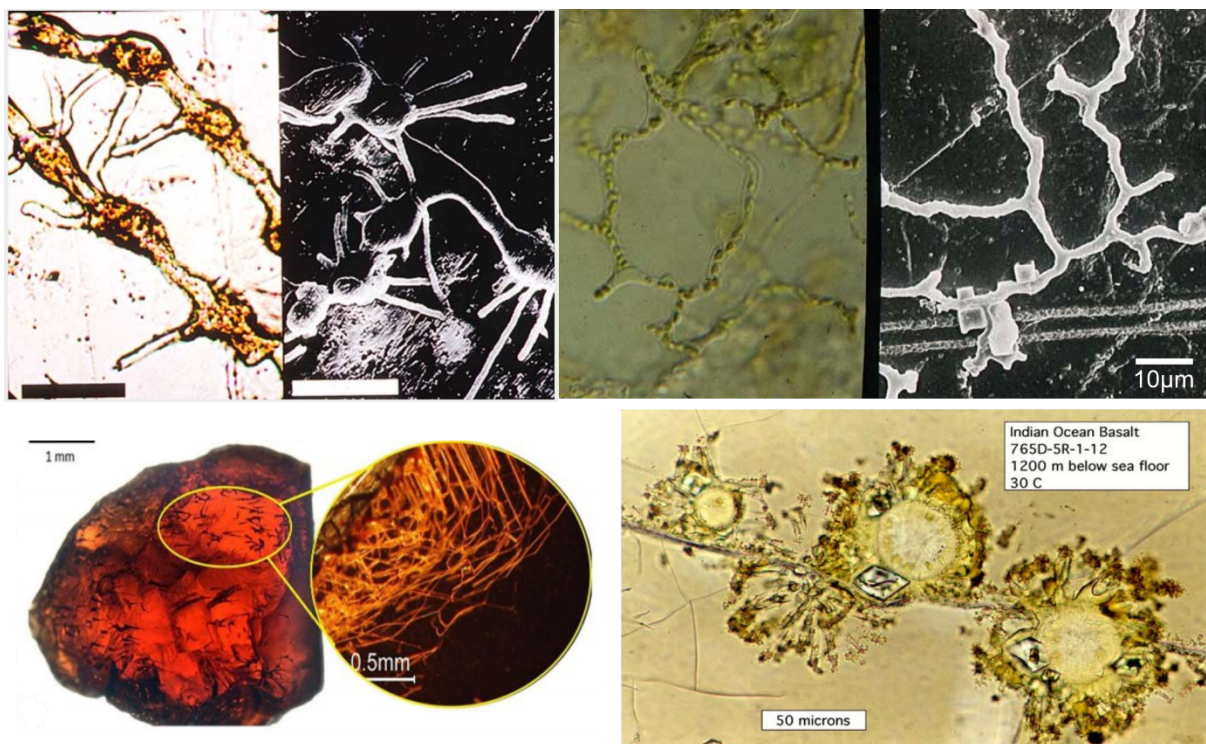


Figure 3 - Boring producers and the pattern on hard substrates. From up left to right, clockwise: Rhopalia catenata (right) and its modern producer Phaeophila engleri (green alga). Scale bars: 30 µm. Ichnoreticulina elegans (right) and its producer Ostreobium quekettii (scale on the image). Intricate tunnels in garnet crystal (after Ivarsson et al. 2018). At bottom right, sample from NOAA Ocean Explorer prospecting from basaltic rocks found at 1.2km beneath the floor of Indian Ocean.

By essence, microendolithic activity is a form of bioerosion (Neumann, 1966). Microbial endoliths are instrumental in destruction of carbonate grains, creating the so-called micritic

envelopes. These organisms are directly or indirectly agents of erosive and early diagenetic processes in carbonate sediments (Planavsky et al., 2009; Schneider and Torunski 1983; Kobluk et al., 1977). Euendolithic cyanobacteria are frequently found in whole assemblages in oolitic grains and sand-sized shell fragments. As the sand grains are moved and stirred by waves and tidal currents, these organisms are frequently exposed to variations in light and nutrients. Ooid grains are home to a number of species of Hyella-type cyanobacteria (Taylor & Wilson, 2003; Klobuk & Risk, 1977). Intertidal and supratidal ranges in carbonate coasts are, in the actuality, the most extensively bioeroded environment on Earth, whose effectively destruction of hard substrates contributes to fine grain sediments production at a geologically significant scale (Glaub et al., 2001; Taylor & Wilson, 2003; Kazmierczak et al., 1996). Epilithic and endolithic cyanobacteria are the main primary producers in these realms and the main responsible for coastal bioerosion (Taylor & Wilson, 2003). Algae bore repeatedly into carbonate grains to create micrite envelopes, which are then filled with precipitated micrite. Although this process decreases intergranular porosity, the algae also create micrite envelopes outside of grains by calcifying (cementing) exposed dead endolithic filaments. These may calcify after death, creating a web of calcified filaments that later forms a cement made of micrite and microsparite (Kazmierczak et al., 1996). The accompanying cements and calcified intergranular filaments serve to bind the grains together and further restrict intergranular porosity (and possibly permeability). By etching and dissolving micrite envelopes beneath algal-mucilaginous coatings, a very microporous residual micrite is created as a byproduct (Mei et al., 2023; Kobluk & Risk, 1977). Hard substrates can be of a biogenic and abiogenic origin and, compared to unconsolidated sediments, shells, rocks, wood, they can provide relatively more stable habitats (Taylor & Wilson, 2003).

Microendolithic organisms affect carbonate substrates by a chemical process called biocorrosion that leaves distinctive patterns (Tribollet et al. 2011). The biochemical mechanism of "calcium pump" is proposed to be the adopted one (Garcia-Pichel 2006; Garcia-Pichel et al. 2010). Boring producers can adopt distinctive pathways in the drilling process. The carbonate dissolution in the majority of filamentous microborers is concentrated on the tip of the filament, and there is no sign of a lateral extension of the dissolution process along the tunnel walls that, as a result, replicates the outlines of the organism. Coccoid cyanobacteria (order Pleurocapsales) exhibit a similar growth pattern, that is facilitated by the directed synthesis of exopolymer stalks. These patterns suggest an effective, presumably rapid drilling procedure. On the other hand, the lateral growth of the drilled structures within the substrate along crystal boundaries, producing large etched fields away from the filament, seems to be related to slower penetration rates and a longer exposure of substrate to corrosion (Golubic et al., 2016). Euendolithic phototrophs are effective in removing the carbonate matrix but are less able to penetrate organic substances present inside skeletal carbonates, eventually resulting in a growth pattern that reflects the crystalline arrangement of the rock. Because they are unable to break through the conchiolin envelopes interlays into bivalve shells, boring algae are frequently trapped within single crystals, when penetrating organic hard parts. However, euendolithic fungi appear to be well adapted to dissolve and digest these materials (Golubic et al., 1975). Their preference for organic *lamellae* appears to be a driving mechanism of growth of the producer that leaves a distinctive pattern, like those presented by *Saccomorpha stereodiktyon* (Golubic et al., 2014).

Dwelling organisms attempting to bore hard substrates must develop mechanisms to secure and defend their attachment space. The study of hard substrate communities allows inferences over spatial competition, ecological succession, oriented growth, and differential utilization of

exposed versus hidden substrate surfaces. Consequently, these communities provide excellent systems for investigating the evolution of communities over hundreds of millions of years (Golubic et al., 2016; Radtke & Golubic, 2011; Taylor & Wilson, 2003). These changes include a general increase in the bioerosion of hard substrates throughout the Phanerozoic Eon, equivalent to the infaunalisation trends observed in soft substrate communities (Zhang and Golubic, 1987, Campbel, 1982, Bromley, 2004). This long history of endolithic lifestyle has been observed also on developmental modifications in the life cycle of the boring producers, that are more frequently observed among eukaryotic euendoliths (Miller III, 2011; Radtke & Golubic, 2005, 2011). For example, some species of red algae *Bangiales* that, during its ontogenetic development, adopt an endolithic lifestyle, being the producer of *Conchocelichnus seilacheri* trace (Radtke et al., 2016) (Fig. 4).

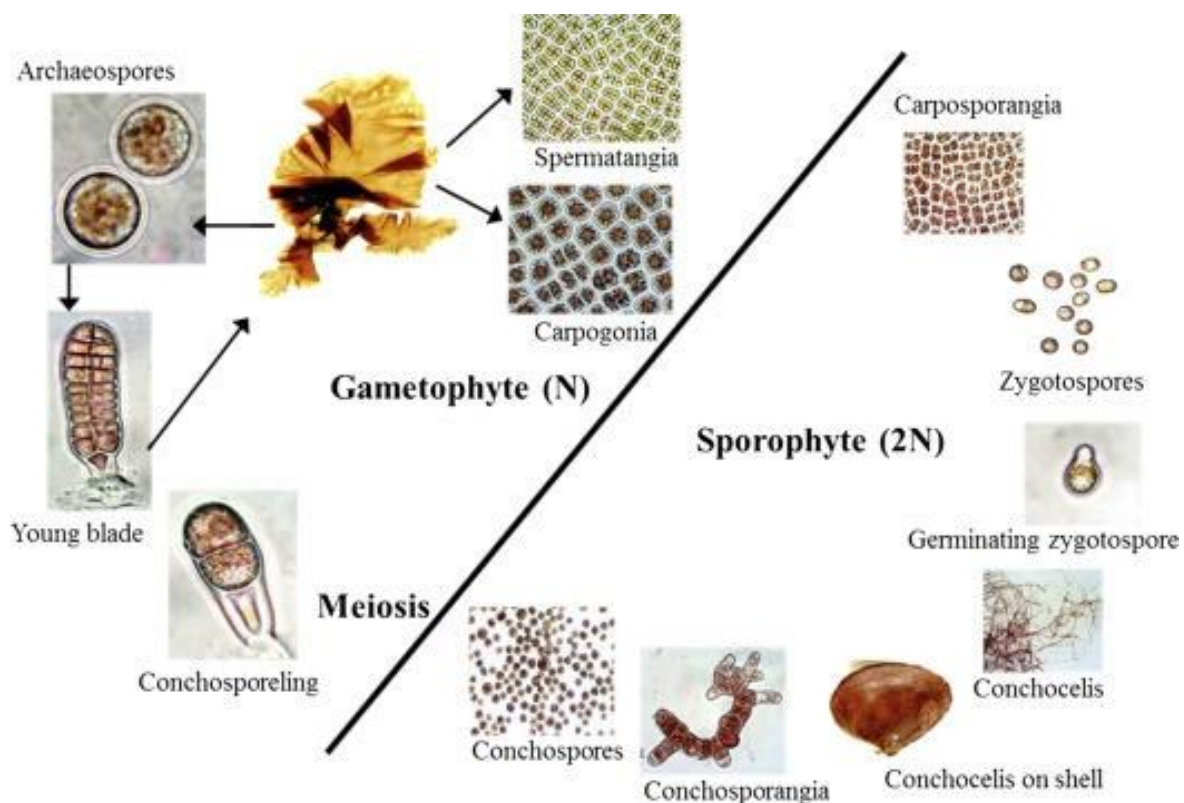


Fig. 4 - Life history of *Porphyra* showing different stages of development in which the first stages pass through the perforating form known as *Conchocelis* isp. Reproduced from Sahoo et al., (2002) and Radtke et al., (2016).

The discovery of endolithic fossils in Precambrian geological formations has been a relatively recent achievement. The endolithic life mode, exhibited by cyanobacteria can be traced back as far as the Early Proterozoic era, as evidenced by the discovery of 1.7-billion-year-old stromatolites in China, which yielded the earliest known record of *Eohyella campbellii* (Zhang and Golubic, 1987). These organisms penetrated lithified stromatolite surfaces, making it the first record of bioerosion (Zhang & Golubic, 1987). Certain members of this genus can still be found in the oceans until the present day, a testament to the evolutionary longevity of microendolithic organisms (Golubic et al., 1975).

The earliest examples of apparent predatory bore are documented from the late Precambrian period, with borings structures consisting of simple circular holes found in the tubular mineralized skeletons of *Cloudina* (Hua et al., 2003; Zhao et al., 1992). Cryptic communities are quite abundant and diverse in the lower Cambrian. These cryptic spaces can be found within archaeocyath and radiocyath reefs, calcified microbial mounds, beneath early cemented carbonate sediments, and beneath skeletal debris. During Siluro-Ordovician, microbioerosion became represented by endolithic rhodophytes and eubacteria (Kazmierczak & Golubic, 1976; Campbell et al., 1979; Campbell, 1980). In the Devonian they can also be attributed to some fungi, including a record with exceptional preservation of soft tissues (Olempska, 2012). Microborings are not commonly found in the Carboniferous period and one of the rare examples relates to the presence of ichnogenera *Eurygonum* and *Scolecia*, which are likely created by cyanobacteria, identified in rocks from the Lower Carboniferous rocks of Utah (Vogel, 1991; Glaub, 1999). Although the composition of microboring communities undergoes changes over time (Fig. 5), their physical expression and ecological requirements exhibit a remarkable consistency (Vogel & Brett, 2009). It is even more evident in modern seas where many euendolithic organisms have shown a cosmopolitan distribution. Neither geographical

variations, nor succession in time have shown effect on the fundamental pattern of microendolithic depth distribution, as presented by Golubic (1970) and latterly verified by experimentation (Gektidis et al., 2007; Färber et al., 2015). In this sense, modern experiments do not identify specialization, nor endemic population of microendoliths (Gektidis et al., 2007). However, a distinct latitudinal gradient can be expected, with a decreasing of diversity and abundance towards the high latitudes (Färber et al., 2015; Wisshak et al., 2012, 2011, 2005; Glaub et al., 2007; Perry & Macdonald, 2002; Vogel et al., 1995).

Irrespective of their metabolic mode, all euendoliths will share interaction with the substrate they occupy, yet the nature of this interaction and the resultant textures and traces may vary. Some may mirror the characteristics of the boring microorganism, encompassing their metabolic attributes and their energy source (phototrophy versus organotrophy), while others may disclose features of the substrate itself (Golubic et al., 2016).

(Ichno-)Taxa / Time	Proterozoic	Cambrian	Ordovician	Silurian	Devonian	Carbonifer.	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
<i>Eohyella campbellii</i>	■												
<i>Cunicularius halleri</i>	■	■											
<i>Eohyella elongata</i>	■	■											
<i>Eohyella recto./ Fascichnus frutex</i>	■			■		■	■	■	■	■	■		■
<i>Eohyella dichotoma</i>	■										■	■	■
<i>Graviglomus incrustus</i>	▲												
<i>Parenchymodiscus endolithicus</i>	▲												
<i>Cunicularius isodiametrus</i>		■											
<i>Endoconchia angusta</i>		■											
<i>Eohyella lata</i>		■											
<i>Scolecia filosa</i>			■	■		■	■	■	■	■	■	■	■
<i>Fascichnus dactylus</i>			■			■	■	■	■	■	■	■	■
<i>Fascichnus roigus</i>				■	■	■		■	■	■	■		■
<i>Eurygonum nodosum</i>			■			■	■	■	■				■
<i>Ichnoreticul. elegans</i>			□	□	□	□	□	□	□	□	□	□	□
<i>Cavernula pediculata</i>			□			□		□	□	□	□	□	□
<i>Conchocelis</i> traces			●	●		●	●	●	●		●	●	●
<i>Saccomorpha clava</i>			○		○	○			○	○	○	○	○
<i>Saccom. terminalis</i>			○			○		○	○		○		○
<i>Orthogonum lineare</i>			▲			▲			▲	▲	▲		▲
<i>Orthog. fusiferum</i>			▲	▲		▲		▲	▲		▲		▲
<i>Planobola macrogota</i>			▲	▲		▲	▲	▲	▲	▲	▲	▲	▲
<i>Polyactina araneola</i>				○			○	○	○	○	○		○
<i>Hyellomorpha microdendritica</i>					■					■			■
<i>Rhopalia catenata</i>						○		○	○	○	○		○
<i>Orthog. spinosum</i>						▲					▲		▲
<i>Cavernula coccidia</i>						▲			▲				
<i>Polyactina fastigata</i>						▲					▲		
<i>Scolecia serrata</i>						▲					▲	▲	▲

■ Cyanobacteria □ Chlorophyta ● Rhodophyta ○ fungi ▲ unknown producer

Figure 5 - Temporal distribution of ichnospecies and their respective main taxa. Modified after Vogel and Brett, 2009 (fig. 43, pg. 19).

1.5 Microborings as a complementary element of bathymetric and paleobathymetric studies

Microendolithic traces, both in contemporary and ancient times can function as indicators of water depth. The presence of traces has proven to be a valuable tool especially in areas where there are no visible signs of wave or current activity. The indication relies in the perceived distinction between traces created by photosynthetic microorganisms, which are limited to well litified portion of the substrate, and those made by organotrophic microorganisms, which are light-independent and can occur at any depths (Golubic et al., 2016). Various studies, such as those conducted by Golubic & Perkins (1975), Glaub (1999), Glaub et al. (2002, 2007) and Vogel et al. (1995, 2000), have confirmed the potential of these traces for bathymetric and paleobathymetric analyses. Different sets of index ichnoceonoses have been identified within the euphotic zone (including subzones), the dysphotic zone, and the aphotic zone, with their nomenclature based on the two most prominent ichnotaxa described in Glaub (1994), Vogel et al. (1995), Glaub et al. (2002 and 2007). These fundamental characteristics of the bathymetric scheme of index ichnocoenoses have been observed since the Silurian period. Recent research by Vogel and Brett (2009) suggests that even in the Upper Ordovician, some samples already display identifiable ichnospecies and one or two bathymetric index ichnocoenoses (Fig. 6).

Inherent factors in marine environments affect endolithic biotas dynamics in different ways. Some of these can exercise a stronger influence such light availability as it acts as an ecological barrier for autotrophic and heterotrophic groups and a main factor affecting the shift of assemblages, in terms of compensation depth of algae (Golubic et al., 1975; Perry & Macdonald, 2002).

A vertical pattern of distribution is represented by a bathymetric set of ichnocenoses divided along the photic zone. These zones are defined by the co-occurrence of distinguishable

ichnospecies, along with key ichnotaxas, and composition of each ichnocenosis (Wisshak, 2012; Glaub, 1994; Glaub et al., 2001; Vogel et al., 1995, 2008). The interest in microbial euendoliths has grown due to the possibility of distinguishing between phototrophic and heterotrophic organisms by examining the shape of their borings. This differentiation could offer a dependable method for determining the water depth of the sediment layers of concern (Glaub, 2007). Microborings closely mirror the contours of the microorganisms responsible for creating them, thus they can provide details about the size, growth orientation, and habits adopted by the producers (Radtke & Golubic, 2011).

Microendolithic Ichnocoenoses

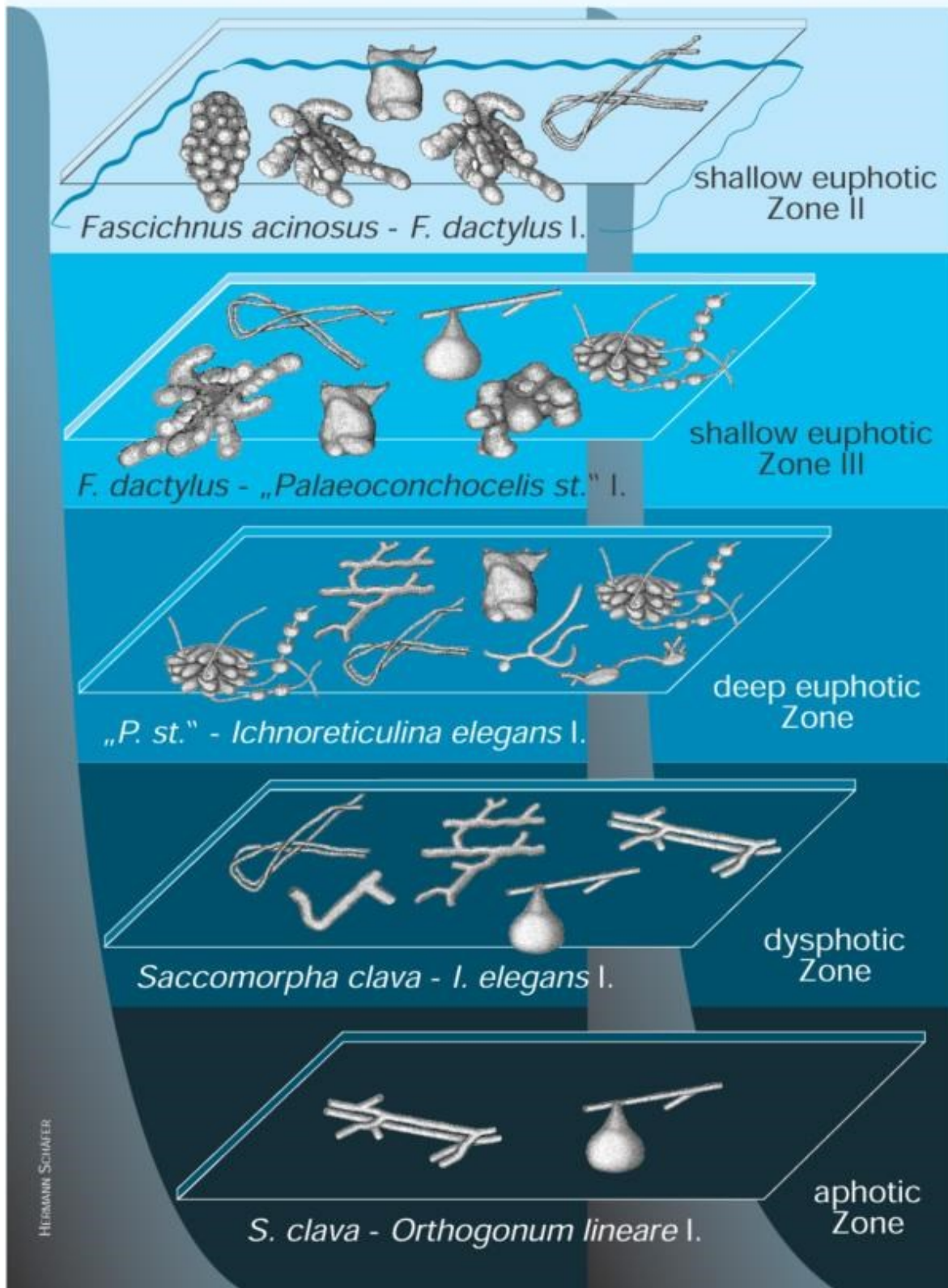


Figure 6 - Schematic determination defined by distinct (paleo)ichnocoenoses at different depths of photic zonation (Glaub 1994, Glaub et al. 2007). From: [https://www.uni-frankfurt.de/69856241/Vogel Bioerosion and Paleobathymetry Results](https://www.uni-frankfurt.de/69856241/Vogel_Bioerosion_and_Paleobathymetry_Results)

Supratidal and intertidal areas of the shallow euphotic zones are dominated by cyanobacteria and their ichnological counterparts characterized by a vertical orientation of the perforations. In the model proposed by Glaub, this ichnocenosis has yet to be defined as a key ichnotaxa. Chlorophytes are most plentiful in the deeper regions of the photic zone where the main element, from subtidal towards the deepest portions of the photic zone, is the shifting of vertical to horizontal orientation of the borings. *Rhopalia catenata* and *Ichnoreticulina elegans* are the key taxa for this ichnocenosis (Wisshak, 2012; Glaub, 1994; Glaub et al., 2001; and Vogel et al., 2008). In the depths where surface illumination is lower than 0.01 percent, only heterotrophic and chemotrophic organisms are found (Akpan & Farrow, 1984; Budd & Perkins, 1980; Golubic et al., 1975; Günther, 1990; Perkins and Tsentas, 1976). These are the Dysphotic and Aphotic zones, and the occurrence of *Saccomorpha clava* and *Orthogonum lineare* are the key elements for these ichnocenoses (Glaub, 1994; Glaub et al., 2001).

Despite microendolithic biota usage as paleobathymetrical indicators, it is important to highlight the use of these assemblages as a primary indicative of the photic zone instead, therefore a relative paleobathymetry. Attention must be given to the fact that photic zones vary significantly as light penetration changes regionally and globally, seasonal variation and even substrate orientation can interfere on distribution abundance of producers (Meyer et al., 2020 and 2021; Färber et al., 2015; Perry & Macdonald, 2002). In clear water environments of modern tropical regions, the upper photic–lower photic zone transition can occur between depths of 20–30 m. This limit is marked by the shift from assemblages dominated by Cyanobacteria (*Eurygonum nodosum*, *Scolecia filosa*, *Fasciculus grandis*, *Fasciculus frutex* and *Fasciculus dactylus*) and Chlorophyte traces (e.g., *Rhopalia catenata*, *Fasciculus grandis* and *Reticulina elegans*), to assemblages predominantly formed by a mix of *E. nodosum* and *S. filosa* (Cyanobacteria), *F. grandis* (Chlorophyte), *Palaeoconchocelis starmarchii* (Rhodophyte) and

Orthogonum fusiferum and *Saccomorpha sphaerula* (Fungi). In case of high turbidity of the water, this transition occurs at 15-20 m depth and at the most turbid sites, at 5-10 m. Crossed data from light penetration and assemblage composition indicate that the shift occurs whenever the percentage of light penetration is reduced by 10-15%. Extreme cases of lower levels of water crystallinity, due to extreme turbidity, induces a shift in the microendolithic community to be dominated by fungi in an assemblage associated to the dysphotic zone, at 30 meters depth (Perry & Macdonald, 2002). Another experiment in modern coral reef sea, comparing clear water with shaded spots, also shows a gradual overlapping of communities towards higher depths (Gektidis et al., 2007).

Temperate mid-latitude experiments over seasonal variation of water depth in the Ionian Sea, showed some patterns in the succession and the effect of ecological conditions. In a similar experiment, set at the Azores archipelago, the occurrence of cyanobacterial producers was documented up to depths of 150 meters, for the *Plectonema terebrans*. This algae is the endolithic organism responsible for the production of the trace *Scolecia filosa* in modern seas (Wisshak, et al., 2011 – Table 1, pg. 498). The occurrence of fungal microborings were documented from 15 m station up to 500 m depth. General bathymetrical zonation shows a dominance of cyanobacteria in the intertidal to shallow subtidal ranges, chlorophytes at deep euphotic to dysphotic zones and an exclusive occurrence of fungi and chemotrophs in the aphotic zone (Wisshak et al., 2011).

In higher latitudes from Arctic Circle, lower ichnodiversity is to be found in the shallow euphotic zone, probably a result of temperature fluctuation, seasonality of light availability and harsh fluctuation of weather, even on a daily rate, while in deeper waters, variation of temperature and salinity are less extreme (Meyer et al., 2020). Another factor to take into account is the polar night. In higher latitudes, the water depth, an indirect indicator of light availability, show

to be the most significant driver of microbioerosion assemblages in the setentrional higher latitudes around 74° and 80°. It is hence expected a lower ichnodiversity in higher latitudes, due to harsh conditions, and it is the depletion of cyanobacteria that mostly reflected in these numbers. The polar night works overlapping and condensing the photic zone during winter and summer, plus the transitional months, imposing a significant limitation for phototrophic organisms (Meyer et al., 2020). This can reflect in the predominance of low-light specialists such as *Ichnoeticulina elegans* (produced by the chlorophyte *Ostreobium quekettii* Bornet & Flahault, 1889) and *Conchocelis seilacheri* (a developmental stage microboring, produced by rhodophytes), opposing to the occurrence of colonizing cyanobacteria. Independent of their light necessity, they will develop strategies to adapt to the low light and low temperatures that, either physiological or ecological, will allow perennial algae to survive the polar night (Wiencke et al., 2007). However, higher latitudes areas around the Svalbard archipelago display an example of the characteristic disposition of assemblages at high latitudes. In an overall context, the bathymetric range of microendolithic assemblages tend to decrease towards higher latitudes (Meyer et al., 2020 and 2021; Akpan & Farrow, 1985). At these range, cyanobacterial borings are to be usually found in the deep euphotic zone, chloro- and rhodophyte traces domines from the deep euphotic down to the dysphotic zone, and fungi traces primarily abound in the aphotic zone (Golubic et al., 1975, Glaub, 1994, Wisshak, 2012). Nevertheless, euendoliths are typically quite resilient when it comes to environmental changes as they are protected within the microenvironment of their drilled dwellings (Vogel & Glaub 2004). Consequently, it is reasonable to anticipate their survival during the polar night as well. Light availability is irrelevant to organotrophs and, as temperatures tend to be more constant at higher depths, these groups will thrive, and higher similarities can be found by comparing ichnodiversity inventory with those from lower latitude areas. *Ichnoeticulina elegans*

dominated deep euphotic to dysphotic zones in both Svalbard archipelago and Azores. Fungal microborings such *Saccomorpha clava* were commonly found at dysphotic and aphotic zones in Azores, while *Orthogonum tubulare* or *Saccomorpha guttulata* dominated aphotic zone from Svalbard (Meyer et al., 2020; Wisshak et al., 2011).

Despite similarities in deep-water conditions between low and high latitudes, certain ichnotaxa commonly found in warm and cold-temperate regions, such as *Eurygonum nodosum* and *Scolecia filosa* (cyanobacterial traces) and chlorophyte microborings in the genus *Rhopalia*, are absent in the polar region. On the other hand, specific ichnotaxa unique to cold-temperate and polar regions, including *Flagrichnus baiulus*, *Entobia mikra*, *Nododendrina europaea*, and *Saccomorpha guttulata*, were present (Meyer et al., 2020). While *Saccomorpha clava* is typically a widespread fungal ichnotaxon in cold water from lower to mid latitudes, the presence is rare in high latitudes, whereas *S. guttulata* was commonly found as a substitute for this trace (Wisshak et al. 2011; Färber et al. 2015).

Therefore, accumulated data from surveys conducted in different regions along both sides of the North Atlantic, varying numbers of microboring traces have been documented. Freiwald (1998) discovered 14 microboring traces on the northern Norwegian shelf. Moving to the tropical end of the latitudinal spectrum, research from both sides of the North Atlantic provides insights. In the coldwater carbonate setting of Mauritania, characterized by upwelling, Glaub (2004) reported 17 ichnotaxa. Meanwhile, the tropical Bahamas has seen research by Vogel et al. (2000) and Radtke (1993), with a total of 14 and 21 taxa documented, respectively. Further south in the Caribbean, various studies have documented microborings, such as 24 taxa in a comprehensive bathymetric transect off Puerto Rico (Budd & Perkins, 1980), 25 forms from a shallow water transect at Yucatan (Günther, 1990), and 17 ichnotaxa from the coral reef in Jamaica (Perry & Macdonald, 2002). In summary, the limited data available so far suggests

that regions in temperate zones host the highest diversity of microbioeroders. This includes 37 ichnotaxa in the Azores, in contrast to the 14–25 microboring ichnoforms reported from polar and tropical areas. Notably, the Azores region exhibits remarkable higher ichnodiversity despite its isolated position, significantly distant from the continental shelf area (Wisshak et al., 2011).

1.6 Taphonomy and bias of microendolithic traces

In both phototrophic and organotrophic euendoliths, adaptive mechanisms have evolved to facilitate their growth and survival within their unique environments. These adaptations reflect distinctions in ecological niches and similarities highlight solutions to common challenges. It is plausible that similar morphological traits have arisen through convergent evolution, independently manifesting in phototrophic and organotrophic euendoliths. Such convergences, both shared and distinct, impose limitations on their employment as environmental indicators (Golubic et al., 2016).

The taxonomy and biology of the microorganisms that drill rock substrates remains limited, with a more pronounced lack in the fossil record, and a particularly notable gap in the case of organotrophic euendoliths. Consequently, a more comprehensive investigation of organotrophic euendoliths traces is better conducted in deep-sea sediment collections, where the presence of analogous phototrophic euendolith traces can be excluded (Golubic et al., 2016).

The well-known correlation among modern trace producers and their environment and conditions where they can thrive is the key element used in reconstruction of paleoenvironmental conditions and facies description (Golubic et al., 2016; Vogel & Glaub, 2004). The process of data collecting in paleoenvironmental reconstruction thus goes the opposite way of modern environments, starting with the morphology of boreholes traces, their

diversity and association and then we compare them to their contemporary counterparts (Golubic et al., 2016, Wisshak et al., 2012, 2011). The interaction between euendoliths and the substrate they infiltrate starts by the entry (Golubic, 2016). These are often marked by holes perpendicular to the rock surface, which can be truncated by grazers (Radtke et al. 1996). Whether in shallow subtidal waters or abyssal depths, carbonatic substrates typically exhibit small perforations on their surfaces, which expand into open galleries within the grain (Golubic, 2016). Once inside the substrate, the euendolith expands in various directions from their point of entry, extending either parallel to the surface of the substrate or while some exploring deeper into the substrate. A predominantly horizontal distribution of branched filaments with repeated tube widening characterizes specific phototrophic euendoliths. Horizontal branching with repeated widening along the tubes is a characteristic of the chlorophyta *Phaeophila dendroides* reflected in its trace *Rhopalia catenata* Radtke. A common behavior of microboring organisms is to grow parallel to the surface of the substrate without exiting it, a strategy also shown by the avoidance of producers for pre-existing tunnels (Golubic et al., 2014, 2016).

Species that adopted an endolithic strategy evolved in unrelated and remotely related groups, but at the light of similar problems, similar strategies may evolve. Reproductive strategies among microborers may include storage spaces prior to their release, usually in the form of clavate-like cavities containing reproductive and dissipating structures that are connected to the exterior by openings in the substrate surface. Pear-shaped boring trace *Planobola macrogota* Schmidt, produced by pleurocapsalean cyanobacterium *Cyanosaccus piriformis* Lukas et Golubic, produces spherical dormant/germinative cells (baecocytes) that have direct opening to the substrate surface. Germinative pulses of this cyanobacteria along the substrate surface produces populations of *P. macrogota* traces in distinct stages of growth and size (Golubic et al., 2016). Similar chambers can be produced by sporangia portions of the fungus

Dodgella priscus Zebrowski, which will result in the boring trace *Saccomorpha clava* Radtke. The remarkable distinction between *P. macrogota* and *S. clava* is the narrow tunnels produced by fungal hyphae, producing a net of tunnels that are associated with cavities (Golubic et al., 2016).

Substrates can be often and repeatedly colonized and bored, by different generations of microborers. The result can be a palimpsest, a superposition of two or more different ichnocenosis, or suits of fossil traces overlapped in the same substrate, producing a unique window of fossilization (Bromley & Asgaard, 1991; Kidwell et al., 1991). This taphonomical view allows the understanding of processes related to colonization and residence time of the producers and their substrate, before the final burial (Powell et al., 1989; Kowalewski, 1996; Olszewski, T. 1999). The comprised set of ichnocenosis can serve as a tool for elucidating the identity of ecosystem processes, particularly in instances involving the sedimentation rates, temporal availability of substrates and even transport of materials from shallow environments to higher depths, offering insights into ecological processes and sedimentary dynamics within these systems (Bromley, 2004; Olszewski, 2004; Bromley & Asgaard, 1991).

1.7 Microbial endolithic role on carbonate substrate cycling

The mechanics of microendolithic erosion was at first taught to be ecologically irrelevant (Dievart et al., 2022). In more recent years, however, many works have pointed the role of the endolithic microbiota in sediment stabilization and construction, sediment and rock recycling, by contributing to karstification of coastal limestone (Golubic et al., 2019; Tribollet 2008; Tribollet et al. 2011; Wisshak 2012), by generating fine sedimentary particles (Schneider and Torunski 1983), as well as by promoting mineral recycling in the process (Golubic et al. 1979; Berner 1999; Archer 2010). Microborers have been involved in the transfer of carbon, from its most abundant environmental pool, into biota and/or solution (Campbell, 1982). They are

actively involved in the carbon budgeting in marine environments all throughout the Phanerozoic (Golubic, 1975; Campbell, 1982). Microborers are exclusively chemical borers and different groups have created different metabolic pathways for obtaining carbon dioxide from the substrate. For example, Chlorophyte *Ostreobium* uses carbonic anhydrase while cyanobacterium *Mastigocoleus* ATPases, calcium pumps cause dissolution via undersaturation on the filament apex of the algae (Tribollet et al., 2006, 2009; Mwachireya et al., 2018) As for the reason why microorganisms bore, Garcia-Pichel et al. (2010) suggested that autotrophs do it so they can obtain carbon dioxide (CO₂), released during excavation, and use it for photosynthesis. Whenever this gas is not sufficed in the environment, algae such *Mastigocoleus testarum* will adopt an euendolithic growth and by doing so, they can release, by excavation, the carbon from the mineral substrate they had bored (Guida et al., 2017).

In modern environmental analogs, the rising of nutrient intake (C, N, P, Fe and Mo) acts a trigger for bioeroders populational increasing and infestation, including microbial counterparts, while inhibits reefs growing (Chazottes et al., 1995; Holmes et al., 2000). The ability of breaking down and fractionate consolidation of hard materials into smaller constituents and micritization of bioclasts, may serve as a proxy for nutrient availability in shallow carbonates environments previously taken as oligotrophic (Peterhänzel & Pratt, 2001). For their response to inorganic nutrients and organic matter concentrations, photoautotrophic euendoliths have a potential to be adopted as indicators of water quality (Cherchi et al., 2012). Oil pollution, as found in waters of Arabian Gulf, are pointed as responsible for a shift of abundance and microbioerosion rates in foraminifera, while in heavy metal polluted sites in coastal areas of Italy, euendolithic infestation have increased in tests of benthic foraminifera (Cherchi et al., 2012; Al-Thukair, 2002). In summary, the response of phototrophic communities to environmental changes (natural or man-driven) in the intertidal zone is translated into a

loss of diversity and a shift in the abundance in this group (Campbell, 1982, Mwachireya et al., 2018).

2 APPROACHING MICROBIAL BIOEROSION

2.1 Methods of Studying Microbial Structures

For carbonate substrates, the key method for the study of microboring morphology is by the embedding/casting protocol, developed by Golubic et al. (1970), lately adapted by Wisshak et al. (2012). The casting and impregnation of the samples in epoxy resin (Fig. 7) is processed under vacuum, obtained in vacuum chambers as CitoVac® from Struers® manufacturer. After the incorporation of hardener, liquid resin is poured over the samples while they are inside the CitoVac chamber, under vacuum.

After embedding and curing, samples are cut and abraded to expose the surface of the substrate. Next step consists of the dissolution of the carbonate matrix in order to expose the epoxy casts. In this process, it is employed the use of a weak acid, commonly a HCl solution of 3-10 percent, depending on the hardness and size of the samples. After washing and completely dried, samples are gold-sputtered and imaged by Scanning Electron Microscope. Details on mechanisms of coating will depend on the requirements of different types of microscopes and the electrical capability.

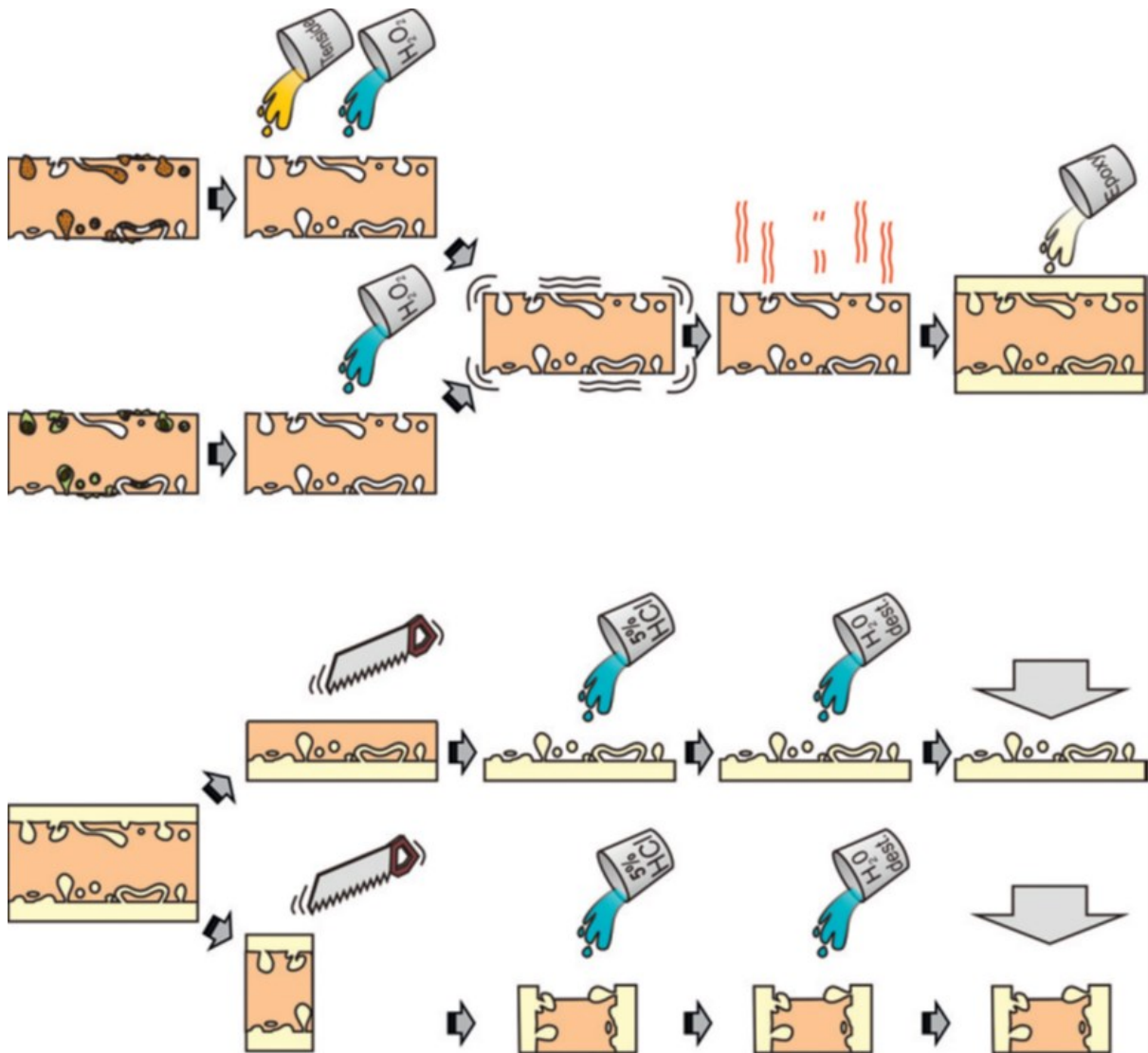


Figure 7 - Conceptual model for impregnation and dissolution for carbonate substrates, such as foraminiferal tests. The calcareous substrate is depicted here and submitted to removal of sediments and organic matter by ultrasonic bath and/or hydrogen peroxide. Cleaned substrate is dried to ensure the removal of moisture. The most critical part of the process encompasses the infilling of the pores and perforations by epoxy resin under vacuum. After curing period, they are cross-sectioned or sanded to expose the original calcareous material. Next step involves the removal of calcareous substrate by treating the blocks with diluted hydrochloric acid, thereby leaving the cast samples intact. Lastly the samples were washed and left to dry and coated with a layer of gold using a sputter-coating technique before being subjected to SEM visualization. Some samples can be only partially etched, due to the frailty of the sample. Modified after Wisshak, M. 2012. *Developments in Sedimentology*, Vol. 64.

The embedding technique, despite having promoted great advancement in the study of boring traces, has the big disadvantage of being totally destructive. This becomes a watershed in

decision making whenever the options are restrictive, in the case of few samples available, holotypes or in historical pieces that become the only source of microendolithic structures (Wisshak, et al., 2017). A multi-technical approach in the study of endolithic boring is crucial to support the use of these traces as indicators, for fossil or recent context. The combination of different methods helps to complement and limit the "artifacts" resulting from techniques and preparations (Golubic et al., 2019). Techniques are being developed using the natural fluorescent properties of organic pigments, under confocal laser scanning microscope (CLSM) microscopy, in order to keep the natural 3D position of the boring structures (Schätzle et al., 2021). This process is suitable for recent and wet material by providing an alternative to the laborious and irreversible process of cast-embedding. Advanced imaging techniques of Micro-CT and Nanno-CT have also been reached in the past few years, with the enormous advantage of being totally non-invasive and non-destructive (Heřmanová et al., 2020; Jacques et al., *in prep.*).

2.2 Ichnotaxonomy Evaluation of Microendoliths traces

Trace fossil classification, also known as ichnotaxonomy, is a parallel system to the Linnean classification denominated parataxonomy as it is based on the vestiges of the activity of an organism, not been directly part of tree of life. However, most ichnologists consider ichnotaxonomy primarily as a morphological classification. There is a consensus that adopting a formal nomenclature that identifies microbial endoliths based on their traces is essential before utilizing them as indicators in paleoecology, stratigraphy, and paleobathymetry (Golubic et al., 2019; Bromley, 1981). The difference resides in the approach and practices from ichnotaxonomy and (formal) taxonomy. The ichnotaxobasis debates relies around shape and substrate, and the current acceptance that a traces form, general geometry and morphology is a direct reflex of the geometry, shape and behavior of the producer, while its identity is

irrelevant for the ichnotaxonomical treatment (Golubic et al., 2019; Bertling, 2007). The external structure of a boring trace conforms and casts the outlines of the organism that produces it, leaving a specific trace, so they can be studied and classified at the level of microbial population and trace assemblages. Comparison with modern producers can provide taxonomic affinities, with some limitations (Radtke and Golubic, 2011; Campbell and Hofman, 1979).

A modified version of the guild concept is applied to boring producers, which groups them based on their behavior, trophic level, and habitat (Tapanila, 2008). Trace fossils must be treated taxonomically in a consistent manner that is unrelated to ethologic classifications. Physical sedimentary features and biological taxa are used to designate trace fossils, with morphology serving as the primary criterion. As ichnotaxobases, size, producer, age, facies, and preservation are disregarded. Ichnotaxa based on well-preserved specimens should replace separate names for undertracks and poorly preserved material. New names can only be based on fossil material, however existing trace fossil taxa can be used to identify recent traces. In systematics, ichnotaxa should not be included in biological taxa. Although compound traces can be designated independently in specific circumstances, composite trace fossil formations lack ichnotaxonomic standing. The only basis for the International Code of Zoological Nomenclature should be trace fossils (Tapanila, 2008).

3 BIOLOGICAL INTERFACES

3.1 Bioerosion and the precipitation of organic byproducts

As rock-dwelling microorganisms present better responses for stressful environments, their activity puts them as good candidates on establishing criteria of bioactivity from remote areas

on recent and young Earth or even in rocks from other planets (Mcloughlin et al. 2007). A robust and reliable protocol (Fig. 8) for ancient and extraterrestrial life must fulfill three interdependent lines of evidence which are: (1) a geological context that corroborates syngeneticity of putative biological remains and the substrate; (2) evidence based on morphology and behavior and (3) geochemical evidence for biological activity (Rose et al., 2006). For the ability of endolithic microorganisms to tolerate extreme environments, it makes them the most plausible candidates to search for life on ancient earth and on other planets (Friedmann & Koriem, 1989). In this minute scale of life, even small grains could provide an entire space for occupation at an ecological level and microboring activity could be reported even minute fragments of hard substrates. Therefore, euendolithic organisms have a great potential to be used as biosignatures, from the deep past or even other planets (Brack, 2019; Cady et al., 2003; Wierzchos et al., 2003, 2005; Westall et al., 2000, 2003).

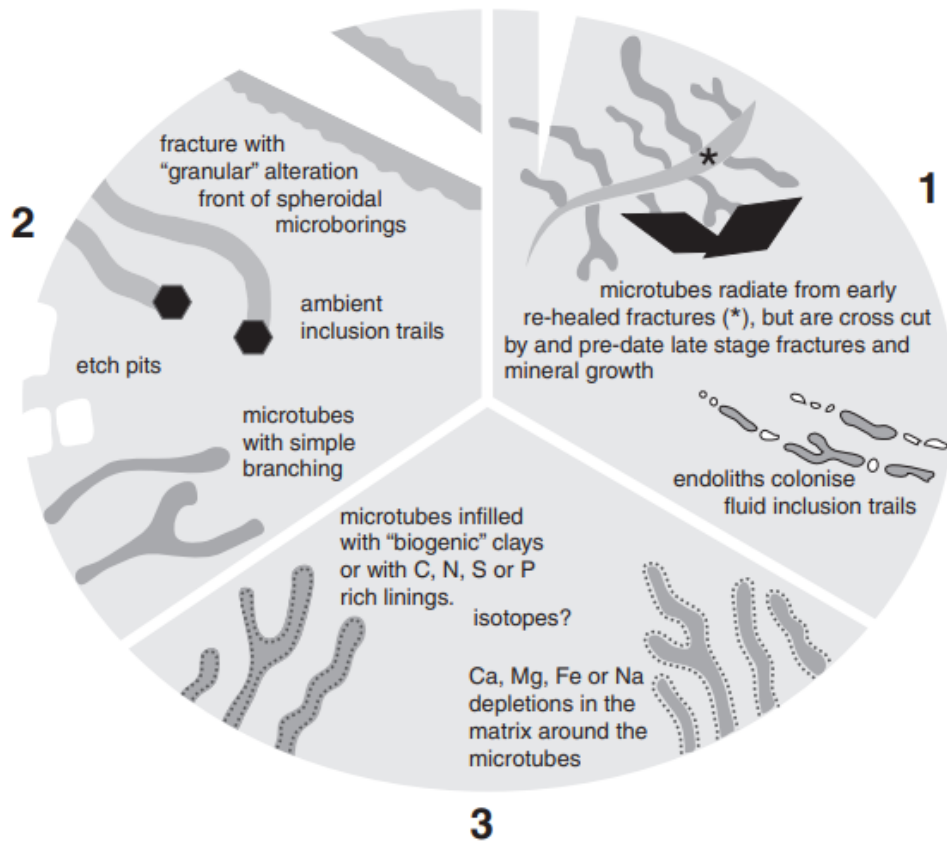


Figure 8 - Schematic summary of requisites biogeneticity criteria for euendolithic traces protocol. (1) syngeneticity and geological context conducive for life; (2) ubiquitous morphology and behavior (3) geochemical trace for biological activity (After McLoughlin et al., 2007).

The process of formation and maintenance of microbial biofilm can also give some clues for the past microenvironment in which fossil groups and microorganisms lived in and the process those environments were subject of (Briggs, 2003). The role of microorganisms in the environment via bioerosion or either its antagonistic counterpart, also known as the precipitation of biofilms and subproducts, is still a prolific field of debate. This topic is still the subject of new protocols of methodologies and chemical analyses, designed for establishment of organic origin, in the fossil record, and the producers, among extant and fossil groups (Iniesto et al., 2016, Briggs et al., 2003). The presence of biofilms can ensure and enhance the fossilization process by creating a microenvironment that either seals organic particles and

prevents them from being washed out by diagenesis or by acting as a barrier for the groundwater during the lithification process (Iniesto et al., 2016).

The sub products of microbial activity, with a potential to preserve in fossil record, includes kerogen, framboidal pyrite and biofilms and in these two last cases, with special contribution by chemotrophic sulfide bacteria (Osés et al., 2017). This last one which specific and traceable morphology and iron and sulfur isotopic composition (Duverger et al., 2020, Lepland et al., 2014).

3.2 Bioerosion and organic products: synergistic interactions of cycling systems in nature

Organic activity will undeniably leave traces behind (Noffke et al., 2001). Apart from endolithic lifestyle, the other group potentially important in the fossil record is the group of microorganisms that leave significant amount of their activity in the form of biofilm and other organic byproducts, e.g. framboidal pyrite (Hoffmann et al., 2021; Folk, 2005; Popa et al., 2004; Schieber, 2002). The widespread distribution of biofilm-producers in modern environments, gives a hint to the fact that episodic accumulation of microbial biofilms may be triggered by stressing situation, perhaps aroused as a natural response for early recovering after harsh conditions (Costerton et al., 1994).

Microorganisms infesting substrates were first thought to be ecologically irrelevant. Over the past 30 years of survey, results have shown therefore, consistent evidence of the role of microorganisms as bioengineers of their environments, with regional and global consequences of their activity (Gomes et al., 2019; Delgado et al., 2014; Posth et al., 2014 and 2013). The involvement of microorganisms in both the formation and recycling of sedimentary structures is widely recognized, and so it is important to understand this very same process on modern

systems, where conditions are known, and outputs can be evaluated and interpreted. Equally acknowledged is the significance of investigating these geological processes in contemporary environments, where we can directly observe and document the conditions, contributing factors, and resulting outcomes. This knowledge is crucial for comprehending and deciphering analogous processes in the fossil record if their effects have been preserved to present days (Dievart et al., 2022; Golubic et al., 2019).

4 CASE STUDIES OF THE THESIS

This chapter compiles a collection of the analyzed material during PhD activities, whose results were published in journals listed in the Web of Science database.

The study of microboring structures has appeared in scientific writings since the mid-19th century with the description of the activity of “perforating algae” and those who would live in the calcareous shells of mollusks (Bornet & Flahault, 1888, 1889). Traditionally, the study of recent endolithic traces, provided by material from coastal limestones of Mediterranean Sea, high latitudes of the Northern Sea, and coral reef areas in Central America and Middle East. Despite the magnitude of all ecological and environmental aspects presented in these environments, most of their microendolithical studies share the aspect of being conducted in relatively well oxygenated and shallow waters. Therefore, indirectly leading to a lack of detailed data from dysoxic environments. This doctoral thesis aims to provide a comprehensive description and comparison of endolithic microbial communities, and their role in ecosystems of variegated ages along the Phanerozoic, and at different hard substrates such foraminiferal tests and even phosphatic shells. The collection of investigated data in this dissertation provides additional examination of ichnofauna across the Early Paleozoic, Mesozoic, and Cenozoic Eras of Europe. While testing long-standing assumptions, it aims to provide novel

data, including those of dysoxic environments, exploring novel and synthesizing existing knowledge about microendolithic structures.

In order to better understand the limits of bioerosional aspects of endolithic activity, it is also compared to the other spectrum of microbial activity, the precipitation of organic subproducts, in this case, biofilms. Data was compiled and analyzed in a semi-quantitative approach for Sassnitz and Western Carpathians samples. Each of these assemblages offer a unique insight into these ichnocoenosis, their evolutionary trajectories and paleoenvironmental aspects.

The Ordovician microboring assemblage from the Prague Basin, offers a glimpse into a crucial stage in the development of the microendolithic niches, illustrating the transition from a predominantly surface-level structures to perforations that explore more and more vertically into the carbonate substrate, known as "Ordovician Bioerosion Revolution". This crucial moment registered not only the diversification of boring activities but also, a great increase of carbonate bioerosion intensity that peaked in the Late Ordovician until the Early Silurian (Wilson & Palmer, 2006). Meanwhile, the ichnofaunal composition from Sassnitz, dating to the Upper Maastrichtian, is situated in a context of global levels of low Mg-Ca (Timofeeff et al., 2006), adding a unique dimension to the study. The dataset derived from the Western Carpathians provides perspective on Cenozoic ichnofauna under dysoxic conditions, and the thresholds dynamics between bioerosional process in opposite to the precipitation and preservation of byproducts deposits. Collectively, these materials encompass distinct episodes, each occurring under unrelated sedimentary conditions, reflecting the dynamic nature of ichnofaunal evolution over geologic time. Through the examination of these ichnofaunal communities, this dissertation aims to shed light on their evolution and adaptation in response to changing paleoenvironments, ultimately enriching our understanding of these structures.

Through the empirical investigation and data analysis, we aim to provide a broader understanding of how these structures can improve paleoecological and taphonomical inferences.

2.1 Methodological dynamics

2.1.1 A multitasking approach

Studying ichnocoenosis is a complex and not always successfully guaranteed process as samples need to achieve a certain condition to provide minimal results before qualitative and quantitative analysis. Around 300 samples from different geological sites of Cenozoic deposits, cores, and profiles, were pre-screened by Scanning Electron Microscope (SEM). For this step, 20 foraminifera tests are separated for a screening process, by SEM visualization and imaging. With the stereomicroscope, we select a variegated set of tests that will be mounted on metallic stubs, intended for SEM equipment. This first screening is intended to check for recrystallization and the general condition of boring structures before embedding. Diagenetic alterations affecting remineralization and the precipitation of clay minerals can obliterate the visualization of the boring structures.

Initially, this thesis was intended to be focused on the register of microboring related to benthic foraminifera from different Epochs of Cenozoic, from tests provided and collected from areas in the Western Carpathians region. Around 300 samples were analyzed, but due to conditions, either recrystallization of the tests, or the scarcity and fragmentary condition of the microendolithic structures, they were therefore considered unusable and not taken as part of this investigation. Thus, the accepted next step was to extend the investigation on boring structures over other ages of the Phanerozoic, that were positive for microboring structures, and could contribute to the scientific discussion over the microendolithic register. Despite the

differences in the geological range of the studied material, it is still possible to provide a semi-qualitative outcome related to their paleoecology, such as the relative paleobathymetry and taphonomical aspects, but focusing on the particularities of each set of samples. Paleobathymetry has been quite similar since the first huge diversification of the microboring groups, during mid-Paleozoic, while the established behavior has presented an important shift during this interval, becoming deeper in the hard substrate (Vogel and Brett, 2009). Maastrichtian samples from Sassnitz provide an opportunity to investigate benthic foraminifera and the associated microendolithic register conditioned to the influence of a global calcitic sea (Wilson & Palmer, 2006). Last, material from Late Oligocene and Miocene, provide the opportunity to analyze the threshold between erosional activity of microborers and their producers of biofilm counterparts, involved in the precipitation and accumulation of bioproducts.

2.2 Applicable techniques

Observation of boring structures can be done by the use of stereomicroscopes, for both tests but more importantly, by using petrographic slides (Holcová et al., 2023; Rifl et al., 2022; Salamon et al., 2019). The transmitted light mode from this equipment allows us to reach certain levels of accuracy and even be able to make evaluations of such infestations and the level of obstruction of the channels and chambers, in a fast and not time-consuming way. This approach is especially useful in fossil tests from recent and Cenozoic, that can retain some level of transparency under transmitted light, or older fossils whenever their diagenetic process allows some level of transparency. Even if it is a useful screening approach for first decisions over samples, it is not able to provide many details. To get the most information from microboring structures related to tests, the most effective known technique is the cold mounting and resin casting one. This consists of casting, under artificial atmosphere generated

inside vacuum chambers, as the CitoVac® Vacuum Impregnation unit from Struers®. When in vacuum, liquid epoxy resin is poured over the samples, the lower pressure ensures the impregnation and filling of any minute void space inside the sample such as chambers, pores and tunnels. Cenozoic and recent tests respond more effectively to pressures of 0.3 Pa during the resin pouring stage, resulting in a reduced occurrence of air bubbles. The next step involves cyclic variations in pressure within the chamber, encompassing a reduction to 0.15 Pa followed by an increase to 0.4 Pa. This procedural repetition aims to overcome the capillary resistance of the resin, to create a gradient that helps the air to escape out of the tests, and to increase resin viscosity, thereby ensuring its penetration into the empty spaces within the tests. This strategy is pivotal for guaranteeing the fidelity and homogeneity of test casting, as it minimizes the likelihood of artifact formation due to trapped air. It is noteworthy that the Mesozoic specimens of tests from the White Chalk Formation, on the other hand, do not respond the same way as Cenozoic samples to the shifts in the pressure. They otherwise show an improved response to pressure at 0.30 Pa. This small change in the methodology had presented a higher efficiency on minimizing the formation of air bubbles that otherwise generate distortions into the samples and compromise the reliability of the casts. Paleozoic samples in general present a higher diagenetic modification due to their longer history of exposure to crustal processes. Samples from the Ordovician-Devonian studied interval from Prague Basin presented a lower density and a higher level of clay minerals obliterating the empty spaces of the tests. Ultrasonic bathing does not apply to these samples as they are too frail and tend to crumble before the natural spaces of the tests have the chance to get cleaned. This set of characters also affects sample performance under vacuum and the casting of the boring structures. In this case, another approach and technique are required. The phosphatic shells from Prague Basin

showed a good level of transparency that allows the examination by transmitted light, ensuring a non-destructive observation of the structures inside the shells.

Trying equipment such as X-ray computed tomography has proven to be a challenge in this study. They provided a suboptimal outcome due to their limited resolution and inability in capturing fine details of small dimensions of the samples of reduced dimensions. Raman spectrometry is a crucial output when dealing with fossil organic residues, but the accuracy of laser beam can be a challenge when using small tests, and thus creating the tendency to biased data. CT measurements of microboring are, right now, also not suitable because of the dimensions required in most of the machines. For imaging of microboring tests, Scanning Electron Microscopy was the main used method. The images were taken using a Jeol in the Faculty of Sciences, Charles University in Prague.

SEM imaging has the inconvenience of being a destructive approach as, due to the nature of this type of observation, microboring structures inside the tests and shells need to be exposed to the electron beam in order to be visualized. MicroCT and especially the NannoCT mode, are the expected next step in the observation and documentation of microendolithic structures, due to the possibility to observe hard substrates without the need to destroy them. Thus, they are promising tools (Jaques et al., *in prep.*).

2.3 Fossil Material – Studied Cases

2.3.1 – Microbial endoliths from test of benthic foraminifera, Western Carpathians

This study is a paleoecological and geochemical determination of microendolithic communities related to tests of benthic foraminifera. The material was collected (Fig. 9) from Cenozoic localities surrounding the Western Carpathians (Kováč *et al.*, 2017) in the Czech

Republic (LOM-1 LKŠ and Mikulov), Slovakia (DNV), and Hungary (Rozalia). Geologically, sedimentary rocks from these areas range from Rupelian to Serravalian (Kováč et al., 2017).

Oxygen content in bottom and pore water was interpreted using the BFOI (Benthic Foraminifera Oxygen Index) proposed by Kaiho (1994, 1999) and Baldi (2006). In these studies, a ratio of index benthic foraminifera establishes the dissolved oxygen of the water and sediment in the environment these organisms lived in, by the means of species composition of the benthic foraminiferal assemblages. This correlation may be applied also to fossil samples. While both dissolved oxygen levels and the flux of organic carbon play the main roles in shaping benthic foraminiferal communities, the BFOI serves as a valuable indicator derived from these communities to assess the dissolved oxygen conditions in Cretaceous and Cenozoic samples (Kaiho, 1994).

Out of 300 individual tests analyzed from the sample collectiveness of these 5 localities, a total of 10 ichnospecies were preserved enough to be identified, and in 4 forms it was possible to determine only approximately. Identified ichnocenosis indicates a deep euphotic to aphotic zones according to zonation proposed by Glaub *et al.* (2007). DNV presented the highest diversity at the epifaunal rotalids, with 4 forms identified, along with LKŠ-1, LOM-1 boreholes, which also presented high levels of infestation. One fully developed organotrophic trace was found in the Mikulov section while the Rozalia section showed a total absence of microborer activities. The BFO index obtained from samples shows a predominance of indicators of suboxic to dysoxic conditions. The Mikulov section is the only locality positive for oxic indicators, while the Rozalia section presents only dysoxic indicators. The anoxic bottom conditions, necessary to preserve the organic matter that will originate oil, may be incompatible with communities other than sulfur-reducing bacteria, being too stressful even

for endolithic heterotrophs. This way, anoxia can explain the notable absence of microboring producers in Rozalia samples. On the other hand, there are abundant deposits of biofilm structures, whose energy dispersive X-ray (EDAX) showed a microenvironment with enriched content of iron, sulfur, and phosphorus. Raman spectroscopy indicates affinity to organic pigments, for these Rozalia biofilms. The present study was the first attempt to describe microbial endolithic communities from this area, and their possible correlation with precipitated byproducts of microbial activity such as biofilms and framboidal pyrite.

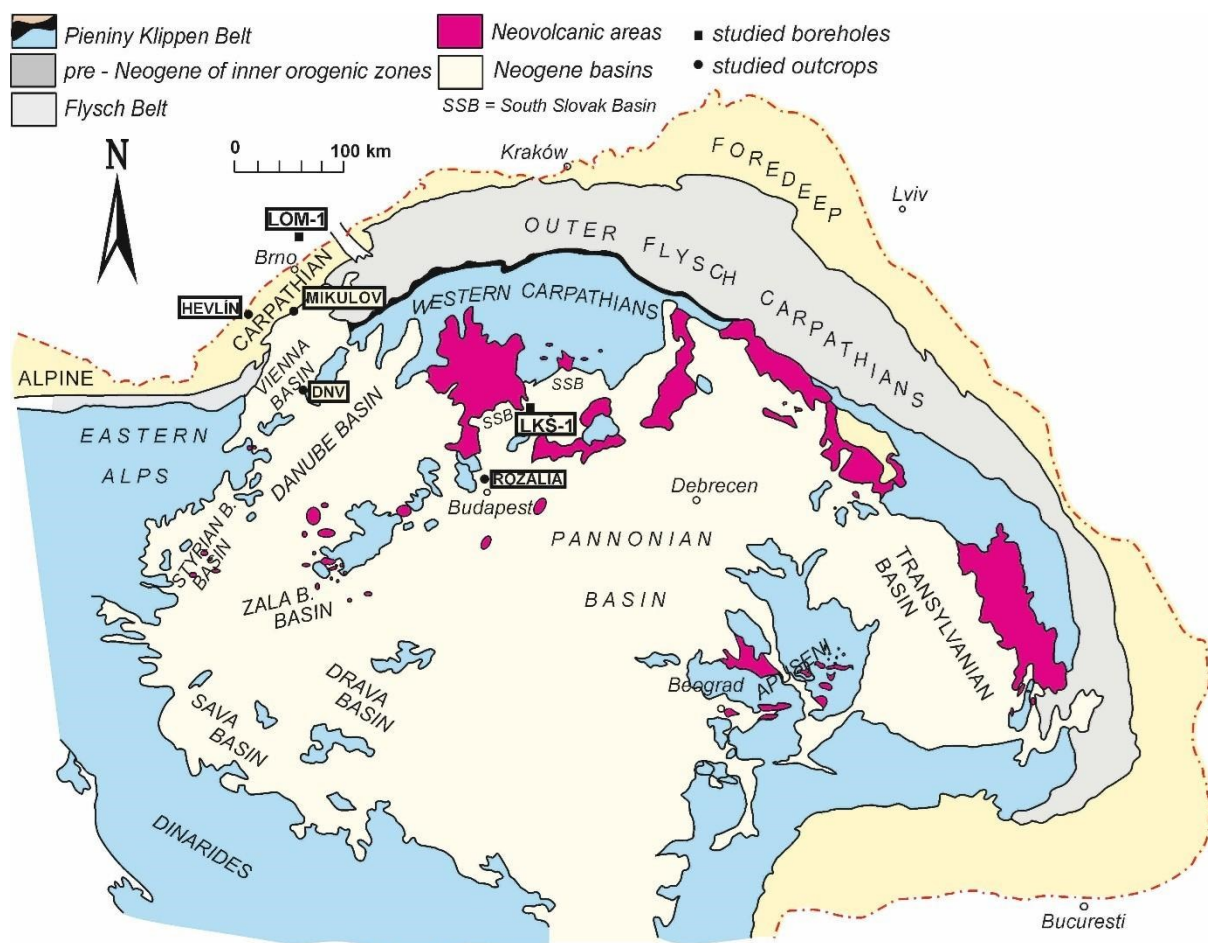


Figure 9 - Geological map of the Western Carpathians region showing the collecting sites of the samples used in this study (modified after Kováč et al., 2017).

2.3.2 – Microbial aspects of Paleozoic deposits from Prague Basin

This study consists of an inspection of microbial endolithic structures, focusing on Ordovician to Middle Devonian marine interval from Prague Basin, Czech Republic (Barrandian area). For this survey, nearly 800 petrographic slides, 10 brachiopod shells and other bioclasts were examined. Microbioerosion was rare in the Ordovician to Lower Devonian and was primarily produced by bacteria and fungi on bioclast surfaces. However, a gradual increase in the abundance of microboring structures and their shift towards the interior of bioclast was observed during the Silurian to Early Devonian interval. This coincides with an increase of the number of bored tunnels found on fossil register, possibly produced by phototrophic microboring organisms (Cyanobacteria and Algae). The interval covered by this survey is also crucial for showing an advance in endolithic paleoecology, represented by early diversification and presumably first appearance of some boring cyanobacterial and fungi ichnotaxa, especially during the late Ordovician (Vogel & Brett, 2009). The abundance of microendolithic structures notably increased from the Emsian onwards. These structures do not exhibit random distribution patterns concerning their paleoenvironments; instead, they are most frequently found in low energy hemipelagic red carbonates. The use of shell and bioclast material as a nutrient source or shelter has been a successful life strategy since the Precambrian period (Campbell, 1982, Glaub and Vogel, 2004). These strategies enable recycling of shell material in biogeochemical cycles, which persisted across all Phanerozoic mass extinctions and subsequent recoveries of the global ecosystem (Tribollet et al., 2011). However, the morphological diversity of boring structures has not significantly changed during this long period of time. Traces of biologically induced erosion in ancient reef structures indicate that bioerosion has probably had some effect on reef carbonates since the Precambrian (Vogel, 1993). In recent years, fossil samples from the Lower Paleozoic of the Prague Basin, Czech

Republic, have been inspected for boring structures. Their presence is relatively rare, which agrees with the data presented by Taylor and Wilson (2003). The morphological variability found in this study was also significantly lower than expected from published data on Paleozoic taxa. Primary factors affecting the occurrence of microboring organisms in modern ecosystems include the amount of light within the photic zone controlled by depth, quality and quantity of both organic and inorganic nutrients, and temperature changes. The type of substrate appears to be more influenced than other environmental factors such as changes in pH, nitrite, sulfate, soluble reactive phosphorus, and dissolved organic content. The study focuses on microboring structures, which are generally produced by chemotrophic and autotrophic bacteria including Cyanobacteria, Algae, heterotrophic fungi and fungi-like organisms. The changes in microbioeroder ecosystems were more likely driven by local factors such as the drift of the Prague Basin from temperate to tropical climate zones, increased oxygen content near the sea floor, or preserved shallow littoral facies (Holcová et al., 2023).

2.3.3 – Microbial endoliths from the Upper Cretaceous of the Boreal Realm

This study consists of the analysis of a sample of chalk from Sassnitz collected in June/2022 and was a chance to make an ichnotaxonomical and paleoecological characterization of a Maastrichtian microendolithic community. A rapid stereoscopical investigation of the tests indicated a good number of clean microboring structures but after preparation, roughly 10 tests presented resin casts of microendolithical structures that were entire enough and in good condition to be identified. Morphology of tunnels and cavities suggests the presence of red algae and fungi and the absence of green algae and cyanobacteria traces were interpreted as a consequence of placement in deep photic to a dysphotic zone. The study also emphasizes the taphonomical aspect of residence time of tests and discusses its importance for the availability of this material as a substrate for endolithic organisms. Miroendolithical studies are

not new in the area, but this is the first description of microborings published in the English language. This study also includes the description of possibly new ichnospecies for the *Saccomorpha* genus. The occurrence of potential new ichnospecies is indicative of novelty and highlights the need for further exploration and research. This paper has been submitted to peer-review process.

2.3.3.1 - Geological settings

During the Upper Cretaceous, approximately 145-66 Ma, extensive portions of the European basin were covered by an epicontinental sea (Tagliavento et al., 2020; Voigt et al., 2008). This epicontinental sea represented a shallow shelf sea, originating from the southern Tethys Ocean, which extended eastward into the present-day Mediterranean region as the North Atlantic Ocean began its formation. This shelf sea encompassed various basins, including the French Basin, North Sea Basin, Norwegian-Danish Basin, and North German-Polish basins, extending as far as Western Asia, southeast of the Urals (Reich et al., 2018; Damholt & Surlyk, 2004).

The Rügen Chalk (German: Rügener Kreide or Rügener Schreibkreide, Early Maastrichtian 70 Ma old) is the common name for a very pure, highly fine-grained, frail, and highly porous chalk, almost entirely of low-Mg calcite (Tagliavento et al., 2021). During this period, the region occupied a position of about 40° paleolatitude of a humid and warm temperate climate, under a greenhouse Mesozoic condition (Price et al., 2013). These conditions were unique to the Cretaceous, and they lack analogs in the Present time. This portion of the basin was located in a distal position far enough for the influence of deltaic and coastal terrigenous input. Carbonate material was precipitated by the accumulation of coccoliths oozes, with minor contribution of other calcareous microfossils and highly specialized benthic fauna of

brachiopods, bryozoans, and other low-Mg content shells (Neumann, 2012; Håkansson et al., 1974). These deposits are nowadays exposed in cliffs on the coast of the Jasmund peninsula in the northeast of the island of Rügen in Mecklenburg-Vorpommern (Neumann, 2012).

Biostratigraphic position of Rügen Chalk is confirmed at the upper part of Lower Maastrichtian by the presence of belemnites from the zones *Belemnella (Pachybellemnella) sumensis* Jeletzky 1949, *Belemnella (Pachybellemnella) cimbrica*, Birkelund 1957 and *Belemnella (Pachybellemnella) fastigata*, Schulz 1979 (*apud* Herrig et al., 1996). Changes in sedimentation processes were reflected in the faunal compositions of the profile sequence, the occurrence of 'chalk band' and variations in flint content. The chalk sea had a depth ranging from 150 to 250 meters, with minor fluctuations. Surface water temperatures in the Rügen area during the Campanian stage were estimated at 12–16°C, with a salinity of less than 32‰ (Hay et al., 1998). The seafloor consisted of soft calcareous mud, occasionally forming secondary hard floors from the remains of organisms like Bryozoa, creating "spotted reefs." Overall, the settlement patterns were qualitatively similar, with variations in settlement density attributed to changes in secondary hard soils and fluctuations in nutrient supply due to varying inputs of limiting nutrients. Evidence for ground currents was limited, suggesting different intensities and local structures and the estimated sedimentation rate was approximately 35 mm per 1000 years. The entire section was deposited over a time-lapse of around one and a half million years to be assumed (Reich et al., 2018; Neumann, 2012, Herrig et al., 1996).

In the Danish-German area, Maastrichtian deposits attain a thickness of about 200-400 meters, and they are assumed to have been deposited as pelagic sediment in moderately shallow waters no deeper than approximately 250 meters but mostly below the photic zone (Håkansson et al., 1974).

The dynamics involving foraminiferal tests from White Chalk, and their ichnological record, have been shown by several taphonomical signs, providing clues on the paleoecology of this microendolithic ichnocenosis. The observance of deep infaunal tests affected by borings produced by Chlorophytes, as well as the existence of clean shallow infaunal tests, gives hints over the dynamics involved in this paleoenvironment. Bioturbation caused by burrowing animals is extensive and well documented in the White Chalk deposits (Ekdale & Bromley, 1984, 1991; Bromley & Ekdale, 1984) and is pointed here as the main interference on the disposition of benthic tests, making them available or not for colonization by endolithic organisms. For this, we proposed a taphonomical model aiming to summarize the way this dynamic environment could have disturbed the expected register of benthic tests and so, interfering in the register of this microichnological assemblage. Another outcome for the analysis of this Cretaceous material is the observance about the diversity of finding remains. Among them, there are the plausible occurrence of Entobian-like microendolithic register and also, a different form sharing deep resemblance with *Saccomorpha* species. This can be summarized as the occurrence of terminal, erect and necked chambers, of an average of 8 μm , connected to straight slender tunnels, with no variations on the caliber along their length. This description fits in the diagnosis proposed by Radtke, 1991, for *Saccomorpha* ichnogenera, and that work has also presented *S. clava* and *S. terminalis*, two forms that share the highest number of morphological similarities with the new form described here. Doing so, in this manuscript, we are proposing a new *Saccomorpha* ichnospecies based on the register present in these samples from the White Chalk and the related forms described originally by Radtke, 1991.

Conclusions

1. During Ph.D study, the protocol of microendolithic methodology was applied in the Institute of Geology and Paleontology, Charles University Prague. It includes preliminary study of the surface of hard substrates by stereomicroscope, resin casting producing 3D microboring structures and detailed study in scanning electron microscopy. Potential of Nanno-CT imaging of microboring activity was also tested.
2. Several microborer communities were studied from three Phanerozoic stratigraphic levels.
3. Early Paleozoic microborer communities were studied in the Barrandien area. Microbioerosions showed low diversity and rarity from the Ordovician to Lower Devonian and was primarily produced by bacteria and fungi on bioclast surfaces. However, a gradual increase in the abundance of microboring structures and their shift towards the interior of bioclast was observed from the Middle Devonian.
4. A new ichnospecies, *Saccomorpha cordiformis* was described from the Upper Cretaceous chalk from north Germany. Detailed analysis of producers of microboring structures in relation to life-strategy of hosted foraminifera, enable reconstructing the paleoenvironment at seafloor, and a model for its dynamics was proposed.
5. The study of the Oligocene and Miocene microborings from the Paratethyan area was focused on the influence of decreased oxygen content on microendolithic communities. The study showed that increased content of oxygen significantly decreased diversity and abundance of microboring structures to their fully disappearing. It means that producers of microboring structures need higher oxygen content inside sediments like deep-infaunal foraminifera.

6. Markers of fossil microbiological activity, associated with microendolithic register, were established in the Oligocene and Miocene samples, from the Central Paratethys. It includes the presence of biofilms and the precipitation of authigenic pyrite in the form of framboids.

List of published and submitted manuscripts stemming from the thesis

Kerkhoff, M., Holcová, K. 2024. ***Saccomorpha cordiformis* isp. nov.: Perspectives on a new form and the microendolithical paleoecology and taphonomy of the Boreal Upper Cretaceous Sea** (*submitted*).

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