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Ichnotaxonomy of microboring traces in marine aphotic depths

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Abstract

Microboring traces in carbonate skeletal fragments deposited in aphotic depths of the oceans are studied, evaluated, and described with respect to their marine ecology and palaeoecology as well as ichnotaxonomy. Sand-size deep sea sediment particles dredged from depths ranging between 600 and 3266 m of the Bermuda Pedestal, Central Atlantic Ocean, the Florida Escarpment, the Mediterranean Sea, the Red Sea and the Indian Ocean were studied. Following ichnological rules, trace fossils are described as ichnogenera and ichnospecies, defined as products of organismal behaviour. This, in our view, refers to the growth habit of microboring organisms in response to environmental stimuli within the substrate they penetrate. The problem of palaeobathymetry is discussed in conjunction with the distinction between light-dependent and light independent microboring organisms, with the emphasis on the latter. We considered this distinction to be important because only the light-dependent microborers have been recognized as indicators of ancient depositional depths, whereas the light-independent ones are expected to occur at any depth, subject to the availability of organic nutrients. Microboring organisms often leave morphologically similar traces due to convergent evolution. Their responses may change during their life cycle; they may produce different traces when pursuing their vegetative vs. reproductive functions. New ichnotaxa are described. All are regarded as organotrophs given their aphotic zone deep sea origin. This work presents the most complete set of deep sea microbial euendolith traces, to date.

Keywords: bioerosion, deep sea, ichnotaxonomy, microbial euendoliths, organotrophy, palaeobathymetry

1. INTRODUCTION

1.1. Microorganisms and mineral substrates

Microorganisms are among the first occupants of mineral surfaces in aquatic environments, forming biofilms (KRUMBEIN et al., 2003) and microbial mats (GERDES et al., 1993). These coatings experience changed physico-chemical conditions upon contact with the substrate (KÜHL & REVSBECH, 2001) which include changes in carbonate saturation levels in the surrounding solution that may induce calcification (KÜHL et al., 2003; KRAUSE et al., 2019). Carbonate dissolution can also occur (GARCIA-PICHEL et al., 2010; GRANGE et al., 2015; GUIDA & GARCIA-PICHEL, 2016; MASSE et al., 2020). Microorganisms that settle on mineral surfaces as epiliths often exude organic acids and chelating agents able to dissolve mineral matter of the rock or shell surface and leave etch mark traces. Microbial settlers use a variety of strategies to enter a rock's interior and become endolithic. The conceptual understanding of microbial activities affecting rocks goes back to their first discoverers, the biologists BORNET (1891) and BORNET & FLAHAULT (1888, 1889). Abbé Pierre Frémy, who published a comprehensive study on African and Mediterranean cyanobacteria (FRÉMY, 1930, 1934), expressed the distinction between etching and penetration for the phototrophs as *"les algues cariant et perforant"* (FRÉMY, 1945). We follow the same distinction in describing microbial traces in the aphotic deep sea, by distinguishing between traces of microboring organisms left in the interior of carbonate substrates from those expressed as etch marks on the surface of carbonate substrates.

The presence of microorganisms in rocks and other mineral-supported hard substrates was noticed by researchers working in the photic zone who observed green, and sometimes, red or black lines about a millimeter beneath the surface of limestone rocks (ERCEGOVIĆ, 1925; LE CAMPION-ALSUMARD, 1969; RADTKE & GOLUBIC, 2011), ooid grains (AL-THUKAIR & GOLUBIC, 1991a, b; AL-THUKAIR et al., 1994), mollusc shells (BOEKSCHOTEN, 1966; RADTKE, 1993; RADTKE & GOLUBIC, 2005; RADTKE et al., 2011), coral skeletons (CHAZOTTES et al., 1995; LE CAMPION-ALSUMARD et al., 1995a, b; KOLODZIEJ et al., 2012; PICA et al., 2016) as well as in stromatolites (REID et al., 2011). Although endolithic microorganisms have been observed for many years, the distinction between epiliths and distinct types of endoliths was defined later by consensus (GOLUBIC et al., 1981). Some microorganisms enter the rock by lining cracks and fissures of a substrate (e.g., DIELS, 1914) as chasmo-endoliths, or by colonizing preexisting cavities inside porous rocks (FRIEDMANN, 1971) as crypto-endoliths, while microboring organisms that actively penetrate limestone rocks (BACHMANN, 1915), dolomites, and carbonatic and phosphatic skeletons are defined as euendoliths though the term "endolith" is often used interchangably. Microboring or euendolithic organisms penetrate carbonate substrates and

reside in the boreholes they have produced. Microbial euendoliths can be prokaryotic, eukaryotic, and potentially also archaea. They leave traces that conform closely to the morphological outlines of their makers (CAMPBELL & HOFFMAN, 1979). A combination of microbial euendoliths and subsequent calcification in the formation of micritic envelopes around sediment particles was studied by BATHURST (1966), who emphasized the importance of comparing ancient and modern environmental settings to ascertain the geological significance of such activities. This phenomenon was thought to be restricted to shallow subtidal ranges but was later found in the deep sea as well (HOOK et al., 1984).

Most studies of organismal impact on sediments (bioerosion) have been carried out in marine coastal regions (TRIBOLLET, 2008a; TRIBOLLET, 2008b), where it was shown that the presence of microborers conducting biocorrosion activity (TRIBOLLET et al., 2011a) attracts grazing and scraping animals, such as molluscs, echinoderms, and parrot fish. Grazers remove the endoliths mechanically (bioabrasion), together with parts of the surrounding mineral substrate (SCHNEIDER, 1976; SCHNEIDER & TORUNSKI, 1983). Together with chemical removal or biocorrosion by microorganisms, these activities described here amount to bioerosion (TRIBOLLET et al., 2011b; WISSHAK et al., 2011). Biocorrosion and bioerosion are widely distributed activities on coral reefs (CHAZOTTES et al., 1995; TRIBOLLET & GOLUBIC, 2005; CLEMENTS et al., 2016). Both also take place in freshwater (SCHNEIDER & LE CAMPION-ALSUMARD, 1999), terrestrial (ERCEGOVIĆ, 1925; GOLUBIC & SCHNEIDER, 2003; GOLUBIC et al., 2015), and in extreme desert environments (WIERZCHOS et al., 2018). The ecologically important activities described here and by those authors differ from those in applied research that centre on the biocorrosion of metals (BEECH & GAYLARDE, 1999; HAMILTON, 2003).

Microbial biocorrosion and bioerosion are gradual but persistent activities affecting and shaping Earth's mineral surfaces. Geologists view bioerosion as an important landscape-modifying force in modern and ancient environments (RADTKE et al. 1997; VOGEL et al., 2000). NEUMANN (1966) and RIOULT & DANGEARD (1967) studied how they contribute to the development of coastal notches. The relationships between microborings and their grazers changes along vertical profiles of coastal notches (RADTKE et al., 1996), as it does across coral reef ecosystems (CHAZOTTES et al., 2009; TRIBOLLET et al., 2019).

Traces attracted the attention of geologists and palaeontologists because they are better preserved generally in the fossil record than the organisms that produce them. If correlated with environmental conditions under which they formed, traces can serve as palaeoenvironmental indicators. Such information needs to be obtained from the study of modern environments (SEILACHER, 1967). Both phototrophic and organotrophic euendoliths leave traces that readily preserve and are common in the fossil record (WISSHAK et al., 2019). Euendoliths and their microboring traces have a long geologic history and an abundant fossil record, extending from the Lower Proterozoic to the Recent. A microboring cyanobacterium *Eohyella campbellii* ZHANG & GOLUBIC, 1987, penetrated lithified stromatolite layers in the early Proterozoic Dahongyu Formation, Hebei Province, North China about 1.7 billion years ago (ZHANG & GOLUBIC, 1987, Pl. 1). Microbial euendoliths bored into ooids in Precambrian time 570 to 700 million years ago (CAMPBELL, 1982a). Endolithic cyanobacteria seem to have been well established and diversified by the end of the Proterozoic (KNOLL et al., 1986; GREEN et al., 1988). The shapes of microorganisms and their boring traces have changed remarkably little over enormous spans of geological time (CAMPBELL, 1982a, b; KNOLL & GOLUBIC, 1992; SCHOPF & KLEIN, 1992; GOLUBIC & KNOLL, 1993). Fossils of non-endolithic multicellular red algae have been dated to 1.6 billion years ago (KRUMBEIN, 2010; BENGTSON et al. 2017), and fossils of multicellular fungi date to about one billion years ago (LORON et al., 2019a, b). The early origin of eukaryotes is discussed in many contributions published in recent years (BUTTERFIELD, 2015; JAVAUX & KNOLL, 2016; ADAM et al., 2017; SANCHEZ-BARACALDO et al., 2017), but no eukaryotic fossil microborings have yet been described from that early age.

The earliest microbial endoliths of the Phanerozoic were reported from the Lower Cambrian (ZHANG & PRATT, 2008). Fossils of the euendolithic phase of a Bangialean red alga *Palaeoconchocelis starmachii,* and its microboring traces were described from the ca. 425-million-year-old Upper Silurian of Poland (CAMPBELL et al., 1979; CAMPBELL, 1980) with the trace later named *Conchocelichnus* (RADTKE et al. 2016) when found without an associated body fossil. The Ichnoname is *Conchocelichnus seilacheri* (RADTKE et al. 2016) in honour of Seilacher. CAMPBELL et al. (1979) recognized the endolithic conchocelis stages of Bangiacean rhodophytes in the fossil record and BUDD & PERKINS (1980) reported their modern distribution to 70 m depth. Descriptions of fossil microboring traces are increasingly plentiful in the Ordovician (VOGEL & BRETT, 2009) and later. They have been described from different periods throughout the Phanerozoic (KAZMIERCZAK & GOLUBIC, 1976; VOGEL et al., 1987; SCHMIDT, 1990; RADTKE, 1991; BRETT et al., 1993; GLAUB, 1994; HOFMANN, 1996; BUNDSCHUH, 2000; GLAUB et al., 2007).

Due to their microscopic dimensions and inaccessible habitat within solid rocky substrates, microboring organisms and their traces could not be studied in any detail until modern technology to create plastic casts of them that enable study by scanning electron microscopy was developed (see GOLUBIC et al., 1983, 2016, 2019; VOGEL & BRETT, 2009). Our views on how to study and interpret fossil microbial euendoliths have developed over time. A key viewpoint that distinguishes our work from others is that traces of microbial endoliths lend themselves to population level studies. This allows multiple morphological features to be discerned as well as how they vary within an ichnotaxon within such populations. After four decades of observing vast numbers of bored substrates and studying many living taxa in great detail, we are confident our work has encompassed the great majority of both modern and

Pleistocene examples of these deep sea ichnotaxa as well as many much older microbial euendolithic traces. This provides us with a perspective that is both broader and more specialized than at the outset of our work and also far more comprehensive than older contributions by colleagues who have contributed taxonomic descriptions of a single taxon from one or only a few localities. Similarly, our earlier and current work has clarified many ichnotaxa previously described.

1.2. Phototrophic vs. organotrophic microborers

Oxygenic photosynthesis that evolved in cyanobacteria, followed by endosymbiosis and then further differentiation into plastids, provided energy generation to various groups of algae and plants (FALKOWSKI et al., 2004), including microbial euendoliths. Boring of carbonate substrates by microbes is known among light-dependent cyanobacteria (ERCEGOVIĆ, 1925, 1932; COURADEAU et al.,2017; PALINSKA et al., 2017), the eukaryotic red (BATTERS, 1892; TSENG & CHANG, 1955; MIURA, 1961; CAMPBELL & COLE, 1984) and green algae (LUKAS, 1974, 1978; MASSÉ et al., 2020). Light-independent microorganisms such as fungi (KOHLMEYER, 1969; HÖHNK, 1969; GOLUBIC et al., 2005; GOLUBIC et al.,2007), protists (WISSHAK & RÜGGEBERG, 2006), and suspected (i.e., inferred, not yet proved) organotrophic prokaryotes, also developed the euendolithic habit. The word "micro-organism" means small living thing and includes animals, like micro sponges. Accordingly, we have included all micro-sized euendolithic traces we found in the deep sea in this work. Bacterial involvement in the decomposition of molluscan periostracum coatings in the abyssal depths has been documented (HOOK & GOLUBIC, 1988, 1990, 1992), eventually also progressing to destruction of shell carbonate (HOOK & GOLUBIC, 1993). Thus, the microorganisms that form the base of the bioerosion process fall into two major metabolic categories regarding sources of energy (and carbon): phototrophs (autotrophs) and organotrophs (heterotrophs).

Phototrophs, such as photobacteria, cyanobacteria and eukaryotic algae, are light-dependent and thus restricted to the illuminated photic zone in the upper parts of the ocean. They were first studied in coastal environments (NADSON, 1900, 1927; ERCEGOVIĆ, 1932). Later, it was suggested that phototrophic microbial endoliths (boring algae) could serve as palaeo-bathymetric indicators to enable the estimation of depositional depths in ancient seas (BOEKSCHOTEN, 1966), with proposed depth ranges based on experiences from modern environments (SWINCHATT, 1969). This hypothesis was important, because clues based on storm-related sedimentary deposition extend only to depths of a few tens of meters. Below that putative water depth, most sediment is a fine-grained cover that leaves no distinction in the fossil record (BRETT et al., 1997). This suggestion stimulated further research (e.g., LE CAMPION-ALSUMARD et al., 1982; WISSHAK et al., 2005), which proved a substantial underestimate of the proposed depositional depth ranges, because their originators did not consider the adaptations of benthic phototrophs to extremely low levels of submarine light. Phototrophs were observed across the tidal ranges (LE CAMPION-ALSUMARD, 1969; GOLUBIC, 1990) and shallow subtidal, typically down to 200 m water depth, though occasionally deeper (VOGEL et al., 2000; GLAUB et al., 2007), down to 300 m for the specialized chlorophyte *Ostreobium queketii* and to 380 m for the cyanobacterium *Leptolyngbya (Plectonema) terebrans* (LE CAMPION-ALSUMARD et al., 1982). Depositional depth in ancient seas is estimated from the depth distribution of foraminifera (e.g., MURRAY, 1973, 1991; BOU-DAGHER-FADEL & PRICE, 2010). Foraminiferal tests in deep sea sediments are widely used substrates to study deep sea euendoliths – including in this paper. Two of our authors, S.E. Campbell and J.E. Hook were the first to identify the absence of borings into foraminifera and pteropod shells while in the water column and that it only occurs following deposition at the benthos (GOLUBIC et al., 1984a). See also Materials and Methods and Acknowledgements section of this paper for details.

Reef corals originate mainly through interactions between phototrophs and organotrophs – both in the polyps and in the coral skeleton. Each coral species has a species-specific endolith composition, bioerosion rates and vertical zonation; the coral skeleton is inhabited by microbial endoliths during life, but the species composition of endoliths may change after the coral's death (CHAZOTTES et al., 2009). The presence of endolithic algae may help corals survive bleaching events (FINE & LOYA, 2002; PERNICE et al., 2020). However, there is some evidence of added damage by phototrophic microborings during bleaching periods (HASSENRÜCK et al., 2013).

Organotrophic eukaryotes, such as most bacteria, protists, fungi and animals, are independent of light and attack any form of organic material in the substrate, and as this work shows, sometimes as apparent parasites of other types of euendoliths. Accordingly, they may occur at any depth, depending on the availability of organic nutrients, but their actual vertical depth distribution remains uncharted. The vertical distribution of microboring traces was studied in polar regions, where the euphotic zone is generally shallower (WISSHAK et al., 2005, WISSHAK, 2006, 2012, 2019; MEYER et al., 2020). These studies determined that organotrophs dominated in deeper ranges starting with the settling of microborers. A kind of "succession" was noted in which microboring organotrophs were followed by dendrinids formed by endolithic foraminifera and related protistan borers. The present study, as in a few earlier ones (e.g., ZEFF & PERKINS, 1979), concentrates on the aphotic deep sea to completely exclude the presence of light-dependent microboring organisms from consideration.

1.3. Marine microbial bioerosion is a benthic phenomenon

We examined numerous shells and other skeletal carbonates of planktonic organisms, and never observed any microborings or etchings in shells of active plankton, something our research also confirmed previously (GOLUBIC et al., 1984a), as well as in the present study (see Materials and Methods below). The light-independent microboring organisms in the aphotic deep sea represent an overprint on deposited skeletal remains before they are buried by sediments and enter the fossil record

(CAMPBELL et al., 1983; GOLUBIC et al., 1984a). Organotrophic microbial euendoliths exploit the organic compounds incorporated within the skeletons of molluscs (MAO-CHE et al., 1996) and corals (PRIESS et al., 2000). They exploit the organic matter incorporated by the host organisms (POULICEK & JASPAR VERSALI, 1984) into their skeletons (PRICE et al., 1976). These compounds include proteins (SAMATA et al., 1999; KOBAYASHI & SAMATA, 2006) that participated in the organization of carbonate crystallites of the host's shell (ALBECK et al., 1993; SARASHINA & ENDO, 2001; MARIN et al., 2005). Concentrations of organic compounds in the bored substrate (e.g., organic lamellae) may influence the orientation of organotrophic euendoliths (MAO-CHE et al., 1996; GOLUBIC et al., 2014). Endolithic organotrophs were also shown to attack coral polyps, which respond by producing special cone-shaped skeletal protrusions in defense (LE CAMPION-ALSUMARD et al., 1995b; BENTIS et al., 2000). So, the substrate can influence the microborers just as they influence the substrate.

In addition to euendoliths, we describe patterns of extremely fine traces that are integrated into the substrate surface, which may be caused by endolithic components of epilithic foraminiferal, thraustochytrid or actinomycete food-collecting systems. Boring sponges, some of them microscopic in size (WISSHAK, 2008), consume microorganisms that are in suspension. Thus, the organotrophic euendoliths, studied in different settings and depths (WISSHAK, 2008; GOLUBIC et al., 2014), may be indirectly supported by a broad range of primary production in the oceans. This includes phototrophy of the phytoplankton (UCHMAN, 2007) raining down from the much shallower water column, as well as chemolithotrophy in the abyssal seeps and vents (PAULL et al., 1984; REYSENBACH & CADY, 2001; GLEASON et al., 2017, 2019). Chemolithotrophy was recently reported in fungi (GLEASON et al., 2019).

1.4. Ichnology, the study of fossil traces

In the present study we describe traces, found in deep sea dredged, grab, and core samples, in accordance with ichnological rules and regulations. Our approach includes the understanding that traces are products of organismal behaviour, i.e., the results of growth and reproduction of microbial euendoliths. We employ the convention that their naming should reflect the shapes of the respective fossil traces (BERTLING et al., 2006; BERTLING, 2007; BERTLING et al., 2022; WISSHAK et al., 2019). We also pay attention to the influence of the substrate that is bored with respect to the endolith cast shape and texture, as this sometimes provides additional clues to the behaviour of the maker.

Descriptions of ichnotaxa were carried out on the assumption that traces of microboring organisms adhere to the morphology of their makers as has always been the case in modern endoliths, when makers are present, as well as in fossil populations preserved both as trace and body fossils (CAMPBELL, 1980). In our description of organism behaviour, we document how the interplay of the boring activity and substrate consistency may have influenced the morphology of the resulting traces. Although most of the taxonomic descriptions are probably complete, in two ichnogenera, *Saccomorpha* and *Orthogonum*, additional investigation may be needed.

There is a tradition in the study of trace fossils based on traces left in soft deposits, to identify them mostly as expressing animal behaviour (VALLON et al., 2016), frequently concentrating on movement (PLOTNICK, 2012), although both movement and growth in response to environmental stimuli are also known for plants and microorganisms. In the present contribution we found that the traces we describe originate from the behaviour of a specialized group of microboring organisms (BERTLING et al., 2006; MILLER III, 2007a), while accepting the general definition of behaviour from the Merriam-Webster Dictionary as "the way that a person, an animal, a substance" (or a microorganism) "behaves in a particular situation or under particular conditions" (endolithic). We confirm the view of BROMLEY & NIELSEN (2015) who noted that bioerosion structures constitute 'ready-made fossils,' suggesting that the onset of fossilization be equated with the death of the bio-eroding trace-maker. In our ichnotaxonomy of deep sea microbial endolithic traces, we subscribed to the understanding that fossilization of microboring traces starts when the boring stops. The rules of ichnology require a strict separation of trace nomenclature and classification from the biological identity of trace-makers. Yet, the distinction in behaviour of phototrophic vs, organotrophic microborers required identification of their physiological, i.e., biological properties. However, the distinction between phototrophic and organotrophic microboring organisms based on the morphology of their traces can be difficult because of trace similarities caused by convergent evolution (GOLUBIC et al., 2016). The behaviour of an organism may change depending on the condition, age, development and reproductive mode, resulting in different traces that may be preserved and persist in the fossil record.

Studies of microbial traces have intensified in recent years (SEILACHER, 1967, 2007; CRIMES & HARPER, 1970; FREY, 1975; BROMLEY, 1990; MILLER III, 2007b; WISSHAK & TAPANILA, 2008; SCHÖNBERG et al., 2019), but by design they have not included the biological identity of trace-makers. Given its importance for palaeoenvironmental interpretation (see SEILACHER, 1967, 2007), avoiding bio interpretation is short-sighted in our view. We emphasize the importance of careful attention to sample collection to rule out post-depositional sediment slumping or other transport in modern as well as fossil studies. We discuss the need for additional research, including comparative research on extant prokaryotic and eukaryotic light-independent microboring organisms, that includes working out ichnotaxonomic descriptions of these fossil microborers in relation to their traces, as well as their vertical distribution along limestone coasts. Such comparative research should be conducted to relate microbial assemblages and processes in skeletal fragments to those in the surrounding deep sea (MAY and PERKINS, 1979; SCHAUER et al., 2010) as well as in fossil settings that are presumed to be deep sea sediments. In our view, descriptions of microbial ichnotaxa should result from analyses of fossil assemblages, and never be based on single

fossils. As new trace assemblages are discovered, some ichnotaxonomic revisions may be called for – as in this paper. Understanding of how modern organisms create the tunnels that can be resin-cast and studied in comparison with casts of ancient microbial euendoliths, and using this knowledge in perspective, will inevitably result in better decisions about lumping and splitting taxa. Lumping and splitting is always an issue when characterizing ichnotaxa and describing them. When consideration is given to what we can learn from the study of modern microbial endoliths, better ichnotaxonomic results can be obtained than if shapes alone are described. Similarly, studying populations of modern and fossil euendolith casts will yield better information about variation within an ichnotaxon and among ichnotaxa. In this sense, biotaxonomic thinking is key to excellence in ichnotaxonomy of the microbial euendoliths.

The present paper resulted from a decades-long multi-investigator collaboration in the US, Croatia, Germany and involved samples from the Mediterranean Sea, the Indian Ocean, the Red Sea, and the Atlantic Ocean and represents the known deep sea microbial euendolith ichnofossil traces as well as including etches. We have sought to produce a quite comprehensive standard for comparisons against which future findings in various fossil sites can be evaluated. We also conclude that the aggregate activity of microboring organisms in the deep sea adds significantly to the overall global cycling of carbon due to the ubiquitous nature of the boring of sedimented shells in the world oceans. There is no information about the geographic distribution or about the diversity of participating microorganisms throughout the abyssal depths, owing to an almost complete lack of information about the biological identity of the microbial tracemakers and etchmark makers, other than that they are light independent. This research paper involves new and revised ichnotaxonomic descriptions. It includes the few previously described by others. In this way, in addition to being a research paper, this work also constitutes a monograph of all presently known deepsea organotrophic microbial euendolithic ichnotaxa.

2. MATERIALS AND METHODS

2.1. Sample collections

All sediment samples in this study were obtained from professional oceanographers who carefully controlled the depth of sampling. All were verified as being collected far below the photic zone. Samples reported on originated from between 600 m (CAMPBELL, 1982) to 2323 m depth (HOOK, 1991).

The sand-size fraction of deep sea sediment dredged or obtained via grab or core sampling techniques was evaluated for evidence of endolithic tunnels. All sediment samples were obtained from sites free of sediment slumping, in order to rule out transport from shallower depths. Autochthony and bathymetric accuracy were assured by the researchers who collected and/or provided the samples. Samples were provided to Stjepko Golubic by Robert Hessler, from the deep sea collections of R. Hessler and Andrew Benson, at station 299, at 2076m depth on an expedition of Scripps Institute of Oceanography in the Gulf of Aden, Indian Ocean. That sample is close to the Gulf of Aden sample location of Radtke outlined below. The Scripps Gulf of Aden sample was studied with C14 at Woods Hole Oceanographic Institute by co-author James E. Hook in 2024. The Hessler and Benson samples were found to be less than 1000 years old. Fossil endoliths reported in this paper that stem from the 1991 PhD thesis of co-author Gudrun Radtke are Palaeocene or older. Samples of oceanographic collections were dominated by fragments of pteropod shells and the tests of foraminifera that represent substrates for microboring traces. They were analyzed initially by dissecting microscope for the presence and shapes of microboring traces.

Deep sea samples dredged and/or grabbed from the northern Mediterranean benthos at Montpellier from 600 to 1500 m, were provided courtesy of D. Belan-Santini, Station Marine d'Endoume, Marseille, France in 1982 to S.E. Campbell. These samples were primarily composed of foraminifera with other shell fragments of planktonic origin. Figure 1a illustrates a representative sediment sample that came from the Gulf of Aden, Red Sea provided to G. Radtke (details below).

Depth-controlled plankton samples presorted to supply a pure pteropod fraction, clearly Holocene in age, were also provided to Campbell 1982 in Montpelier, France by J. Rampal. The purpose was to determine whether any planktonic pteropods were attacked by microbial endoliths during passage through the water column, but there was no evidence of such activity.

Deep sea dredged, grab, and core sediment samples from the central Atlantic grounds of the Bermuda Pedestal, at 1645 m depth were obtained by J.E. Hook via the courtesy of T. Sleeter, at the Bermuda Biological Station (Fig. 1a), as were the sediment samples from the South Atlantic Ocean (36º 53' S', 53º 10' W) at 2195 to 2323 m depth to J. Hook. The materials included foraminifera and other shells of planktonic origin. The following collections of the Senckenberg Expedition *Meteor* 1987 in the Red Sea Me5-158 Port Sudan, 1558 m depth, Me5-176 NE Masamirit 1970 m and Me5-281 Gulf of Aden 1065 m deep were obtained by courtesy of Ronald Janssen, Senckenberg Research Institute, Frankfurt am Main to G. Radtke. 2012. Dredged sediment samples from the Red Sea had outstanding shell preservation involving foraminifera, pteropods and other planktonic shells and shell fragments and provided a high ichnotaxonomic diversity (based on the review of 1100 photographs). Preparation and SEM documentation (Senckenberg Research Institute) followed in Frankfurt am Main. and Wiesbaden by G. Radtke. All specimens from RADTKE (1991) and younger are deposited in the Senckenberg Collection. Discussions, as a part of collaboration with Max Wisshak, Senckenberg am Meer, Wilhelmshaven, Germany, included comparison with samples he collected (WISSHAK et al., 2014b, 2018; GOLUBIC et al., 2014).

2.2. Sample preparation

Shell fragments of fossil pteropods (Fig. 1a) were selected using a dissecting scope from among other carbonate particles as a standard substrate for comparisons whenever possible. Pteropod shells have the following properties suitable for this study: they are optically clear and of uniform thickness,

allowing for initial survey by light microscopy at various magnifications (Figs. 1b; 2).

The uniform internal structure of pteropod shells caused minimum substrate-related morphological alterations of the cast microboring traces, making them suitable for the purpose of comparison.

It is usually impossible with direct visual observation to accurately characterize the nature of microboring traces within shells because of the shells' natural opacity. Also, we have found it necessary to study populations of each taxon to be able to work out which features typify it. This is never possible using direct light microscopy due to optical interference by the subtrate and overlapping traces. Our solution to this problem has been to first embed the shell in resin (through a decreasing acetone dilution series) and then carve the resulting resin block to expose a circumference of the shell. At this point the sample is placed in dilute HCl or similar acid to dissolve the actual carbonate shell. This process can yield a replication of the tunnels to an accuracy of <0.1 micrometres. The two halves are metal-coated and observed and documented photographically under SEM.

The detail of the method of embedding is as follows: selected shells were dehydrated, infiltrated, and cast by multicomponent araldite resin or Spurr Low Viscosity Medium, following procedures of the combined embedding-casting method (GOLUBIC et al., 1970, 1983; WISSHAK, 2006, fig. 5). The resin-casts were exposed by partially or completely dissolving the carbonate substrate by dilute HCl and observed as inverted (replicated) images of microborings. Dissolution of the carbonate substrate is a necessary step in the technique to obtain resin casts of microborings for study by SEM. This always results in destruction of the original material, so it is not possible to preserve type material of the actual microboring traces studied. For further discussion see Section 2.4. As a control, scanning electron microscopy (SEM) was used to observe the bored substrates directly (Figs. 1c, d, and e) and we compared these with resin casts (Figs. 1f, g). This approach permitted study of the trace orientation and the three-dimensional display of the borings within shells (FÄRBER et al. 2015). The close relationship between microbial borings and the bored substrate (GOLUBIC, 1969; GOLUBIC et al., 1975) was studied on deep sea traces using light microscopy and SEM. The methodology employed in the study of microbial endoliths and bioerosion using complementary approaches has been summarized and illustrated in a separate publication (GOLUBIC et al., 2019).

2.3. Measurements

Measurements of the dimensions of euendolithic traces that characterize their shape were carried out at the level of trace populations within mineralized substrates, using light microscopy and the SEM of casts of microborings. Dimensions were measured using Motic-2 (Motic group, China), Sigma-Scan and Sigma-Plot software (Jandel Scientific, CA) and are displayed at appropriate resolution with the support of Photoshop Elements 18 (Table 1). Measurements of properties that appeared to be stable and uniform in appearance, while characterizing the shape of the trace, were carried out in natural populations of traces. The results were used for reconstruction of the 3-dimensional morphology of traces as proportions. Traces with constant morphological properties, such as diameters of tubular traces, were expressed as Mean ± SD (n = number sampled). Structures subject to change, such as reproductive structures in the process of growth, were measured and recorded as ranges, emphasizing the maximum achieved rather than an average. This is a key distinction in the morphometry of microbial endoliths and casts of their borings – especially in the case of globe-shaped forms. Ramifications were measured for branching frequency, with their orientation recorded. The branch diameters were recorded for separate branching orders (Table 1).

2.4. Ichnotaxonomy

Here, the observed trace morphotypes were identified according to formally described ichnotaxa. When these were lacking, the morphotypes were described as new ichnogenera and ichnospecies including their possible varieties. The existing ichnological nomenclature has been based on fossil traces (BAUCON et al., 2012). New descriptions and modification of ichnotaxa can be safely made on the basis of information obtained from borings found in deep sea sediments where the microboring organisms were no longer active (BROMLEY & NIELSEN, 2015).

When a new ichnotaxon is to be established, the type material should be fossilized, according to Article 1.3.6. of the International Code of Zoological Nomenclature (ICZN, 1999, p. 3). As mentioned above, we accept the opinion of BROMLEY & NIELSEN (2015) of what constitutes a fossil: "Because bioerosion structures constitute 'ready-made fossils', it is suggested that the onset of fossilization be equated with the death of the bioeroding tracemaker." Accordingly, all our material should be considered fossil. We disagree with the proposal of BERTLING et al. (2022) to "define 'fossil' as 'not demonstrably postdating the beginning of the Holocene". The arbitrary age of 11,700 years BP (WALKER et al., 2009) for the base of Holocene is defined as the "first signs of climatic warming at the end of the cold phase" and does not have anything to do with being fossil or not. Accordingly, we suggest that the proposal of BERTLING et al. (2022), that is not yet included in the Code and cannot be used as a taxonomic rule at this time, be rejected in the future by the ICZN.

Because "many trace fossils are diagnosed inadequately, either by incorporation of too many different forms, or by using such specific criteria that the ichnotaxon remains monotypic" (BERTLING et al., 2006, p. 265), some ichnogenera needed to be widened in this study to accommodate more ichnospecies (e.g., *Saccomorpha guttulata* WISSHAK et al., 2018). Some ichnospecies, when first described, included morphologically distinct developmental stages (CAMPBELL, 1980; RADTKE et al., 2010) and behavioural expressions, including at different developmental stages, which needed to be formally distinguished and separately named (PLOTNICK, 2012). According to rules, the names of ichnotaxa rely on morphology and substrate as ichnotaxobases, rather than on biological relationships among the trace-makers (BERTLING et al., 2006, 2019; BERTLING, 2007). However, in contrast to most other ichno-

taxa, for microbial endoliths there is a very close relationship between the biological identity of a trace maker and its growth habit, which results in a trace that replicates the surface outline of the trace-maker (CAMPBELL & HOFFMAN, 1979) in the vast majority of cases (see CAMPBELL & COLE, 1984). We applied our knowledge about how to characterize the living microbial euendolithic taxa we have encountered in the course of extensive research of the photic zone and used this thinking in our approach to characterize the fossil deep sea ichnotaxa. We hope this type of work will eventually support identifying extant deep sea euendolithic tracemakers as well as any ancient body fossils that may be found within their traces. Behaviour may change during growth, development, and the functional differentiation of individual trace makers, resulting in production of a variety of trace shapes, especially in those characterized as compound complex traces (MILLER III, 2007a). In addition to morphological differentiation of the trace-making organism (oncogeny), how the trace was formed (ichnogeny) needs to be identified and discussed. With populations of microbial euendolith traces concentrated within very small fragments of shell or rock, such distinctions are possible within and among the ichnotaxa, with a high degree of confidence. Despite the specific requirements of the ichnotaxonomic approach that differs from the biological one, in future it is likely that many biological trace-makers of these ichnotaxonomically characterized borings will be discussed, especially if this morphometric approach is applied at the population level, as a standard part of ichnotaxonomic work going forward which we regard as essential, although the taxonomic code does not require it.

Taxonomy requires that every extant or fossil species has its holotype (ICZN 1999, p. 79). In the case of microboring traces, the technique necessary to obtain these traces involves, as a necessary step, the destruction of the calcareous sample (see section 2.2.). Therefore, the holotype can be an image. It is specifically allowed under Art. 73.1.4. of ICZN (1999, p. 80):

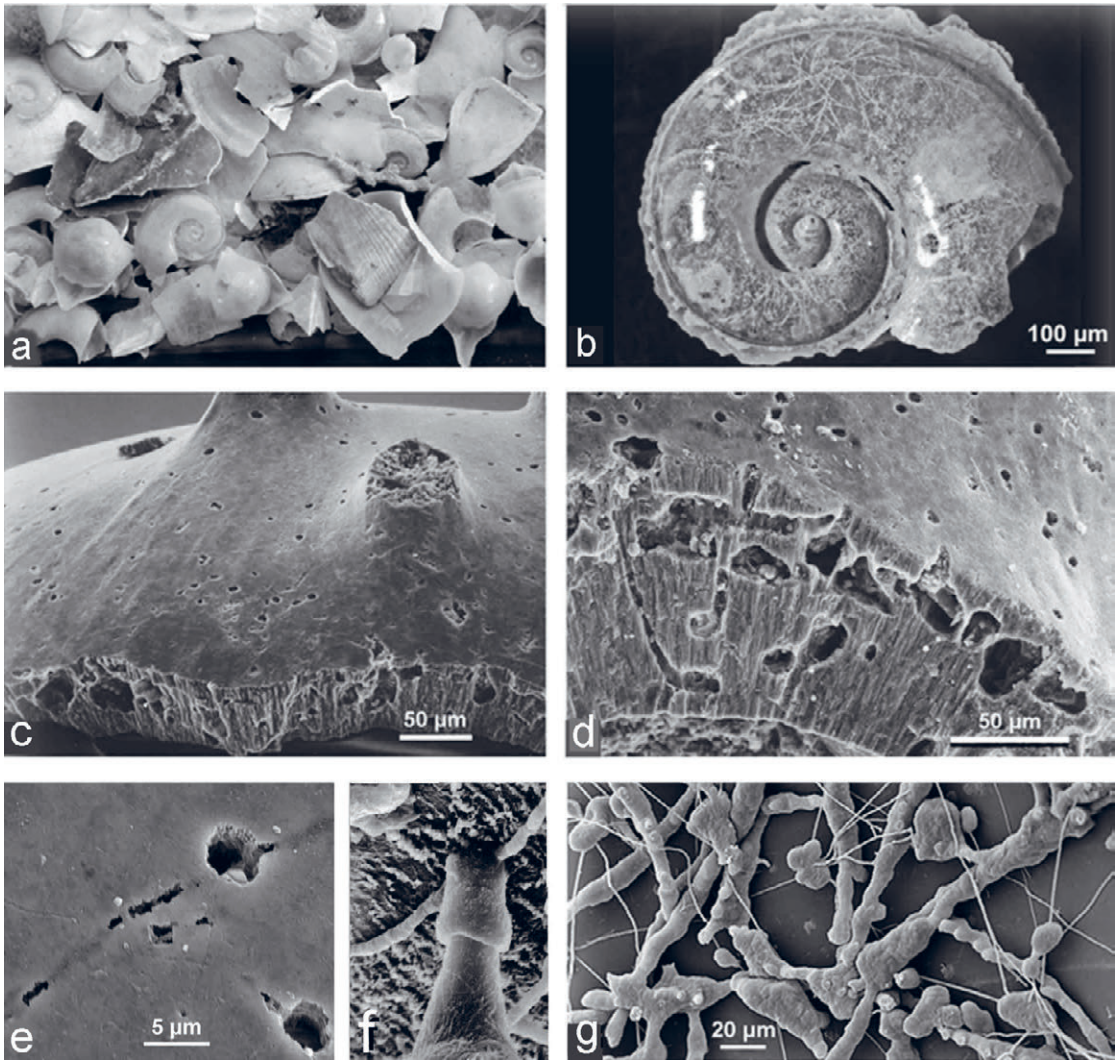

Figure 1. Shell and test fragments of pteropods and foraminifera settled on sediment and exposed to boring by deep sea microbial euendoliths (ca. 10x). **a.** Sand-size fraction of the deep sea (1,553 m) sediment Me-5-158 Port Said, Red Sea. **b.** A pteropod test selected from a., affected by a dense assemblage of microbial borings. **c.** Fractured test of the foraminifer *Oolina globosa* (MONTAGU, 1803) with numerous perforations by microborers. **d.** Detail of c, showing substantial expansion of the excavations in the interior of the test compared to small holes where endoliths entered. **e.** Detail of the external *Oolina* test surface in d, note the collapsed roof of a subsurface hyphal tunnel. **f.** Substrate surface view from the test's interior: resin-replicated neck of *Sacomorpha* isp. with collar and attached hyphal tunnels (same scale as in e). **g.** Microboring assemblage in a test of the foraminifer *Laticarinina pauperata* (PARKER & JONES, 1865), replicated in polymerizing resin. Microborings of *Saccomorpha guttulata* WISSHAK et al., 2018, interspersed with traces of *Saccomorpha* ispp.

"Designation of an illustration of a single specimen as a holotype is to be treated as designation of the specimen illustrated; the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation." Photographic images are accepted as holotypes in nomenclature, if necessary. GARRAFFONI & FREITAS (2017) discuss the use of photographs as type specimens, arguing that in the case of soft-bodied meiofaunal animals, specimens deteriorate and most of their diagnostic characteristics vanish soon after preservation, but sharp photographs and videos instead allow a timeless and correct identification. They suggest a revision of the Code to specifically allow this practice, as do we.

2.5. Study procedures evaluating microbial endolith traces

Our approach to study deep sea euendolithic traces has been standardized as follows: Visual inspection of selected translucent to transparent shell slivers provided the initial way of confirming the presence of microbial euendolithic traces (Figs. 1a, b), followed by a survey using light microscopy, using consistent image scales as far as possible (e.g. in Fig. 2, all scales are 50 µm long), to record and roughly compare the size ranges (Fig. 2a vs. 2b) and size variability (Fig. 2b vs. 2c vs. 2e), to determine the presence of ichnocoenoses (e.g. Fig. 2d), and to evaluate the morphological complexity of individual traces (Fig. 2f). Owing to the importance of size distinctions when morphological features may have limited utility for taxonomic distinctions, we added a table of morphometrics (Table 1) which serves as a type of comparative key. Direct Scanning Electron Microscopy (SEM) is used to assess bioerosional damage to a substrate (Figs. 1c, d, e). The three-dimensional display of microboring excavations is best illustrated by SEM of resin casts, following partial or complete dissolution of the carbonate matrix (Figs. 1f, g), revealing their orientation and distribution within the bored substrates - in

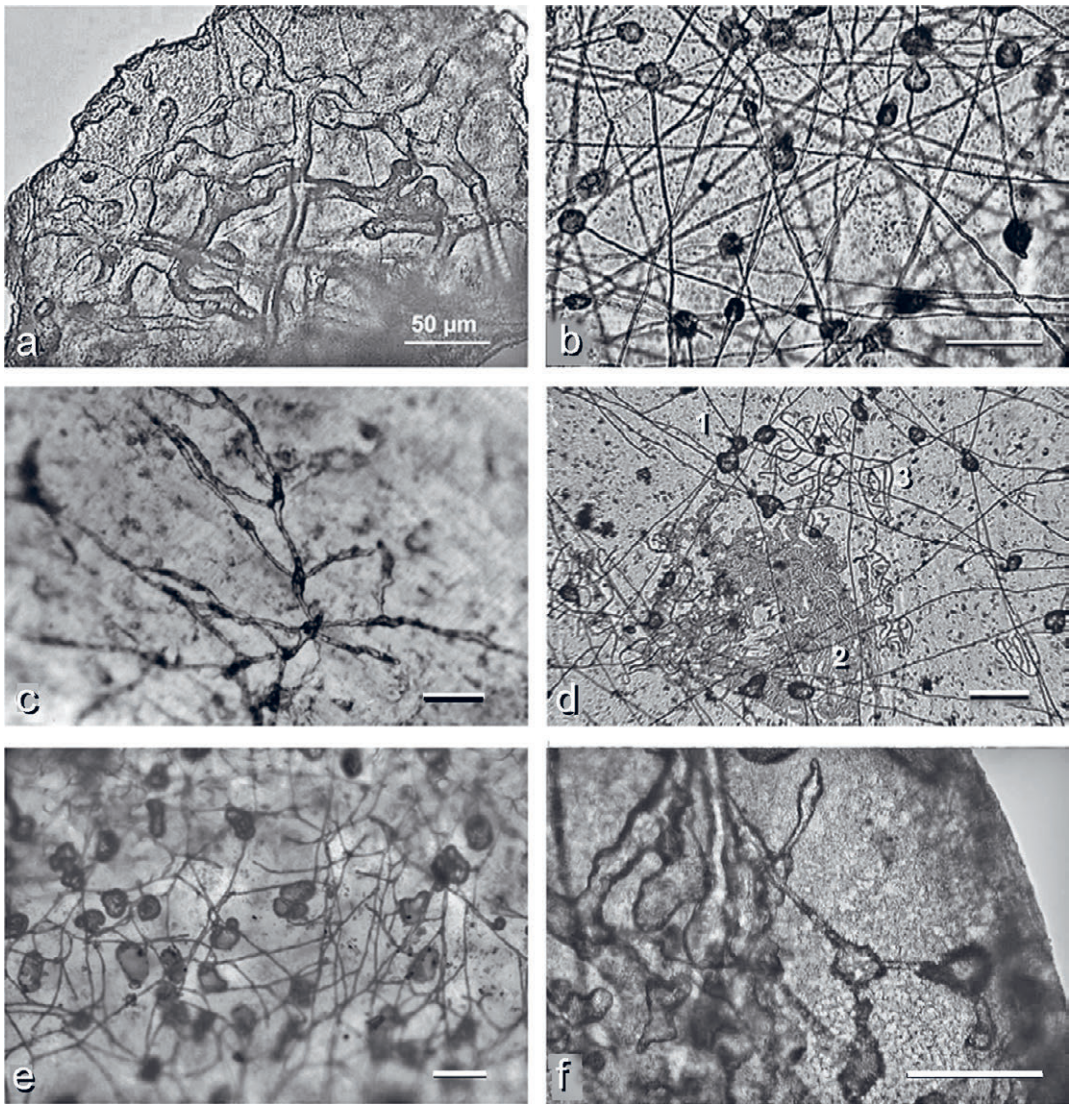

Figure 2. Outlines of various microbial borings in transparent shells from the 1550 m deep Blake Platform – transmitted light micrographs, all scale bars are 50 µm long. **a.** Shell fragment densely bored by *Orthogonum isp.* **b.** A network of crisscrossed hyphal tunnels interconnecting sporangial swellings of *Saccomorpha*. **c.** Outlines of *Saccomorpha guttulata*, with ramified sections and spindle-shaped swellings; note dark content indicating residual organism or precipitate. **d.** A network of *Saccomorpha* (1) superimposed over the shell surface corroded by *Scolecia serrata* (2) and *S. urbimetra* isp. nov. (3). **e.** Network of *Saccomorpha stereodiktyon*, with numerous sporangia adhering to the shell's interior surface. **f.** *Saccomorpha guttulata*, in a transparent keel of the foraminifera *Laticarinina pauperata* (PARKER & JONES, 1865) from 1,645 m depth at Bermuda Pedestal, Atlantic Ocean.

which details of the contacts between endoliths and substrate can be examined (e.g. Fig. 1f). This technique can be applied to modern and fossil euendolithic traces to evaluate the complexity and interrelationships among traces within the endolithic landscapes (e.g., Fig. 3). Microboring traces are evaluated by morphology and size, preferably at an angle to include the relationships between microborings and the substrate surface in perspective (e.g., Figs. 4 and 5). The presence of conspecific or unrelated microboring organisms is documented, e.g. fusions of euendolithic tubules may reflect cases of accidental entering of the preexisting microborings, a biologically specific anastomosing property, a case of intraspecific mating behaviour, or interspecific host-parasite relationship. Possible preparation artefacts are discussed in the interpretation of results.

3. RESULTS AND DISCUSSION

3.1. Photic zone endolithic landscapes

These aspects of research are reviewed and summarized in the introduction section (above). Within the ocean's illuminated photic zone, both phototrophic and organotrophic euendoliths penetrate the skeletons of live and dead molluscs, calcareous algae, and corals (LE CAMPION-ALSUMARD et al., 1995a; RADTKE & GOLUBIC, 2005, 2011), and are often nutritionally interdependent (LE CAMPION-ALSUMARD et al., 1995b), summarized by TRIBOLLET et al. (2011a, b). The light intensity reduction and spectral modification follow the gradient of increasing depth (GOLUBIC et al., 1975, fig.12.2). However, the gradient also depends on the physical properties of the ocean water, which, in turn depends on its chemical composition and water purity. The depth distribution of light-dependent organisms, on the other hand, depends on their physiological properties, i.e., light requirements. (LE CAMPION-ALSUMARD et al., 1982). The subdivision of the illuminated zone of the ocean into euphotic and disphotic ranges is, therefore, arbitrary (GLAUB et al., 2007), and so are the palaeobathymetric estimates as reported and discussed in the Introduction above.

One obvious question is whether microbial endoliths could ever have been bored while the host skeleton was descending through the water column to the benthos. To test that, one of the authors accessed samples collected by a foremost pteropod researcher of the time, Mme Janine Rampal in Montpelier, France who assured all had been collected in the open ocean at discrete depths. Thousands were evaluated in samples that had been collected from numerous depths in the open ocean and none were bored (unpublished research by Susan E. Campbell during a NATO postdoctoral fellowship, 1982).

3.2. Deep sea endolithic landscapes

Deep sea endolithic landscapes contain only light-independent, mostly organotrophic euendoliths which exploit organic compounds incorporated in the shells of molluscs and the tests of foraminifera (Fig. 1a). Many planktonic and benthic organisms produce organic-rich calcareous structures, which *post-mortem* become part of the sediment. These organic compounds are available as nutrients for organotrophic euendoliths (Fig. 1b). The amounts of organic compounds incorporated into the mollusc shells is substantial. It may be as much as 5.5% of the shell's dry weight, which amounts to over 40% of the entire organism's organic matter being invested into its shell (PRICE et al., 1976). It contains diverse proteins (MARIN & LUQUET, 2004; MARIN et al., 2005, 2007) and promotes calcification within organic lamellae such as is known in foraminifera (SPERO, 1988). Thus, deep sea endoliths depend largely on distant extraneous primary production imported from the illuminated parts of the ocean above. The exceptions are those deep sea endoliths that colonize skeletons of organisms in productive deep sea gardens around hydrothermal vents and deep seeps (e.g., PAULL et al., 1984) which may depend on bacterial chemolithotrophy as their source of primary product (GLEASON et al., 2019).

3.3. Carbonate excavation progression

Here, we examined endolithic excavation inside the test of the foraminifer *Oolina globosa* MONTAGU, 1803 var. *saetosa* EARLAND, 1934 (see GOLUBIC et al., 1984, fig. 2C), by analyzing development of the perforation process. The endolith often enters the substrate through a tiny perforation, but subsequently excavates voluminous spaces in the interior of the substrate. There, some taxa develop elaborately branched tunnel systems. A fractured shell of the foraminifer *Oolina globosa*, collected from more than 3200 m depth on the Atlantic Sea floor (32º05'N, 64º15'W), provided the opportunity to examine the extent of bioerosion damage evident from the external surface view (Fig. 1c), compared with the extent of excavation in its interior (Fig. 1d). The volume of the cavities exposed by the fracture of the test was measured and compared with the volume of a cylinder as wide as the surface entry extending into the shell as deep as 50 µm (the average depth of euendolith penetration, see TRIBOLLET et al., 2011a). Results showed that the volume of the substrate removed from the interior of the test marked by small entry openings was almost an order of magnitude larger (8.95 times larger) than the damage calculated based on the size of the euendolith's surface entry, assuming the same average depth of penetration. This insight is significant in calculating and comparing the extent and rates of microbial bioerosion (e.g., CHAZOTTES et al., 1995, 2009). This leads to the realization that the microboring contribution to carbon cycling may be an order of magnitude larger than has been previously recognized. The study of the substrate and the interrelationship between substrate surface and microboring organisms requires a view from the outside (Fig. 1e) as well as from the inside (Fig. 1f). The interior landscape is best visualized by casting microborings in polymerizing resins then observing them by scanning electron microscopy SEM (Figs. 1f, g).

It is important to view the behaviour of carbonate penetrating organisms in developmental terms, starting from the moment of the euendolith's settlement and the initial entry into the rock or shell, and then by following the direction and changes of their boring strategy in the pursuit of shelter, nutrition, or reproduction. Euendoliths' responses may vary, depending on the stage of a taxon's life cycle. They may be different in the vegetative state while seeking food than in the generative state pursuing reproduction. Increase in branching

frequency has been observed when microborers approached organic lamellae inside the shell (MAO-CHE et al.,1996). Sporangial cavities frequently expand toward the substrate surface apparently to release the spores (Figs. 4c. d). Reconstruction of the developmental sequences of euendoliths from their fossil traces was possible in cases where the microboring traces were present in sufficient abundance to assess their morphological variability in relation to the structure and composition of the bored substrate. The shape and orientation of microborings, including avoidance of contact vs. anastomosis, are all indicative of sensing and responding, and have genetic control in the background of that behaviour. Concentrations of organic compounds may have a positive effect on a euendolith's orientation, while the mineral matter may represent an obstacle to its progress. We have observed deep sea endolithic landscapes (Fig. 3d), where representatives of complex (a), tubular (b) and vermicular (c) euendolithic traces co-occur. Morphometric properties of the studied deep sea traces are summarized in Table 1.

4. SYSTEMATIC ICHNOLOGY

4.1. Complex traces in deep sea shells

Complex euendolithic traces are defined as products of organisms with biological complexity. MILLER III (2007a, p. 461) discusses the distinction between compound and composite traces. Only compound traces are legitimate and require description and naming, while the composite traces do not, because they may have been produced by more than one organism. They do require the identification of the components. Euendolithic microborings may also constitute a cumulative historical record, involving more than one microboring organism. Such cases would constitute composite, rather than compound traces, which require recognition but do not require naming (MILLER III, 2007a). Although some individual ichnotaxa illustrated here are located within larger groups of different ichnotaxa in a few photomicrographs, we carefully selected photomicrographs that unambiguously illustrate the type for each ichnotaxon described to ensure clarity. Complex traces that are also compound are produced by specialized parts of the same organism. These distinct structural elements serve different functions and may change during the organism's growth and development. The ichnogenus *Saccomorpha* (RADTKE, 1991) from the Tertiary of the Lower Rhine embayment, Upper Oligocene is a good example of a compound complex trace.

4.1.1. Historical background

The microborings of the *Saccomorpha* type were first observed by George Zebrowski within sand grains on an Australian beach. He believed that he could recognize in this trace a lower fungus belonging to the Family Cladochytriaceae and described these forms as organisms, adding the customary Latin diagnosis (ZEBROWSKI, 1936). Zebrowski first presented his results at the 1934 meeting of the Mycological Society in Pittsburg, PA, and subsequently described the new genus as *Dodgella*, with the type species *D. priscus* and two other species *D. inconstans* and *D. radicatus* (ZEBROWSKI, 1936).

Zebrowski's observations of biological structures were limited to fine, rarely branched hyphae inside shells and sponge spicules, proliferating from the spherical bases of the sporangia and radiating in fairly straight lines for distances up to several hundred micrometres, while remaining just beneath the substrate surface. He noticed that the sporangial swellings were positioned along the hyphae terminally or sub terminally, with the longitudinal axis at right angles to the hyphae, whereas the sporangial neck reached the shell surface, opening a pore to the outside. Zebrowski also extracted the spores using dilute hydrochloric acid, and found that they stuck together forming a clump, as they would if released and settled on a new carbonate substrate. Our specimen (Fig. 2b) corresponds well to Zebrowski's descriptions and to his original drawings (ZEBROWSKI, 1936, pl. 27, figs. 1–4).

4.1.2. Development of the tracemaker

When a spore of the *Dodgella* fungus settles on a carbonate substrate it germinates and forms a hypha, which subsequently penetrates into the substrate. Further development can be recognized by following the boring trace that the hypha has left in the substrate. The sporangium forms in a terminal position on the hypha (Fig. 3c, right). The hypha can subsequently continue with undifferentiated growth, leaving the sporangium in a subterminal or an intercalary position (Fig. 3c, left). Differentiation of sporangia starts as a minor hemispherical swelling of the hyphal tube, which deepens and expands to form the club-shaped cavity. The position of contacts between hyphal tunnels and sporangial swellings and the sizes of these swellings in the sequence along hyphal progression, indicate the direction of growth in the development of the tracemaking organism. Spores that germinate inside sporangial structures appear to have produced tunnels that emanate from the sporangial cavity and continue on through the shell (Fig. 3b, c). In modern taxa that produce similar structures, spores are released through the sporangial neck, transported through the water column, and settle on a new substrate, which they then penetrate following germination. Furthermore, as sands and sediment shift in present-day seas, shells especially friable ones such as pteropod shells, will often fracture and break, especially in areas that are densely bored, which is a likely additional conduit of spores to the modern environment. Similar fossil structures are likely to reflect an equivalent reproductive strategy by the tracemaker.

4.1.3. Classification – the ichnogenus *Saccomorpha*

The original diagnostic features defining the ichnogenus *Saccomorpha* RADTKE, 1991 were based on the type ichnospecies *S. clava,* holotypus Bo 7/161 Sophia Jacoba 8 II/ *Pecten*. It is Oligocene in age. The author contrasted it with two additional new ichnospecies *S. sphaerula* and *S. terminalis* (RADTKE, 1991, p. 92–98). The same author investigated trace fossils from the Palaeogene (Early Tertiary) on the basis of mollusc shells from well-studied depositional areas, in order to demonstrate the bathymetric dependence of trace fossils and other environmental parameters. RADTKE (1991) established 7 new ichnotaxa with 19 ichnospecies based on extensive sample material, (circa 200 samples, 550 resin samples, 5500

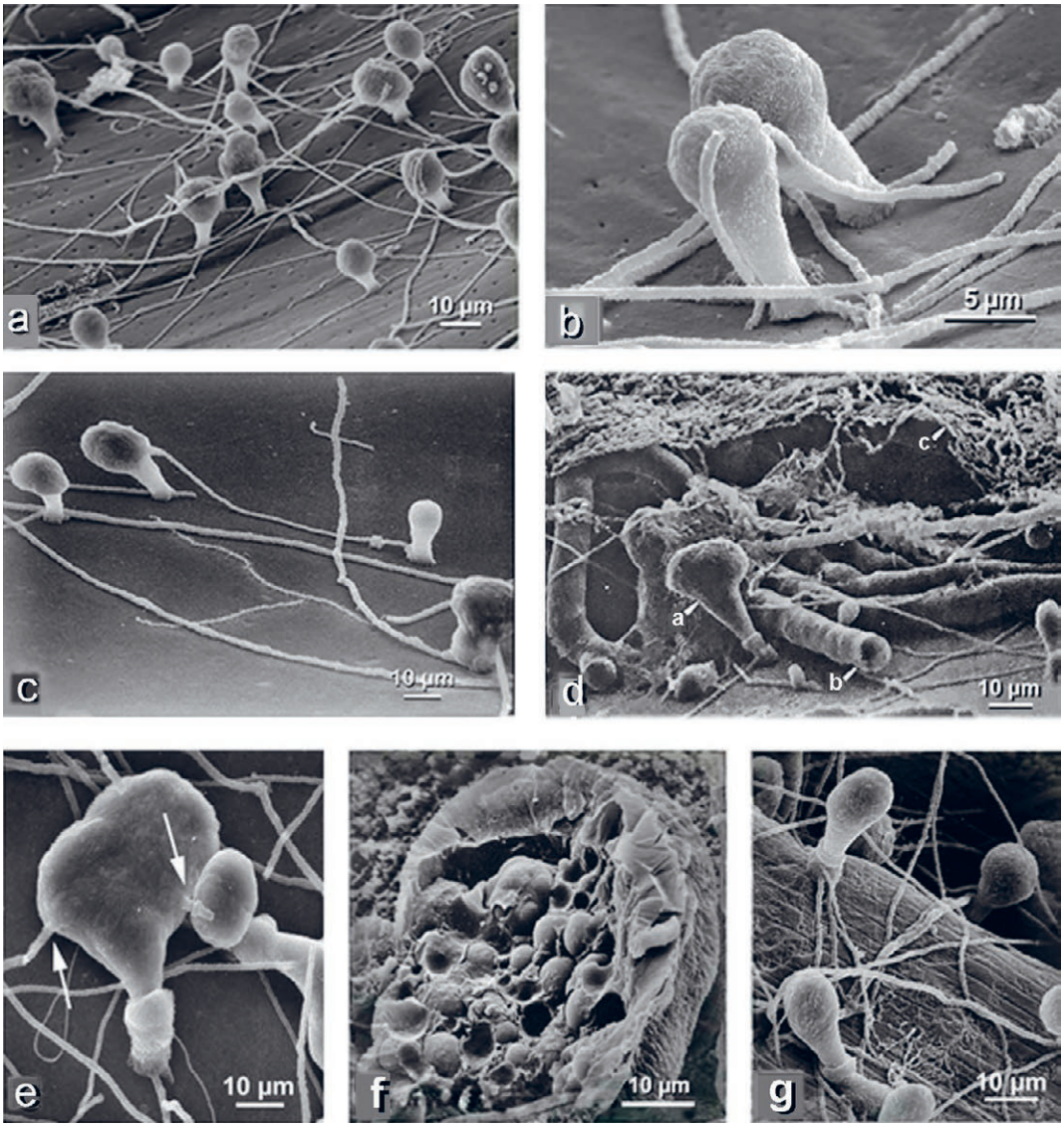

Figure 3. Microscopic landscapes with traces within a bored pteropod shell, displayed as resin-replicates. **a.** A population of traces of *Saccomorpha clava* RADTKE, 1991 with sporangial swellings attached to the interior shell surface by necks that are interconnected by hyphal tunnels. **b.** Two *S. clava* sporangia with hyphae attached to both sporangial bodies as well as the neck. **c.** Proliferation of a sporangium of *S. clava* in subterminal position (left), with a hyphal tunnel extended from its sporangial body that probably resulted from germination of an unreleased spore. Note the differentiation of another sporangial swelling in terminal position (right). **d.** Euendolithic trace assemblage in a pteropod shell with the complex trace *Saccomorpha collaris* isp. nov. (insert a), next to a large tubular *Orthogonum tubulare* RADTKE, 1991 (insert b), both under a cover of a vermicular trace *Scolecia serrata* RADTKE, 1991 (see also HOOK, 1991, fig 6-3.). **e.** *S. collaris* isp. nov. with two additional hyphal tunnels connected to the sporangial swelling (arrows). **f.** Broken sporangial swelling cast with spores exposed. **g.** A group of expanding collared sporangial swellings of *S. collaris* isp. nov and tunnels.

SEM images). Four ichnotaxa (*Orthogonum, Saccomorpha, Polyactina, Scolecia*) are relevant here.

The size of hyphal tunnels for this ichnogenus was initially narrowly conceived and was later modified to accommodate more ichnospecies, by removing the diameter constancy of the interconnecting hyphal tunnels as an ichnogeneric criterion (WISSHAK et al., 2018). Original descriptions of ichnospecies are usually based on limited observations of traces, which often include morphological variations without identifying their causes, such as changes due to growth, development, substrate specificity and behaviour, as well as the possibility of biological taxonomic distinctions. Once these have been identified as expressions of ichnospecies behaviour, the conventions of trace fossil naming require that they be named separately. Biological identity of the trace-makers is not part of the ichnotaxobasis, but it is helpful to distinguish between light-dependent and light independent trace-makers as well as their traces, when pursuing work in ichnotaxonomy.

As our store of microbial endolith collections increased, a feature noted in 1991 on a small number of *Saccomorpha clava* sporangial cavities, was a ring-shaped widening of the neck, which we perceived in resin-replicated specimens as a collar and was found to be more common than originally thought. Because we regard the collar as a clear morphological distinction which is how an ichnofossil must be described, we are splitting Trace 1, *S. clava* with no collars from Trace 2, *S. collaris* with collars commonly seen in larger sporangia. We have recognized other additional distinctive features in *Saccomorpha* such as a bent flag sporangium, a lobate

sporangium, and a few others that we describe below as distinct ichnotaxa.

Ichnotaxonomists as well as biological taxonomists tend to be "lumpers" or "splitters." Sometimes this is mindset or viewpoint, but at other times, lumpers have identified features that are no longer deemed distinctive (e.g., WISSHAK et al., 2018), or they identify previously unrecognized transitions that undermine the original taxonomic distinctiveness. Splitters may identify previously unrecognized features that proved to be distinctive when more examples were found. Here, we encountered a need to split the *Saccomorpha* ichnogenus into several ichnospecies.

Several morphologically distinct traces have been observed and described under different informal names, but were revised upon detailed comparative observations, and are reclassified within the ichnogenus *Saccomorpha: S. velum, S. radiata, S. stereodiktyon, S. papilio* and *S. guttulata*. We start by summarizing *Saccomorpha clava* (RADTKE, 1991) and then split it to yield *S. collaris* isp. nov. The first *Saccomorpha* ichnospecies to be formally described, *S. clava* (RADTKE, 1991) *is* a complex trace comprised of club-shaped to pear-shaped cavities connected by tubes. As with the chytridiomycote *Dodgella priscus* ZEBROWSKI, 1936, the club-shaped cavities likely contained sporangia, whereas the tunnels probably were made by fungal hyphae. The sporangial function of these club-shaped cavities has been demonstrated in a few broken resin casts exposing spores (Fig. 3f), and in fractured skeletal fragments (GOLUBIC et al.,1984a, fig. 2E, F). Fossilized spores have been shown to persist for hundreds of thousands of years (CAMPBELL, 1980) and should be anticipated to be more frequent than vegetative cells in the fossil record owing to their generally protective, more robust cellular structure.

Trace 1: *Saccomorpha clava* RADTKE, 1991

(Figs. 3a-c)

1991 'plain *Dodgella*' – HOOK, 1991, p. 126, fig. 5-3

1991 *Saccomorpha clava* isp. nov. – RADTKE, 1991, p. 92–95, pl. 13, figs. 1-3, 5

1991 non *Saccomorpha clava* (= *Saccomorpha velum* isp. nov.) – RADTKE, 1991, p. 93, pl. 13, Fig. 4

1991 non *Saccomorpha clava* (= *Saccomorpha collaris* isp. nov.) – RADTKE, 1991, p. 93, pl. 13, Fig. 6

Key feature: The simple variety of sporangial swellings (ca. 25 µm long, 15 µm wide and 10 µm thick) circular or elongated in cross section. The name *clava* derives from Latin *clava*, a club. The formal description as a trace with the name *Saccomorpha clava* was given by RADTKE (1991, p. 92).

RADTKE (1991) described the *Saccomorpha* ichnogenus as a complex and compound trace comprised of club-shaped to pear-shaped cavities, on purely morphological grounds. Names and terms that could indicate possible biological makers of the traces were deliberately avoided. The cavities expand from the substrate surface into the interior of the bored substrate, perpendicular (less frequently slightly inclined to the surface plane). They are interconnected by uniformly thin 1 to 3 µm wide (except in *S. guttulata*, see Table 1) with occasionally branched tunnels. The length of the interconnection tunnels and the frequency of branching vary. The club-shaped cavities vary in shape and size. They are circular or slightly elongated in cross section. The size of the *S. clava* club-shaped cavities is age-dependent, reaching up to 25 µm in height (= penetration depth), and up to 15 µm in width, expanding inward from the shell surface. In resin cast preparations, these cavities appear as pear-shaped bodies positioned on top of a narrower 6–8 µm wide stalk (neck) up to 20 µm long, erected from a planar interior surface of the shell (Figs. 3a-c).

Comment: *Saccomorpha clava* may represent early transitional states during the expansion of sporangial cavities. Such smaller specimens of simple shape lacking a collar are often associated with morphologically different *Saccomorpha* ispp, Fig. 4f shows that situation with *S. lobata*.

Saccomorpha clava is the type species of the ichnogenus *Saccomorpha*. It was described from the Tertiary of the Lower Rhine embayment, Upper Oligocene, Grafenberg Formation, holotype Bo 7/161, Sophia Jakoba 8, from a shell of *Pecten* (RADTKE, 1991, p. 92–95, pl. 13, figs. 1–6; holotype image, Pl. 13, fig. 1). As a part of the original description, this complex trace was interpreted to be formed by the chytridiomycote fungus and compared with *Dodgella priscus* ZEBROWSKI, 1936 (RADTKE 1991, p. 93). PORTER & ZEBROWSKI (1937) expressed a certain departure from biological classification in favour of a classification of the observed borings as fossils, considering that their specimens might be of any age from the Cambrian to Recent, and that the organisms which produced the described pattern may or may not exist at the present time. Well-preserved microboring traces are common in sand particles at all marine depths, although it is rare to find the trace-makers inside the boreholes except in the coastal intertidal zone and in coral reefs. We have not found hyphal makers in their boreholes in the aphotic zone sediments, but we encountered spore-like reproductive units (GOLUBIC et al., 1984a). Spores typically are tougher than vegetative cells that form hyphae and are far more prone to fossilize as previously mentioned.

The interpretation that this complex trace was assumed to be formed by the chytridiomycote *Dodgella priscus* ZEBROWSKI, 1936, suggested that the club-shaped cavities contained sporangia, while the tunnels contained fungal hyphae. The sporangial function of these cavities has been shown in broken resin casts exposing spores (Fig. 3f), and in fractured skeletal fragments (GOLUBIC et al., 1984a, figs. 2E, F).

The fine tunnels containing fungal hyphae that interconnect the sporangial swellings are attached to them at the point at which the sporangial neck meets the shell surface (Fig. 3c, left). They are less frequently attached anywhere on the body of the sporangial swelling (Figs. 3b, c). The appearance of this feature is explained by spores germinating inside the sporangium and then continuing to penetrate the substrate from there, instead of being released through the neck into the water column and settling and germinating elsewhere.

A conspicuous feature observed in a few *Saccomorpha* casts (RADTKE, 1991) is a ring-shaped widening of the sporangial neck, observed in resin-replicated specimens as a collar. This widening of the stalk into a collar is steep on the side of the swelling and gradual and conical toward the surface

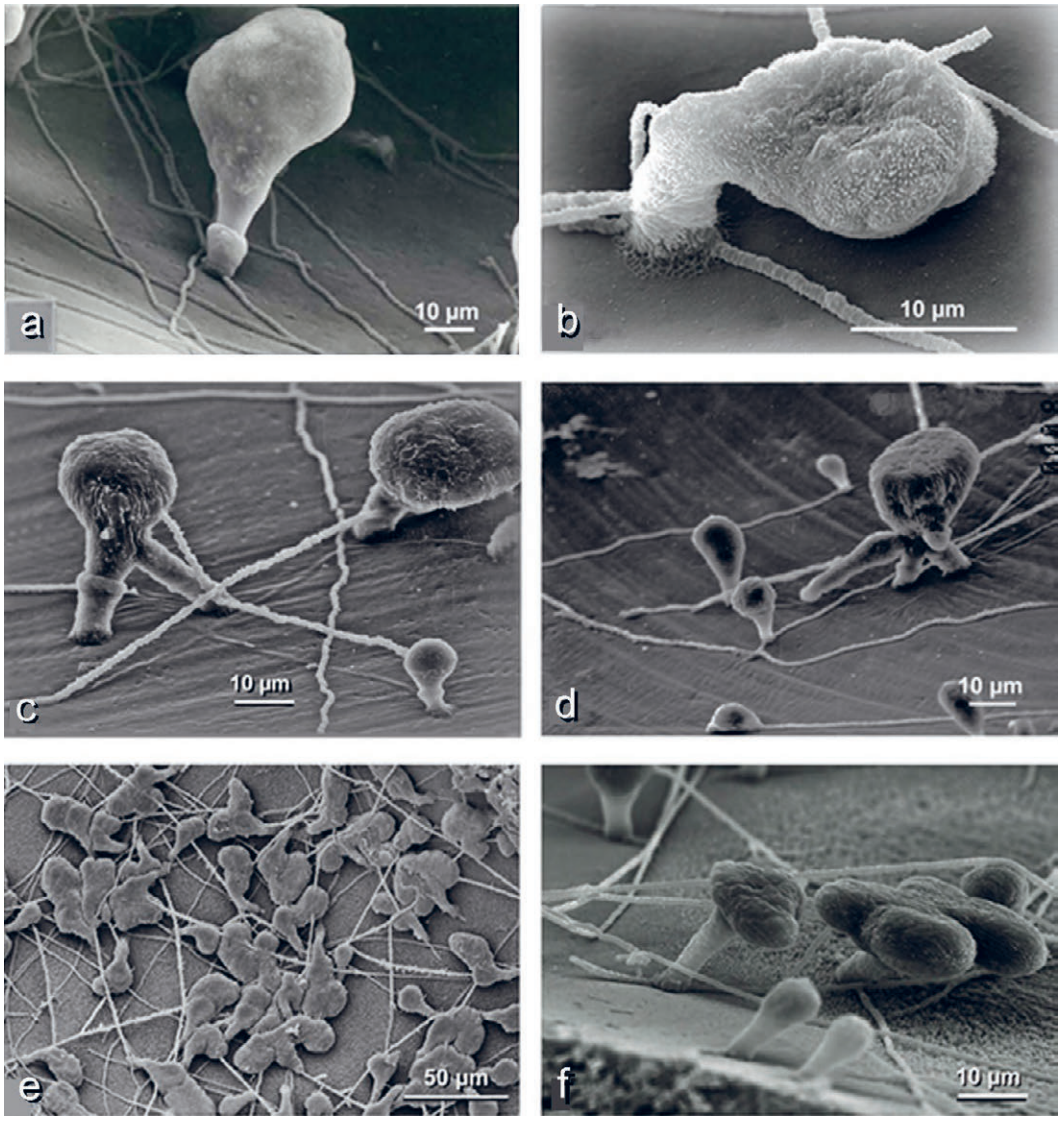

Figure 4. *Saccomorpha* ispp. traces. **a.** *Saccomorpha collaris isp. nov.*, sporangial swelling with collared neck connected to a hyphal filament at the base. Holotype. **b.** *S. curvata* isp. nov. with a bent flag – note the etched shell surface around the sporangial neck attachment (see HOOK, 1991, fig. 5-4). **c.** *Saccomorpha polypoda* isp. nov. connected by two necks with the substrate surface. **d.** *S. polypoda* with two necks and two additional protrusions; note that only the "primary necks" have collars (see HOOK, 1991, fig. 5-5B.). Holotype. **e.** *Saccomorpha lobata* isp. nov. with lateral lobes widening sporangial cavities that tend to fill the available space. Holotype. **f.** *S. lobata*, detail; note the presence of two sporangia of *S. clava* morphology, possibly representing similar appearing earlier stages in development of *S. lobata*.

(Fig. 3b, c). It was noted as 'not always present' (RADTKE, 1992). It is a morphological feature that may also have had a biological origin. We now regard the collar as the key feature of *S. collaris* (see Trace 2, below). When populations of this morphotype have numerous members with a well-developed collar and sporangia attaining larger sizes than described for *S. clava*, we recognize it as S. *collaris* isp. nov. (See Trace 2).

Trace 2: *Saccomorpha collaris* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Figs. 3d-e, g, 4a)

1991 'collar *Dodgella*' – HOOK, p. 126, fig. 5-4

1991 *Saccomorpha clava* - RADTKE, p. 93, pl. 13, Fig. 6

Holotype image Fig. 4a; paratype RADTKE 1991, Pl. 13 fig.6.

Etymology: Latin *collaris* = equipped with a collar.

Key feature (diagnosis): The largest cavities have a "neck" with a collar (Figs. 3d,e; 4a), suggesting a feature of maturity, however a few smaller cavities show collared necks suggesting an occurrence of the collar feature early in its process of development (Fig. 3g). The largest cavities of *S. collaris* are 40 x 30 x 20 µm. In *S. clava* they are smaller. Like *S. clava*, most of the sporangial cavities in the process of development lack collars (Fig. 3a,b).

Comment: The collar around the sporangial neck is a feature marked as "not always present," both in the original descriptions of *Dodgella priscus* (ZEBROWSKI, 1936), and in the description of that trace as *Saccomorpha clava* (RADTKE, 1991, p. 92). These observations raise the question of whether the collar is an expression of a taxonomically specific distinction, a feature expressed at a certain stage in the development of the sporangium, or a response to environmental conditions within the bored substrate, such as a structural obstacle in the process of penetration into carbonate? RADTKE (1991, p. 93, pl. 13, fig. 6) found isolated instances of collar in *Saccomorpha clava* and included that in the *clava* description as a paratype.

However, we now hold it to be indicative of a separate ichnospecies. Collar presence is indicative of *S. collaris.*

We observed that the sacs are initiated terminally or subterminally as small hemispherical swellings on the interior surface of hyphal tunnels (Fig. 3c, right). The connection of a sporangial swelling to the substrate surface is often accompanied by a small area of etched substrate surface (Fig. 4b).

Filaments interconnecting the sporangial cavities often encounter one another, but do not fuse and anastomose. Most commonly, one of the filaments dives deeper into the substrate, bends under, and bypasses a preexisting one (Fig. 5d). Another response by the arriving filament is to stop short of the preexisting filament and form a terminal sac. Thus, the hyphae act as primary and the sacs as secondary structures of this compound trace. The third type of response is deflection of the arriving filament and continuation of its growth parallel to the preexisting one. Euendolithic hyphae seem to react to inhabited and empty borings in a similar fashion. They persist in their endolithic mode and tend to develop groups of sporangial clusters when they encounter fissures in the rock or shell. This is likely where and how the ichnotrace creators released their spores in life.

Distribution: *Saccomorpha*-type complex and compound traces are common in carbonate fragments on the deep sea floor and are widely distributed. They have been found in all the oceans examined from the intertidal to the abyssal depths. In habitats deeper than a few hundred metres these forms are usually dominant (Fig. 3a). They have been reported in fossil substrates from the Ordovician onwards (VOGEL & BRETT, 2009).

The curved flag-shaped traces represent a distinct morphology, and are possibly a product of a separate biological entity, so according to ichnological rules they deserve to be considered a distinct trace, which we name as *Saccomorpha curvata* isp. nov.

Trace 3: *Saccomorpha curvata* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Fig. 4b)

1991 'Bent flag' – HOOK, fig. 5-4

1991 HOOK, fig. 5-12d

Holotype image: Fig. 4b.

Etymology: Latin *curvatus* = bent, curved.

Key feature (diagnosis): *S. curvata* is characterized by its curved flag-like shape, usually occurring in forms with a plain, non-collared stalk, ca. 25 μm long, up to 15 μm wide and only 6 μm thick. Bending of the sporangial flag-shaped cavity correlates with neither the thickness of the shell nor with any discontinuity observed in the shell's architecture.

Comment: The bending is considered an inherent morphological characteristic, possibly an environmentally induced one. The morphological distinction of the curved flag-shaped sporangial cavity justifies the description of a separate ichnospecies. Both collared and plain *Dodgella* shapes with different curvature have been seen in shells at 480 m depth by ZEFF & PERKINS (1979) as well as in all deep sea collections presently under study.

The new species of *Saccomorpha curvata* stems from the original observation of RADTKE (1991) that *clava* sporangial cavities includes some that are wide and flat, elongated in cross section, forming a straight, inclined, or bent "flag". The flattening and curvature of the flag are often combined, yet no correlation with the structure bored was observed. Because of the conspicuous shape of this flag, we split it out in this paper as a separate ichnofossil.

Some sporangial swellings are connected with the substrate surface by more than one neck. We recognize this feature as one worthy of a separate ichnospecies:

Trace 4: *Saccomorpha polypoda* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 4c, d)

1991 'multipedal *Dodgella*' – HOOK, p. 127, Fig. 5-5

Holotype image: Fig. 4d**.**

Etymology: Greek: *poly* = many, *podos* = leg.

Key feature (diagnosis): *S. polypoda* is a morphotype similar in height to *S. clava*, but wider. Each sporangial sac extends from a primary stalk with a collar and widens into an relatively isodiametric shape (30–40 μm in diameter), often with a flat top (Fig. 4c, d). Secondary, relatively wide tubular protrusions emerge from the main body of the swelling and connect to the substrate surface without forming a collar. This results in bipedal and tripedal structures. Additional protrusions that do not reach the surface are observed as projections from the main body (Fig. 4d, right).

Comment: It is conceivable that the secondary stalks served as additional portals for the release of spores. The flat top may reflect the thickness of the shell. Hyphae-containing tunnels (ca. 2 μm across) are connected to the swellings or to the stalks, and to the substrate surface.

A different variant, distinct from *Saccomorpha clava,* refers to lateral lobate widening of the sporangial swellings, that develops from simple juvenile shapes and expands later by laterally protruding sporangial lobes. This very characteristic shape of sporangial cavity deserves to be described as a new ichnotaxon:

Trace 5: *Saccomorpha lobata* isp. nov. HOOK, CAMPBELL, RADTKE & GOLUBIC

(Figs. 4e, f)

Holotype image: Fig. 4e.

Etymology: Latin *lobatus* = lobed.

Key feature (diagnosis): *S. lobata* represents a different form of proliferation in which the sporangial cavity widens laterally, forming two to several horizontal lobes (GOLUBIC et al. 1984a, figs. 3D, E). This type of expansion often extends to a point of crowding, forming a layer of expanding sporangial cavities, often occupying a large area. Interconnecting hyphal tunnels are not different from those in S. clava.

Comment: *S. lobata* forms appear to develop from small *simplex*-type stages with the sporangial cavities expanding laterally to occupy an area of the shell, often crowded, and mutually flattened as they develop into shapes resembling interlocking puzzle-pieces or cookies in a pan as they swell during baking (Fig. 4e) – swelling that expands later into a multi-lobed form (Fig. 4f), covering areas up to 60 μm across. *S. lobata* type traces have been observed previously in the tests of foraminif-

era exposed to boring in sediments of the Atlantic Ocean at depths of over 3000 m (GOLUBIC et al. 1984a, figs. 1E–H). The above four newly described ichnospecies have several properties in common with the *Saccomorpha clava* as originally described, although they are also morphologically different.

Trace 6: *Saccomorpha velum* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 5a-b, d–e)

1991 'IC-*Dodgella*' – HOOK, p. 127, Fig. 5-6b, d

1991 *Saccomorpha clava* – RADTKE, p. 93, pl. 13, Fig. 4

Holotype image: Fig. 5e top centre.

Etymology: Latin *velum* = sail.

Key feature (diagnosis): *S. velum* consists of euendolithic traces with flat-based, sail-shaped intercalary, and arrowhead-shaped terminal sporangial swellings, interconnected by straight hyphae-containing tunnels, 1.5 to 2.5 µm in diameter (slightly wider than those interconnecting sporangial swellings in *S. clava*), extending straight for long distances. Intercalary sporangial swellings form along these tunnels 40 to 150 µm

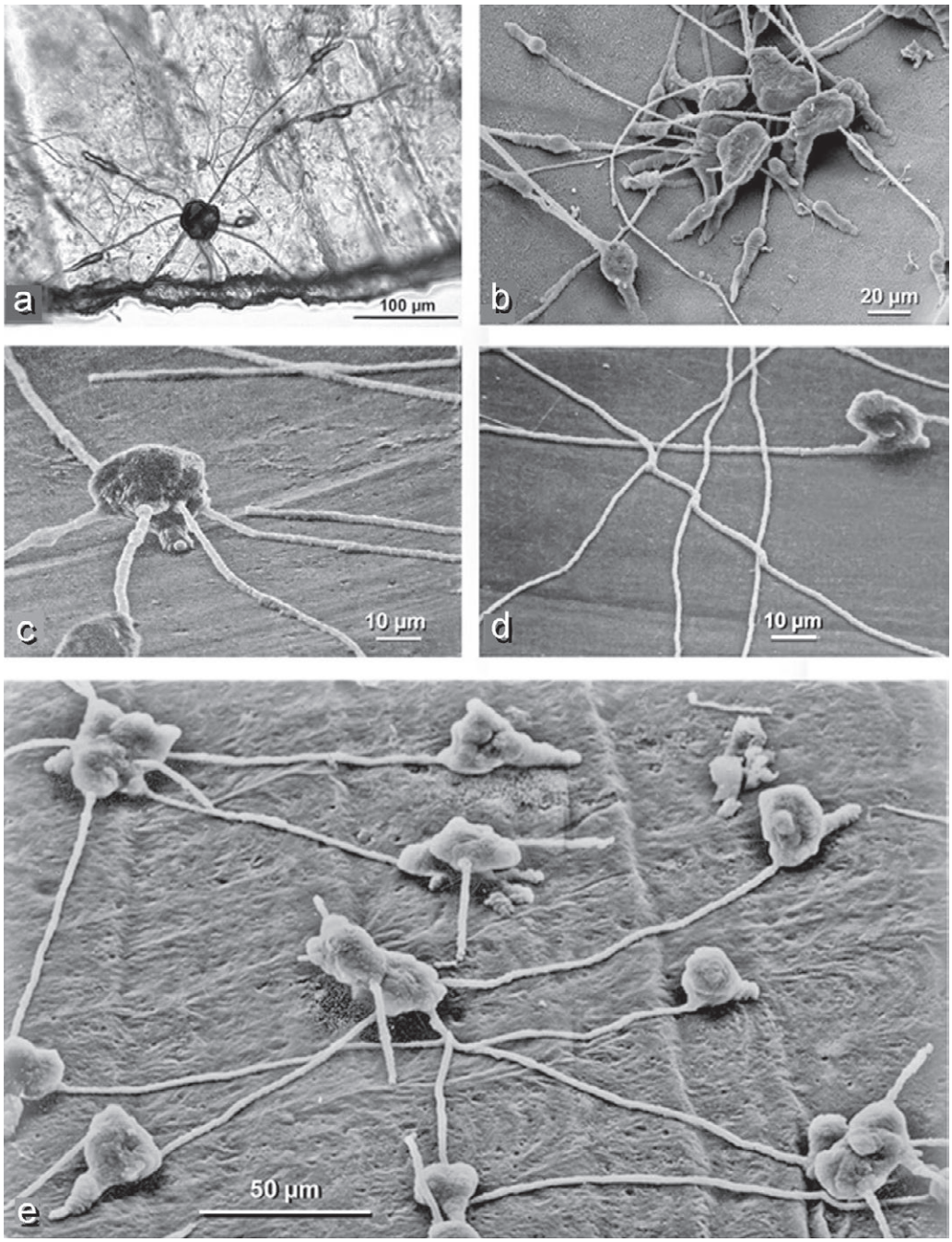

Figure 5. *Saccomorpha velum* isp. nov with arrow-shaped swellings along hyphae vs. *S. radiata* isp. nov. that lacks the hyphal swelling. **a.** Light microscopic image of *S. velum, s*howing the radiating boring pattern departing from a central group of distributive sacs and typical arrow-shaped terminal and subterminal swellings. **b.** The resin-cast replica of a similar distributive group of sporangia with radially departing hyphal tunnels and terminal arrowhead-shaped swellings. **c.** *Saccomorpha radiata* isp. nov.; a single distributive sporangial swelling with six departing hyphal tunnels (one broken). Holotype. **d.** *Saccomorpha velum* with a sail-shaped swelling in subterminal position next to several tunnels bypassing each other, without fusion. **e.** An area of the interior shell surface dominated by a *S. velum* network of straight hyphal tunnels with sail- and arrowhead-shaped sporangial swellings (see HOOK, 1991, fig. 5-6.). Holotype top centre displaying sail shape

apart. The trace network usually starts from a central distribution centre composed of one to several sporangial swellings in a group (Figs. 5a, b) connected with the substrate surface by a slightly inclined neck. Less frequently, the network originates by spores germinating inside sporangia, producing several hyphal tunnels exiting in all directions from a single central isodiametric swelling, described below as a separate morphotype *S. radiata* (Fig. 5c). The intercalary swellings are elongated, ca. 10 μm wide, up to 18 μm long and 10 to 12 μm tall (deep) adhering directly to the hyphal tunnels (without a neck) usually in the form of a flat upright sail (Fig. 5d). The terminal swellings have a distinctive arrowhead outline (Fig. 5a, b, and e, lower left).

Comment: The property of straight radiating filaments, combined with the distinctive sail-shaped and arrowhead-shaped sporangial swellings distinguishes *S. velum* from other *Saccomorpha* ispp. as recognized by light microscopy of an affected shell, (Fig. 5a) and by SEM of resin casts (Fig. 5b). The morphological properties of this trace provide some insight into the processes of development of this and similar traces. This morph, described here from the Bermuda Pedestal, has not been previously reported, but may have been present in photomicrographs published by ZEFF & PERKINS (1979, fig. 7). It has also been observed in material collected from the intertidal zone in the Gulf of California. This morphotype may be more common but is difficult to distinguish from the more ubiquitous types of *Saccomorpha* when using light microscopy or SEM images in vertical projections. It is classified within the ichnogenus *Saccomorpha* because it follows the basic pattern of resin-replicated sporangial swellings interconnected by fine filaments (tunnels).

Trace 7: *Saccomorpha radiata* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Fig. 5c)

1991 'part of the IC-*Dodgella* morph' –HOOK, figs. 5-6a, c

Holotype image: Fig. 5c.

Etymology: Latin *radiatus* = beaming or radiating.

Key feature (diagnosis): *S. radiata* produces a trace in which a single stalked swelling serves as a point of departure of hyphal tunnels exiting from the body of the sporangial swelling. Solitary occurrences have been observed in early Tertiary fossils, which remain the basis of this formal trace description (GOLUBIC et al., 2005, fig. 1d). However, we have observed the same morphotype as part of the development of the trace *S. velum,* as described above and *S. guttulata* (WISSHAK et al., 2018, figs. 2f–h; 3b, c). Thus, it is possible that this morphotype expresses similar function and strategy in different *Saccomorpha*-type traces or might even been part of the developmental sequence of *S. velum*.

Comment: The direct departure of many hyphal tunnels from the sporangial swellings, rendering them an apparent distribution centre, appears to be a strategy, beneficial to and possibly used by different complex organotrophic microorganisms. We cannot ascertain to what extent a particular occurrence is supported by the genetic background of the organism. However, our observations do confirm that the radiating pattern of the trace *S. radiata* fulfills an important function of distribution that is morphologically expressed and, thus we conclude it deserves to be described as a separate trace. ZEBROWSKI (1936, pl. 27, fig 4) described a similar chytridiomycete *Dodgella radicatus* with subterminal sporangia 17–21 x 27–43 μm in size and mentioned up to 8 "rhizoids" to a sporangium, which may refer to radiating hyphae described here.

Trace 8: *Saccomorpha papilio* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 6a–f)

1991 'ptero morph' – HOOK, figs. 5-8, 5-9

Holotype image: Fig. 6c.

Etymology: Latin *papilio* = butterfly.

Key feature (diagnosis): *S. papilio* is the name for the trace characterized by flat sporangial swellings widened into two opposite lateral lobes that resemble the shape of a butterfly with spread wings (Figs. 6a, b), diverging at angles between 45º and 180º. Alternatively, the swelling may fuse to form a semicircular disk with several shallow lobes (Figs. 6c, d, e). The flat sporangial blade is itself anchored to the interior shell surface by numerous short (ca 2.5 μm long), thin (1 to 3 μm wide) tapered tunnels. On the opposite side, at the centre of the flat (the concave side) of the sporangial swelling is a spine (4–5 μm in diameter) extending toward the opposite shell surface (usually broken in cast preparations) Figs. 6b. Several (typically 4–7) tapered, monopodially branched tubular extensions originate between the swelling and the shell surface from a single centre, radiating in all directions (Figs. 6a, c). The main filaments, resin-replicated tunnels departing from the central body arch mildly counterclockwise for the first few hundred micrometres (Fig. 6c). They are initially 1–2 μm wide, and narrower with each subsequent ramification. These tubules form an extensive flat network, covering an area of 1–2 mm in diameter (Fig. 6a, c). The branching is monopodial and alternating, producing up to at least 7 orders of progressively thinner branchlets that adhere to the substrate surface, depart at an angle of about 70º, and run in remarkably straight lines. Filaments taper and become progressively finer as they ramify. The main filaments have a diameter of 1–2 μm at the base (Fig. 6d, e), while the finest branches are less than 0.1 μm wide (Fig. 6f). The extremely fine filaments originate at all ramification orders, appearing to have been created by tunnel-makers densely exploring the area. Very fine networks were observed to affect the substrate surface forming a small yet distinct etchfield around the termini of these finest grooves (Fig. 6f, Insert).

Comment: The function of the spiny protrusion (Fig. 6b) is unknown. It may represent the original entry of the microborer but may also represent a neck for spore release. During the preparation process, it is conspicuous that, unlike resin-casts of other very fine filaments, these networks remain in place following the carbonate dissolution process and are not displaced (compared to e.g., resin-cast tunnels in *Saccomorpha* and *Scolecia*). Their stability indicates that they are integral parts of the substrate surface. They appear to be traces that are grooved into the shell and are probably epilithic in origin (Fig. 6f). *S. papilio* is a complex trace. The microorganism that produces this trace is unknown, but the pattern of this ichnotype is reminiscent of foraminifera and thraustochytrids that are

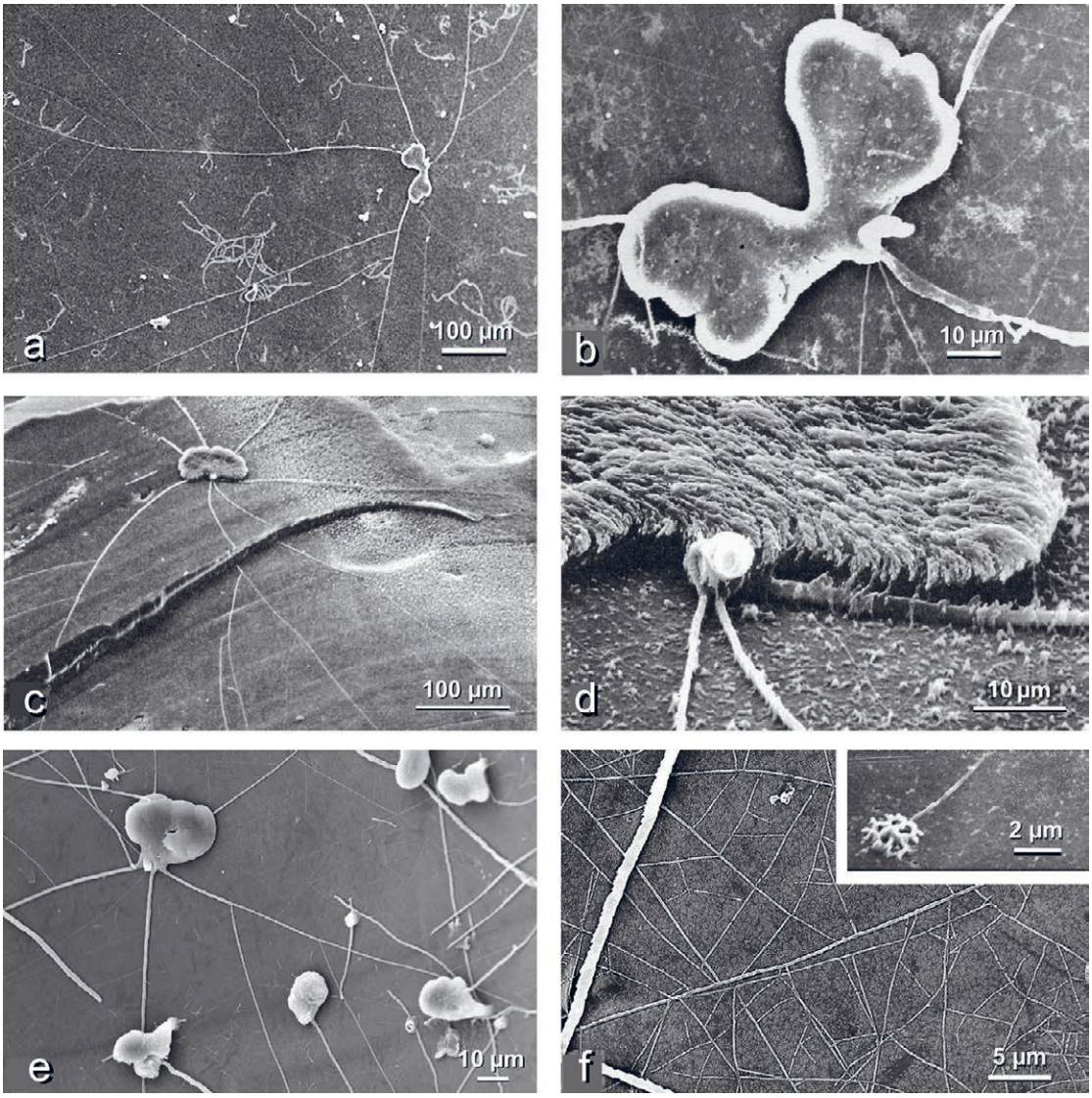

Figure 6. *Saccomorpha papilio* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC. Resin casts (HOOK, 1991) of the butterfly-shaped and fan-shaped traces in a pteropod shell from the Bermuda Pedestal (1,645 m deep). **a.** Internal surface area of a pteropod shell showing *S. papilio:* flat, butterfly-shaped sporangial cavity and expanding, branched, tunnels, narrower with each subsequent branching order (note Scolecia *urbimetra* isp. nov. background, low centre). **b.** Detail of a flat sporangial cavity of *S. papilio* with a neck and departing tunnels of different diameters. **c.** A fan-shaped sporangial cavity of *S. papilio* trace with radiating tunnels, distributed on the interior surface of a cracked pteropod shell. Holotype. **d.** Detail of c: note the texture of the swelling's surface and filaments of different diameters. **e.** *S. papilio* swelling with some tunnels accompanied by *S. clava*. **f.** Distal branching network of *S. papilio* tunnels: note the diameter difference between subsequent ramification levels. **Insert:** Terminal etching pattern of a *S. papilio* trace (see HOOK, 1991, fig. 5-8).

characterized by having a central body from which emanates an extensive, fibrous cytoplasmic network, which serves to collect particulate matter and move it to the central body for consumption. The very close shell surface integration of this trace indicates that the trace-making organism may have fed on material falling onto the mineral shell surface rather than exploiting the organic matrix incorporated in the shell, or both.

Trace 9: *Saccomorpha guttulata* WISSHAK & NEWMANN, 2018

(Figs. 1g, 2c, f and 7a–f)

1991 'the fusiform morph' – HOOK, 1p. 131, Fig. 5-7a, b

1991 *Orthogonum tubulare* – RADTKE, p. 61-64, pl. 5, fig. 5, 6

2018 *Saccomorpha guttulata* isp. nov - WISSHAK & NEUMANN, 2018, p. 525-533

Etymology: Latin *guttula* = droplet.

S. guttulata consists of a complex euendolithic trace system of a relatively irregular, multiply branched network of round tubes that gradually increase in size to distally form swellings detectable by light microscopy (Figs. 2c, f). We refer to this pattern as "sections." In fully grown networks, the swellings are seen to be regularly spaced at distances of 30–80 µm and are the most frequent sites of branching. Each cast section starts with a filament of circular cross-section, 3–7 or 4.4 $\pm$ 1.0 (n = 100) µm wide, gradually increasing to form distal swellings 20–40 or 21 $\pm$ 5.5 (n = 131) µm wide and up to 60 µm long. In fully grown networks, the swellings are seen to be regularly spaced at distances of 30–80 µm and are the most frequent sites of branching. The swellings are fusiform but asymmetric, distally emphasized, creating an impression of droplets of different lengths (Fig. 7a, b). The distal ends of sacs are commonly wider and often forked, producing two or more

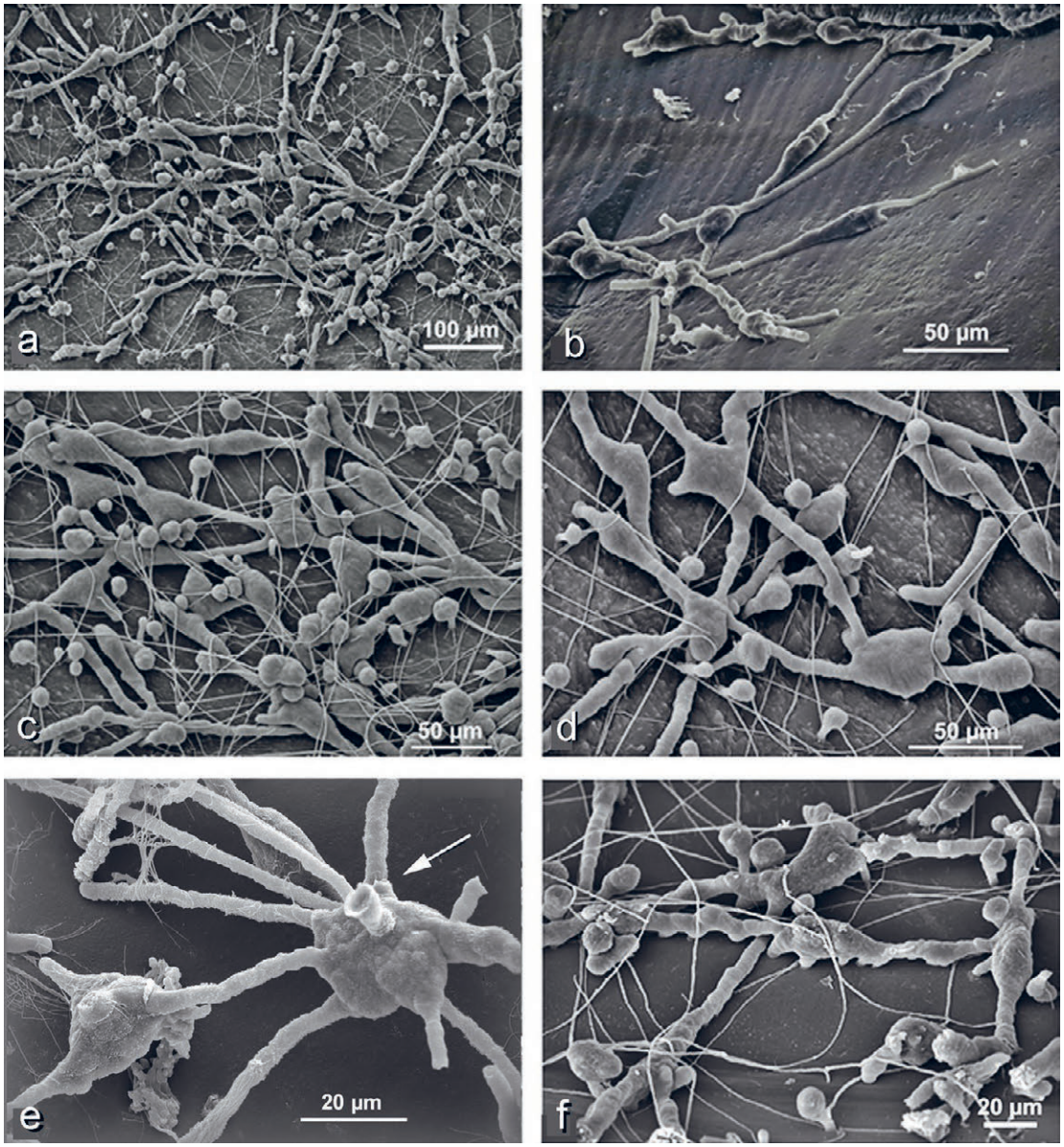

Figure 7. *Saccomorpha guttulata* WISSHAK et al., 2018, a complex segmented trace (see HOOK, 1991) with gradual transition between proximal hyphal tunnels and distal swellings. **a.** Dense segmented and branched network; expanding in the picture from right to left. **b.** Young peripherally expanding filaments of *S. guttulata;* note the transition between the proximal tubules and distal asymmetric spindle-shaped swellings. **c.** Detail from a (centre), with spaced ramifications of segments; note the presence of *Saccomorpha ispp.* **d.** Formation of secondary distribution centres of *S. guttulata.* **e.** Detached cast of a sporangial swelling acting as a secondary distribution centre, with surface attachment (arrow). **f.** A branch of *S. guttulata* showing multiple connections to the substrate surface (see HOOK, 1991, fig. 5-7b.).

branches (Fig. 7c) diverging at narrow angles. Branching directions may vary forming secondary distribution centres (Fig. 7d, e,), but the growth of the network is largely directional, maintained at a level parallel to the substrate surface (Fig. 7a, c). This system consists of distally enlarged sections that conform to the rhythm of branching by connecting the branch points. Each section starts as a tube, which expands very gradually, reaching a maximum diameter at the distal end of the section, followed by a steep decline in diameter, resulting in an asymmetric spindle (dimensions in Table 1.).

Comment: The size distribution is supported by numerous morphometric evaluations (WISSAK & NEUMANN, 2018, Table 2). There is commonly a ramification and/or a contact with the substrate surface at the wider end of each section. Less commonly, the sections follow each other in a linear fashion (Fig. 7b, top). See symmetric spindles (WISSHAK & NEUMANN, 2018, fig. 2) and in linear arrangements (Figs. 7b, right, c, top). More commonly, at the wider, distal end of the section, the diameter of the swelling is sharply reduced and associated with branching.

Trace 10: *Saccomorpha stereodiktyon* GOLUBIC et al., 2014

(Figs. 2e, 8a–c)

2014 *Saccomorpha stereodiktyon* isp. nov. - GOLUBIC et al., p. 106, Figs. 1-4

S. stereodiktyon is a three-dimensional (stereo) complex trace, with specialized parts that appear to have different functions and different responses to the microecological composi-

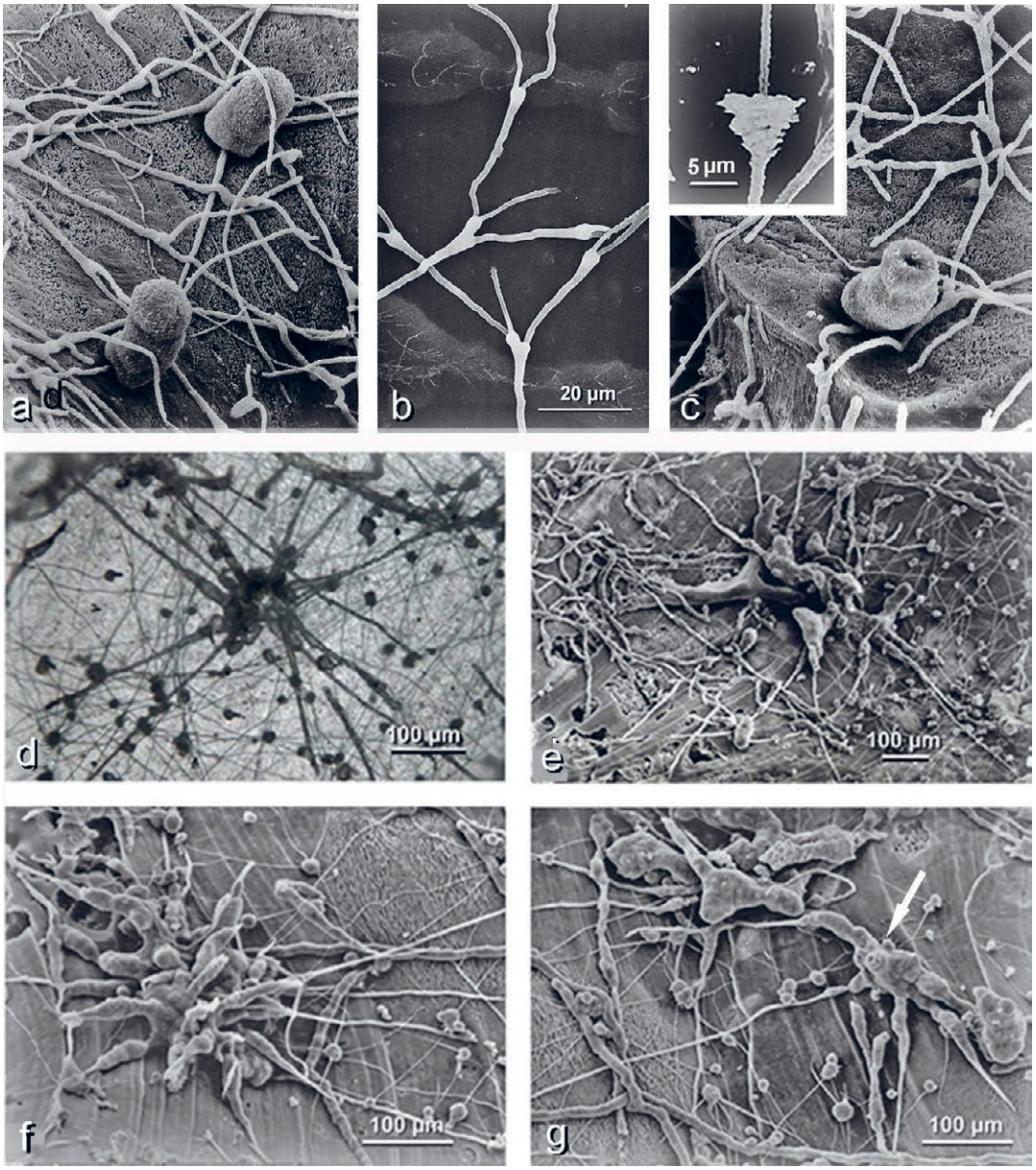

Figure 8. *Saccomorpha stereodiktyon* GOLUBIC et al., 2014 (a-c) and *Polyactina araneola* RADTKE, 1991 (d-g). **a.** *S. stereodiktyon:* Sporangial swellings attached to the substrate surface interior, interconnected by a network of hyphal tunnels (note ultrafine tunnels may belong to a different microborer). **b.** *S. stereodiktyon:* Dichotomous and trichotomous branches of hyphal tunnels (the scale in b is also valid for a and c). **c.** A sporangial swelling with a depression facing the interior of the substrate, **insert:** Proliferation of conical excavations when hyphae encounter organic lamellae in the shell. **d.** Transmission light photomicrograph of *Polyactina araneola* RADTKE, 1991, in a transparent pteropod shellof a trace indistinguishable from *Conchyliaster enderi* ZEBROWSKI, 1936, surrounded by *Saccomorpha* ispp. **e.-f.** Resin-replica of a *P. araneola* trace among traces of *Saccomorpha guttulata* (SEM images). **g.** Detached *P. araneola* trace replica, showing the connection to the opposite shell surface (arrow).

tion of the bored substrate. The trace consists of a network of hyphal tunnels with regular dichotomous and trichotomous ramifications that interconnect sporangial swellings (Figs. 8a, c). The boring strategy is differentiated by two differently oriented hyphal systems: A 'horizontal' and a 'vertical' network (GOLUBIC et al. 2014, fig. 5) The 'horizontal' network spreading parallel to the substrate surface (GOLUBIC et al. 2014, fig 1, 3), seems to be exploring the shell by spreading the filaments similar to the hyphae of a fungus). Tubules are 1.0–3.0 µm wide, increasing in diameter approaching bifurcations and trifurcations. Sporangial swellings 15–30 µm or 22.4 ± 5.5 (n = 375) µm long appear to arise from tunnels at right angles to the surface and adhere to the internal substrate surface (Figs. 8a. c). A "vertical" network of hyphal tubes departs from the "horizontal" one by dichotomous or trichotomous ramifications (Fig. 8b, centre), which swell slightly. Each dichotomy generates one horizontal and one vertical branch. Each trichotomy generates two horizontal branches and a third upright one. The upright branches penetrate toward the interior of the shell, where they apparently engaged in digestion of organic lamellae incorporated in the shell, leaving a clearly discernable trace of that activity (GOLUBIC et al. 2014, fig 2G, H).

Comment: When encountering organic lamellae incorporated within the host's shell, the upright branches, oriented perpendicular to the sub-surface network, form a special cloud-like optical disturbance, which is detectable by light microscopy (GOLUBIC et al., 2014, fig 1D). The same texture is

revealed as an upward diverging set of interconnected spaces forming an inverted cone around the replicated hyphal tunnel (Fig. 8c, insert). GOLUBIC et al. (2014) described reproductive branches that are often bent into flat helices as they produce terminal sporangial swellings at the substrate surface in an apparent reproductive phase of this trace-maker. The swellings are cylindrical (Fig. 8a, c) but also can be bi-lobate to multi-lobate (GOLUBIC et al., 2014, fig. 2E).

The trace was first observed on marine underwater cliffs of the Kornati Islands in Croatia at 70 m depth. Later, it was found at different sites (COURADEAU et al., 2017; ROUSH & GARCIA-PICHEL, 2020), including the intertidal zone of the North Sea, but it is also frequent in shell fragments from the deep sea sediments of the Gulf of Aden in the Red Sea at 1558 m depth; Early Tertiary occurrences from the Eocene have also been confirmed (RADTKE, 1991; GOLUBIC et al., 2014).

By re-examination of the early work on the *Dodgella* traces by Zebrowski, we could recognize among his drawings (ZEBROWSKI, 1936, pl. 27, fig. 8) a similar trace of what he described as a Cladochytriacean fungus *Arborella kohli* ZEBROWSKI, 1936. The ten ichnospecies listed above represent the presently known morphological spectrum of the genus *Saccomorpha* RADTKE, 1991.

Trace 11: *Polyactina araneola* RADTKE, 1991

(Figs. 8d–g)

1991 *Polyactina araneola* isp. nov. - RADTKE, p. 86-88, pl. 12, Figs. 1, 2

P. araneola was described by RADTKE (1991). It was the type ichnospecies of the ichnogenus.

Polyactina is defined as being "composed of many radially branching arms" (RADTKE, 1991, p. 86-88, pl. 12, Figs. 1, 2) and was compared with the trace of a cladochytrid lower fungus that fits the description for *Conchyliaster enderi* ZEBROWSKI, 1936.

It is a complex trace with two types of sporangial swellings. A central isodiametric cavity approaching 100 μm in diameter) apparently contains the primary sporangium, while several outward radiating cylindrical chambers may contain secondary sporangia. Such secondary sporangial swellings are often separated from the central body by a slight constriction. The secondary sporangial swellings extend distally into long radiating and gradually tapering tunnels (Fig. 8d), that are significantly thicker than the adjacent hyphal filaments of *Saccomorpha* ispp. The three-dimensional display of *P. araneola* cast in resin and viewed by SEM shows the relationships between different parts of *P. araneola*, and some variation that is reminiscent of a small spider (Figs. 8e–g).

Comment: The trace corresponds closely to the original description and illustration of *Conchyliaster enderi* (ZEBROWSKI, 1936, plate 27, figs. 7, 9*),* where it was described together with *Dodgella priscus* ZEBROWSKI, 1936 as a separate microorganism. Traces of both organisms are commonly found together (Figs. 8d, e).

The ichnogenus *Flagrichnus* WISSHAK & PORTER, 2006, with the ichnospecies *F. profundus* (type) and *F. baiulus* were described as compound traces and marine cold-water indicators (WISSHAK & PORTER, 2006, p. 135–145). They were distributed at depths that include the aphotic zone. A new species is described here that shares some but not all the properties of the ichnospecies above.

Trace 12: *Flagrichnus polyfloges* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 9a–c)

1991 HOOK, p.106-112; fig. 4-3., 4-4

Holotype image: Fig. 9b.

Etymology: Greek *poly* = many; *floga* = flame.

Key feature (diagnosis): *Flagrichnus polyfloges* isp. nov. consists of complex traces composed of a basal fairly isodiametric, sporangia-like swelling having multiple tapered, flame-shaped to thread-like extensions that penetrate and permeate the shell (Fig. 9a). The new trace shares several morphological properties with the type ichnospecies *F. profundus* (WISSHAK & PORTER, 2006, p. 139). Similar to *F. profundus* and *F. baiulus*, the new ichnospecies has a simple isodiametric body adhering to the substrate surface. Unlike *F. profundus* and *F. baiulus* with simple and forked filamentous extensions (WISSHAK & PORTER, 2006, fig. 4), the new trace is beset by numerous flame-like tapered extensions 2-3 μm wide at base, sufficiently unique to be described as a new ichnospecies: *F. polyfloges* isp. nov. Light microscopy (Fig. 9a) shows the isodiametric outlines of the lobed sporangial swelling with numerous tapered extensions, which fill the spaces between the substrate crystallites they have preferentially dissolved (HOOK & GOLUBIC, 1993). Adherence to the substrate surface and the flame-like shape of the extensions are best observed on SEM images of resin-casts (Figs. 9b, c).

Comment: Our SEM images of *Flagrichnus polyfloges* isp. nov. (Fig. 9b, c) compare well with *F. profundus* and *F. baiulus* regarding the adherence of the basal swellings to the substrate surface (WISSHAK & PORTER, 2006, fig. 2H). Similarly, the tapered extensions emanating from the basal swelling (Fig. 9c) in *F. polyfloges* correspond to the distal portions of filament extensions of *F. baiulus,* (WISSHAK & PORTER, 2006, fig. 3B) permeating the shell's carbonate matrix. The borings of *F. polyfloges* dominated the interior of *Bathymodiolus shells* collected at the Florida Escarpment at a depth of 3,266 m (PAULL et al., 1984).

Boring sponges have been known for well over two centuries. Fossil traces were named *Entobia* Bronn 1837 (SCHÖNBERG, 2008; WISSHAK, 2008; WISSHAK et al., 2014b). WISSHAK (2008) described two ichnospecies *E. micra* and *E. nana* as parts of the microbioerosion in aphotic depths. In our study, we observed, characterized, and illustrated the following:

Trace 13: *Entobia micra* WISSHAK, 2008

(Figs. 9d, e)

1991 'knobby morph' – HOOK, 1991, p. 138, 171; fig. 5–16

2008 *Entobia micra* isp. nov. – WISSHAK

E. micra or the mini-sponge trace is a complex trace characterized by the penetration and progression of sponge tissue forming a bumpy irregular, sometimes branched cylindrical body, approximately 200 μm in length and varying between 20 and 35 μm in width (Fig. 9d). It is said to be

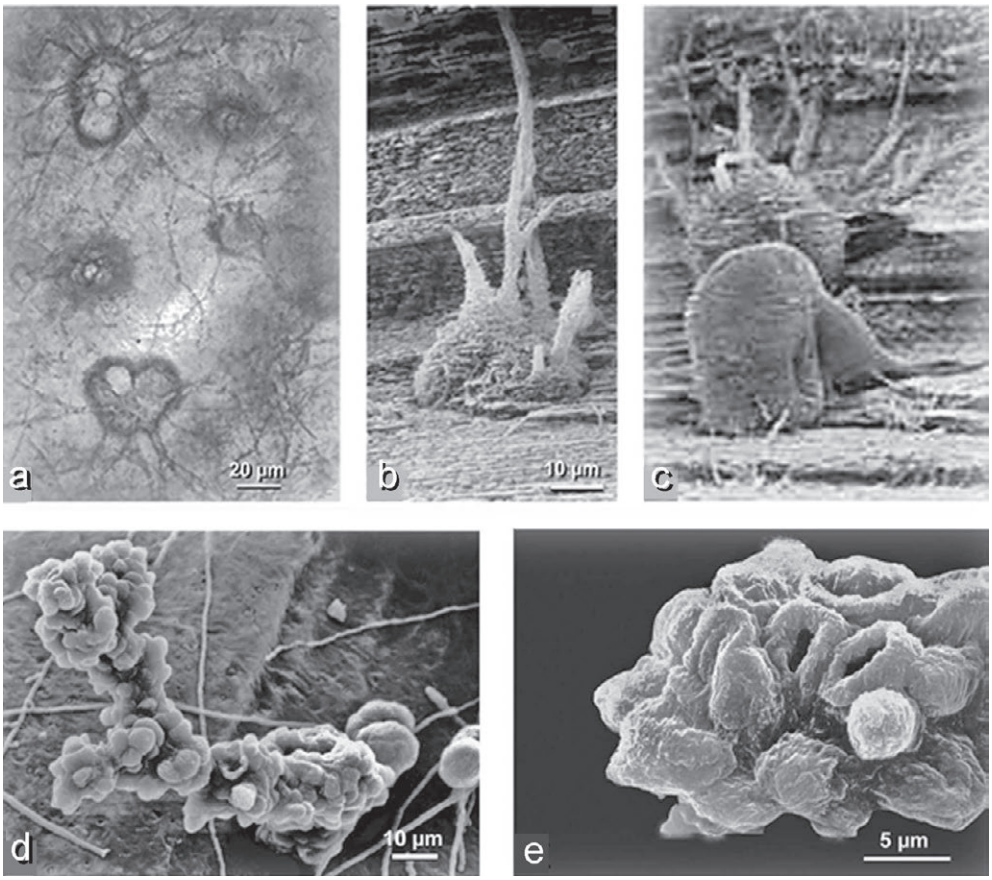

Figure 9. Complex deep sea traces *Flagrichnus* WISSHAK & PORTER, 2006 (a-c) and mini-sponge trace *Entobia micra* WISSHAK & NEUMANN, 2018 (d and e). **a.** *Flagrichnus polyfloges* isp. nov. – light photomicrograph taken through a translucent shell of the deep sea *Bathymodiolus* sp. clam from the Florida escarpment (3,266 m depth). Characteristic are :isodiametric, sporangial cavities with tapered and fibrous hyphal extensions (see GOLUBIC, 1984b and HOOK, 1991 fig. 4-4.). **b.** Resin cast of a *F. polyfloges* sporangial cavity in profile view, adhering to the interior of the shell surface, with branched and tapered extensions; the scale in b is valid for c. **c.** Dome-shaped, partially collapsed resin-cast sporangial cavity and partially exposed intact cast with protuberances; (GOLUBIC, 1984b; HOOK, 1991 fig. 3-3. and fig. 4-4.). **d.** Deep sea mini-sponge trace *Entobia micra* WISSHAK, 2008, a branched tunnel with carbonate-carving functional units, each 4–5 µm in diameter (see HOOK, 1991, fig. 5-15c). **e.** Detail of d: some of the carbonate-boring units are open outlining the size of carbonate chips carved by the *E. micra* sponge (see HOOK, 1991, fig. 5-15d.).

produced by a boring sponge that was noted to be much smaller than the known *Cliona* type of boring sponges (WISSHAK, 2008). The trace is considered complex, as is its surface interface, as revealed by the casts. They consist of hemispherical knobs, averaging 5 µm across, at the points where the actual carbonate bioerosion takes place. Some knobs appear in casts as open and hollow with a lip-like rim (Fig. 9e).

Comment: The description above is consistent with the distinctive boring mechanism known for boring sponges, except that the size of this one is a full order of magnitude smaller. Boring sponges have specialized cells, each of which removes substrate by encircling and separating a piece ca. 50 µm across, which is then exported to the shell exterior. The hollowed hemispherical knobs of this form would suggest removal of smaller than 5 µm diameter particles (see also "scalloping borer" HOOK & GOLUBIC, 1988). This morph has been observed in the deep sea sediment of the Bermuda Pedestal and in other sites of the northern Atlantic (WISSHAK, 2008).

4.2. Tubular microboring morphotypes

Tubular traces are simple, but also subject to a wide range of variability regarding the size, orientation in relation to the substrate surface, modes of branching, relationships to surface texture and interactive behaviour with other traces: avoidance vs. anastomosis. In the deep sea, different prominent traces often occur together: the complex traces of the ichnogenus *Saccomorpha* (Fig. 3d-a**)**, tubular traces of the ichnogenus *Orthogonum* (Fig. 3d-b) and the thin and intertwined vermiculate traces of the ichnogenus *Scolecia* (Fig 3d-c). The tubular traces are described here. The ichnogenus *Orthogonum* with the type ichnospecies *O. tubulare* RADTKE, 1991 was described as predominantly two-dimensional networks of robust, often rectangular, multiply branched tubular traces, extending parallel to the substrate surface, with frequent, often widened ramifications, which may cover areas of up to several mm². Branching angles commonly approach 90º (40 % of measured angles are between 85º and 90º), which inspired its formal ichnogenus name: *Orthogonum*. The trace has been formally described from a shell of *Turritella* in the Priabonian, Upper Eocene (RADTKE, 1991, p. 60, pl. 5, fig. 3 – holotypus Bo 7/110). The original description of the type species *O. tubulare* RADTKE, 1991 included a wide spectrum of morphological variations, which may have represented the work of different microboring organisms. Here, the genus is refined by modifying diagnostic criteria for *O. tubulare* and

O. lineare and refining *O. spinosum*, as well as adding the species *O. arbor, O. tenue*, and *O. cellexpressum*.

Trace 14: *Orthogonum tubulare* RADTKE, 1991

(Figs. 10a–c; 11a–c)

1991 *Orthogonum tubulare* isp. nov. – RADTKE, p. 60-64, pl. 5, figs. 3-4

1991 non *Orthogonum tubulare* (= *S. guttulata* WISSHAK & NEUMANN, 2018) – RADTKE, p. 61-64, pl. 5, fig. 5, 6

1991 non *Orthogonum tubulare,* RADTKE, p. 61-64, pl. 6, figs. 1, 2

1994 non *Orthogonum tubulare* – GLAUB, p. 98-100, Fig. 35

The original description of *O. tubulare* is given by RADTKE (1991, p. 60-64, pl. 5, and now refers only to fig. 3 and 4). Some former paratypes are now interpreted as other ichnotraces.

Updated diagnosis: A large tunnel system parallel to the substrate surface with thick, straight, and usually right-angled branched tunnels. The distances between branching points vary. The diameter of the tunnel can increase at branch points.

Updated description: The form is characterized by branching tunnels (diameter 8–15 µm), some of which run in a very straight line and occasionally appear to create wide arches. In the case of unilateral branching, right angles prevail, although angles between 20–60 degrees can be found. Vertical branching into the shell is also present. Some side passages branching off from the main passage, briefly turn deeper into the substrate to later arc back to the shell surface. Often the branching points of the tunnels are conically thickened (diameter 20–30 µm). Sometimes the tunnels show an oval, flattened cross-section. Anastomosis formation can be observed (RADTKE, 1991, pl. 5, fig. 3).

In the description of *Orthogonum tubulare* the author combined several observations into one ichnospecies, which occurred in different localities, which could finally be corrected here. Some of the paratypes have now been assigned to other

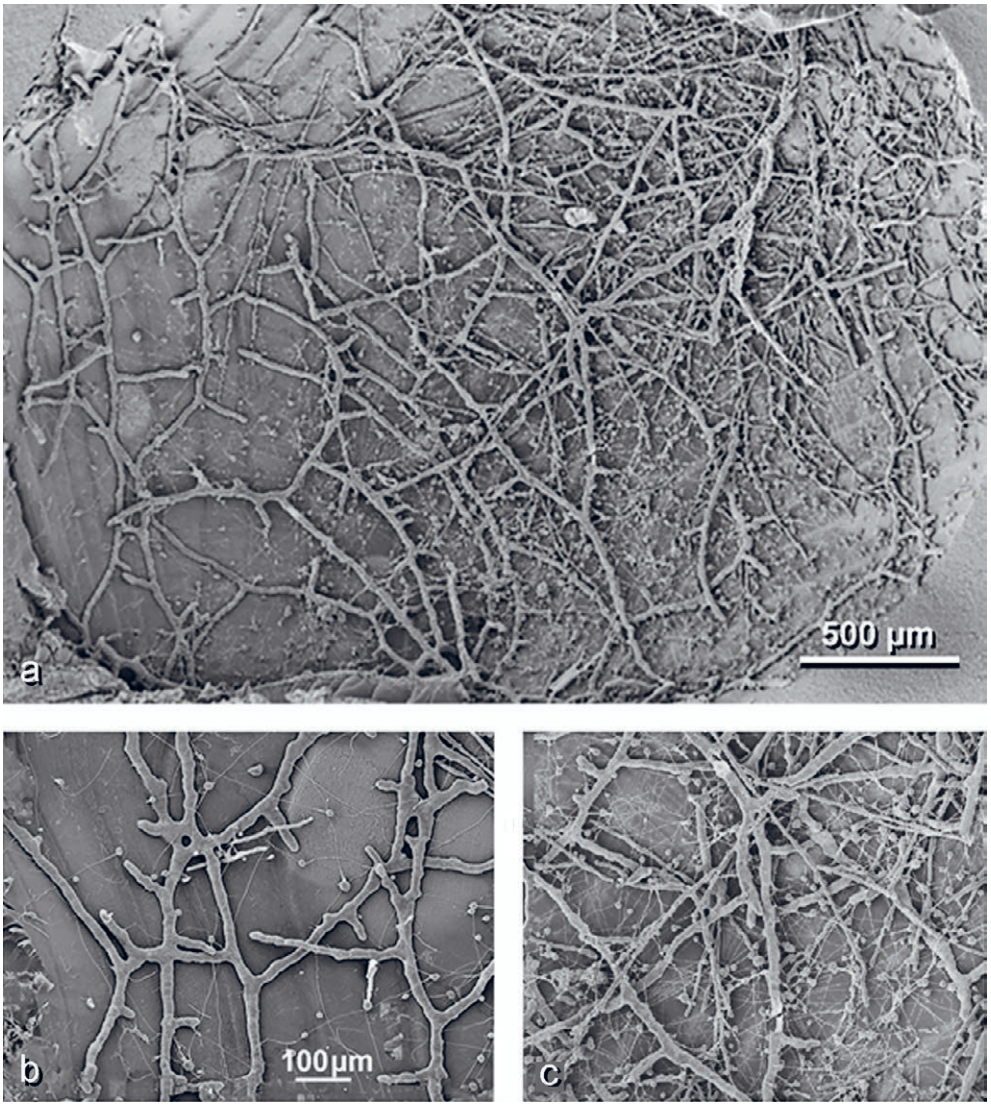

Figure 10. *Orthogonum tubulare* RADTKE, 1991, SEM of resin-cast tunnels (sample RAJ 158-1a_29); also see SEMs in HOOK (1991). **a.** Interconnected network of repeatedly ramified and periodically anastomosing tunnels of very variable diameters, branch length and location, distributed along the interior surface of a pteropod shell, shared with *Saccomorpha* ispp. **b.** Detail of a (upper left): showing moderately branched exploratory tunnels with several anastomoses. **c.** Detail (centre): showing the range of size variability of ramified tubules of the same trace (see also HOOK, 1991, fig. 5-2d. and fig. 6-1.). Photos b and c are at the same scale.

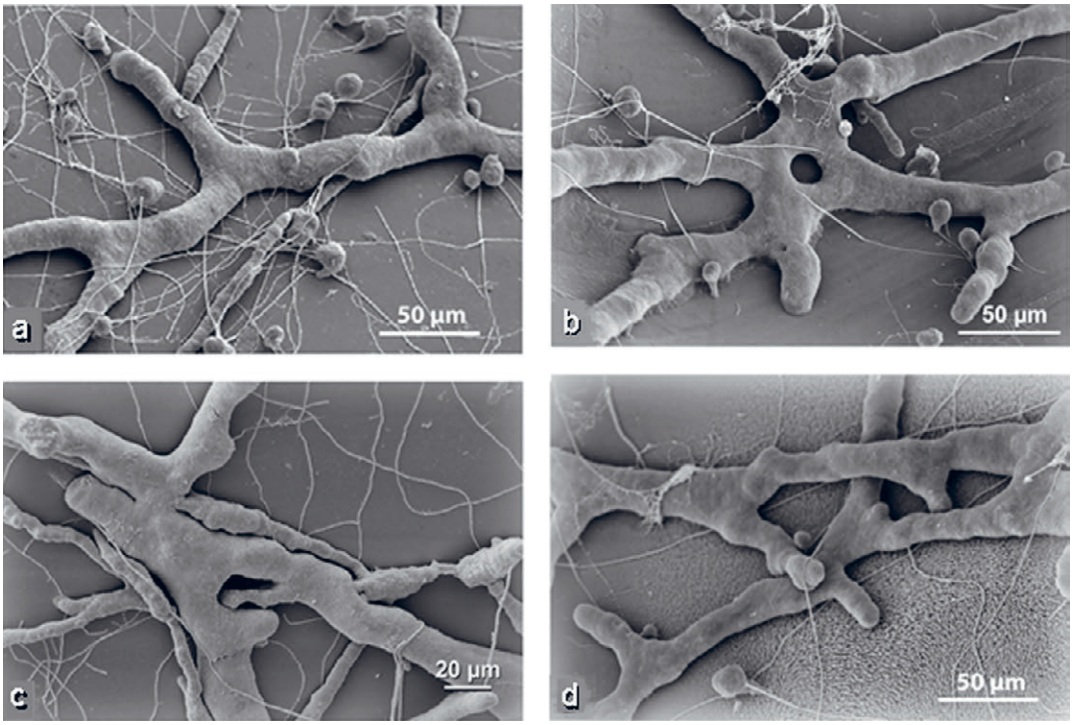

Figure 11. *Orthogonum tubulare* RADTKE, 1991, details. Note the irregularity of branching pattern and the wide variety of branch diameters. **a.** Regular branching pattern intermixed with *Saccomorpha* network. **b.** Anastomosis, detail from Fig. 10b. **c.** Example of a fusion of several branches with a wide range of branch diameters. **d.** Branching with flat branch points showing avoidance of anastomosis.

ichnospecies. A few specimens from Northern Italy and the Aquitaine Basin have since been assigned to the new ichnospecies *Saccomorpha guttulata* WISSHAK, et al. 2018. A large number of specimens with very detailed observations were described by RADTKE,1991 (Table 11, p. 62-64, 92 specimens).

O. tubulare is a euendolithic trace that forms an extensive network of tubules within a skeletal carbonate substrate, characterized by high variability in diameter, branching frequency and considerably varied branching density as observed by light microscopy in transparent shell fragments (Fig. 2a) and by SEM of resin-cast replicas of tunnels (Figs. 10, 11). The network exhibits, in part, a loosely configured "exploratory" phase (Figs. 10a, left; 10b) with straight branches, relatively uniform in size, 16.5 ± 1.8 µm (n = 35) wide, becoming significantly wider (25–30 µm) and slightly flattened when approaching ramifications (Figs. 10a, c) or anastomoses (Figs. 10b, 11b). Sometimes, the same microborer generates densely branched areas with branches that successively narrow in diameter, reminiscent of the ramification of branches of a tree, thereby forming a dense "substrate-exploiting" region (Fig.10a, centre; 10c, 11c). Branching occurs at various distances, 20 to 200 µm apart, and at highly variable angles (mostly less than 90º), with diameters ranging from 10 to 60 µm (Fig. 11c). The network of the *O. tubulare* tunnels is largely two-dimensional, forming at one or two levels parallel to the substrate surface, with few branches departing deeper into the substrate (Fig. 11d). The outlines of the tunnels are mostly irregular and the surfaces contacting the substrate are rough.

Comment: The original holotype figure of the ichnospecies *O. tubulare* RADTKE, 1991, p. 65, pl. 5, fig. 3 is confirmed.

Trace 15: *Orthogonum lineare* GLAUB, 1994 – modified

(Figs. 12a–c)

1991 'cylindrical morph' - HOOK, p. 131, 153; Figs. 5-7c, d

1994 *Orthogonum lineare* isp. nov. – GLAUB, p. 103, Fig. 37

O. lineare consists of tubes of relatively constant diameter of 7 to 12 (9.96 ± 1.7, n = 59) µm wide (Fig. 12a). This was previously described by GLAUB (1994) with diameter 7–16 µm, pl. 7, fig. 1–4.). *O. lineare* has a smooth surface and round cross-section (Fig. 12c). Ramifications occur at variable intervals, at nearly right angles (Fig.12b) conforming to the ichnogenus diagnosis. Tunnels have smooth surfaces (Fig. 12b) and rounded, sometimes slightly inflated tips (Fig. 12c). The lack of anastomosis and the avoidance of pre-existing tunnels is consistent, even when there is a high density of filaments. Filaments arch over each other or are deflected (Fig. 12c). Tubules often run parallel to each other (GLAUB, 1994, fig. 37; pl. 7, figs. 2 and 4), avoiding the edge of the substrate as well as each other. In light-microscopic preparations, the tunnels were found to contain gray-coloured content. The SEM of fractured tunnels shows some of our samples to contain spore-like bodies.

Comment: GLAUB (1994) describes the ichnospecies *Orthogonum lineare*, mirroring the approach made by RADTKE (1991) for *O. tubulare*. Glaub's diagnosis, based only on the more narrowly defined description of *O. lineare,* lists clearly discrepant size ranges for what she regards as the same ichnotaxon. She appears to have studied them as populations but assigned those size ranges incorrectly.

Glaub documented her new ichnospecies based on a very idealized drawing (GLAUB, 1994, p. 103, fig. 37). Also, her

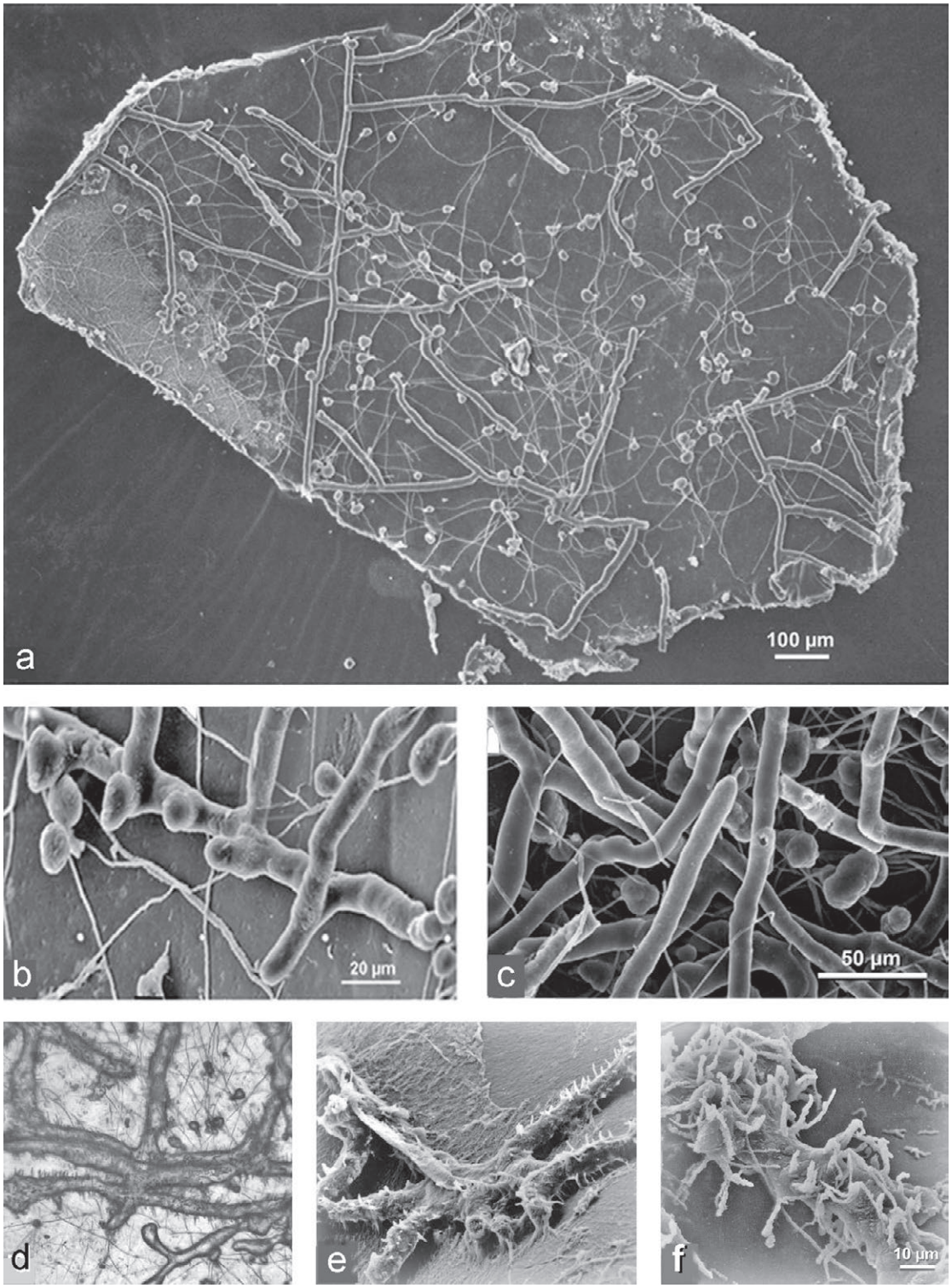

Figure 12. Tubular microboring traces of *Orthogonum lineare* GLAUB, 1994, displayed as resin replicas (a-c) and *O. spinosum* RADTKE, 1991 (d-f). Also see images in HOOK (1991). **a.** *O.lineare* spread over the interior surface of a pteropod shell fragment from 1,645 m deep Bermuda Pedestal sediment (see HOOK, 1991, fig. 5-7a.), with *Saccomorpha* ispp. and *Scolecia* in the background, left (see HOOK, 1991, fig. 5-15.). **b.** Typical display of *Orthogonum*-type filaments with orthogonal branching; note that the branches are often slightly narrower at the initiation. **c.** Filaments of *O. lineare,* showing smooth surface and rounded tunnel tips, with *Saccomorpha* ispp. in the background. **d.** Light photomicrograph of *Orthogonum spinosum* RADTKE, 1991 in a transparent shell together with *Saccomorpha* ispp. and a tip of *S. guttulata* WISSHAK et al., 2018 (in the lower part of the photo). **e.** Resin-cast of *O. spinosum* RADTKE, 1991. Fig. 12d and e are at the same magnification. **f.** Detail of e: at a different place, showing spines (see also HOOK,1991, fig. 6-4.).

drawing (p. 99) combines features from different taxa, which is a by-product of a "lumping" approach. For this reason, as well as the incompatible size ranges. *O. lineare* is being modified here. HOOK (1991) described *O. lineare* as the "cylindrical morph." His size range matches our description.

Orthogonum lineare GLAUB, 1994 was described as a tubular microboring in the brachiopod *Linguithyris aspasia* (Holotypus: Bo 13/203) as an ichnospecies with a predominantly straight (linear), frequently branched borehole system, characterized by tubules with smooth surface and rounded

tips. *O. lineare* is now modified to restrict it to one of the two originally mentioned size ranges: 7–12 µm wide. In contrast, Glaub wrote that *O. lineare* encompasses populations between 7 and 16 µm diameter (GLAUB, 1994, p. 102). Yet, the tables in that publication included in the original description list two size-distinct populations with diameters of 7–8 vs. 14–16 µm (l.c. p. 104). We found this ichnotaxon to avoid anastomosis (mentioned in the diagnosis), which explains the common deflection and parallel advancement of borings described by Glaub (see GLAUB, 1994, Pl. 7, fig. 3). The added information calls for modification of the diagnosis of this trace which appears to have initially encompassed more than one taxon with similar behavioural properties.

Trace 16: *Orthogonum spinosum* RADTKE, 1991

(Figs. 12d-f)

1991 HOOK Ch. 6, p. 176, 187; fig. 4

1991 *Orthogonum spinosum* isp. nov. – RADTKE, p. 65-66, pl. 6, Figs. 3, 4

O. spinosum (RADTKE, 1991, p. 65-66, pl. 6, figs. 3, 4) or "spiny tubule" varies in diameter from 20 to 50 µm, producing a complex pattern comprised of two morphological elements: frequently branched tubules and pointed spinose extensions. The traces are clearly recognizable by light microscopy in transparent pteropod shells (Fig. 12d), as well as in SEM images of resin casts (Figs. 12e, detail in f). The tubules' shapes and sizes are both widely variable in diameter, including the flexible spiny protrusions which characterize this ichnotaxon (Fig.12f). HOOK (1991, ch. 6, fig. 4) Found similar tubes 30–70 µm or 33,5 ± 7.6 µm (n = 69).

Comment: We discovered that spiny tubules in the aphotic depths are relatively rare. Our illustrated examples correspond to those in the original description of this trace (RADTKE, 1991, pl. 6, figs. 3, 4).

Trace 17: *Orthogonum arbor* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 13a–d)

1991 'arboreal morph' - HOOK, p. 132, 153, figs. 5-10

Holotype image: Fig. 13b.

Etymology: Latin *arbor* = tree.

Key feature (diagnosis): *O. arbor* is a solitary, relatively short, tubular form with a notable resemblance to a tree (Fig. 13a). Like a tree, it consists of a "trunk" which terminates with a dense "canopy" of branches. The trunk begins its growth at the point of entry into the substrate and curves to continue to grow, mostly parallel to the shell surface, as a straight or gently arched tunnel for 100 to 600 µm. It is circular in cross section with a diameter of ca 10 µm, gradually increasing distally to 12 µm. It may sometimes ramify (Fig. 13a) or change direction if encountering obstacles (Fig. 13b). It mostly remains unbranched and mildly curved (Fig. 13c). The "canopy" results from a burst of ramifications at the end of the straight "trunk," with an average branch point distance of 30 µm. The branching pattern is planar, sympodial, expanding up to 5 orders, with a circumference of about 150 µm (Fig. 13a). The planar growth of the tree trace may be dictated by the thinness of the shell. Departures of this pattern were noticed in thicker shells where the taxon develops a three-dimensional canopy (Fig. 13b). Branches are up to 130 µm long, sometimes arched, and always shorter than the main trunk. Their diameter is narrower at the branch point, and gradually widens distally, up to 50 µm, assuming a clavate shape. Older branches also enlarge laterally, becoming flat and oval in cross section. As the widened branches fill most of the space between, they

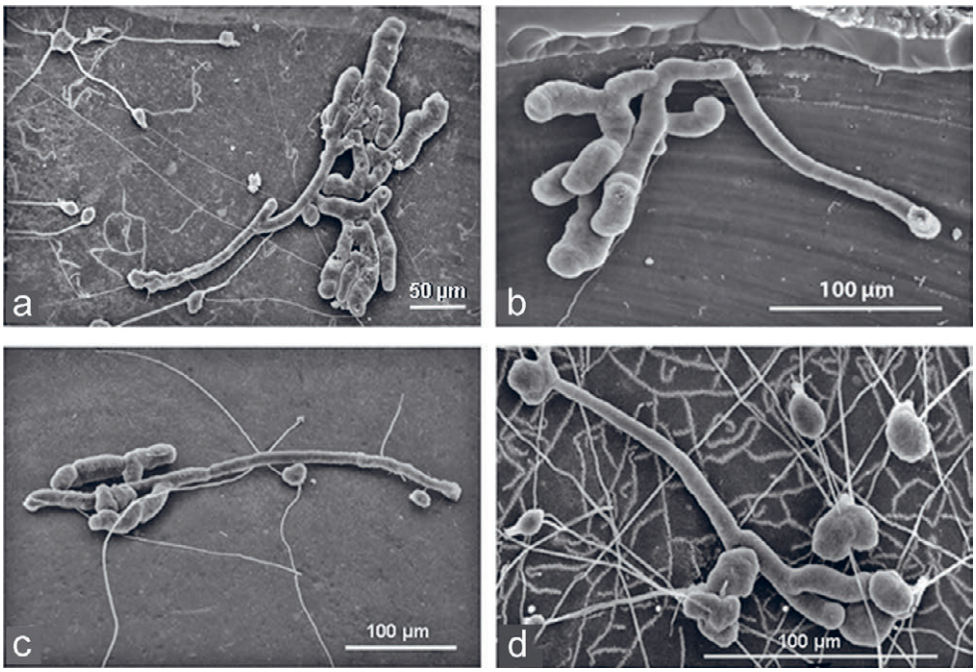

Figure 13. *Orthogonum arbor* isp. nov. in a pteropod shell from the Bermuda Pedestal (1,645 m deep); images in HOOK (1991, fig. 5-10). **a.** The tree-shaped microboring with a flat, two-dimensional canopy, spread parallel to the shell surface, with *Saccomorpha velum*, isp. nov. (Upper left) and other traces. Magnification is the same as in c. **b.** *O. arbor* with a branches become gradually wider in the "canopy" region. Holotype. **c.** Early development of *O. arbor* with *Saccomorpha* traces. **d.** *O. arbor* in the context of a dense deep sea ichnocoenosis with *Saccomorpha* ispp. and *Scolecia urbimetra* isp. nov. on the shell surface in the background.

crowd and become mutually compressed and rectangular in cross section. This trace is typically an integral member of the deep sea ichnocoenosis (Fig. 13d).

Comment: Images of *O. arbor* adhere closely to the substrate surface. This may be a result of displacement following removal of carbonate support. In that case, these borings may originally have penetrated deeper into the shell. During the examination of shell fragments, it was noted that the tunnels of this form weaken the shell, which then becomes particularly susceptible to breakage along this feature probably due to its propensity to tunnel close to the surface of the substrate. Due to shell fracturing, the frequency of this trace in shell fragments may be underestimated.

Trace 18: *Orthogonum tenue* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Fig. 14a-a)

Holotype image: Fig. 14 a-a.

Etymology: Latin *tenuis* = narrow.

Key feature (diagnosis): *O. tenue* consists of narrow, very straight, rarely branched tubular traces, with irregularly wound, crowded terminals (Fig. 14 a-a). Lateral branches are short with attenuated ends. The main tubules are 5.5 to 10 (6.9 ± 1.35, n = 32) µm wide.

Comment: This trace needed to be described as separate *Orthogonum* ichnospecies as it forms trace assemblages that are consistently narrow, and distinct from *O. lineare*. The main trunk diameter of *O. tenue* corresponds to the diameter of the secondary branches of *O. tubulare* Radtke 1991. The trace was observed in the shell of the pteropod *Limacina*.

Trace 19: *Orthogonum cellexpressum* isp. nov. GOLUBIC, CAMPBELL, HOOK & RADTKE

(Figs.14a, b. Detail: Figs. 14b, -c)

Holotype image: Fig. 14b.

Etymology: Latin *cella* = cell, *expressus* = distinct.

Key feature (diagnosis): *O. cellexpressum* trace is a product of a highly variable microborer leaving tubular traces that appear to distally change in size and shape, possibly reflecting

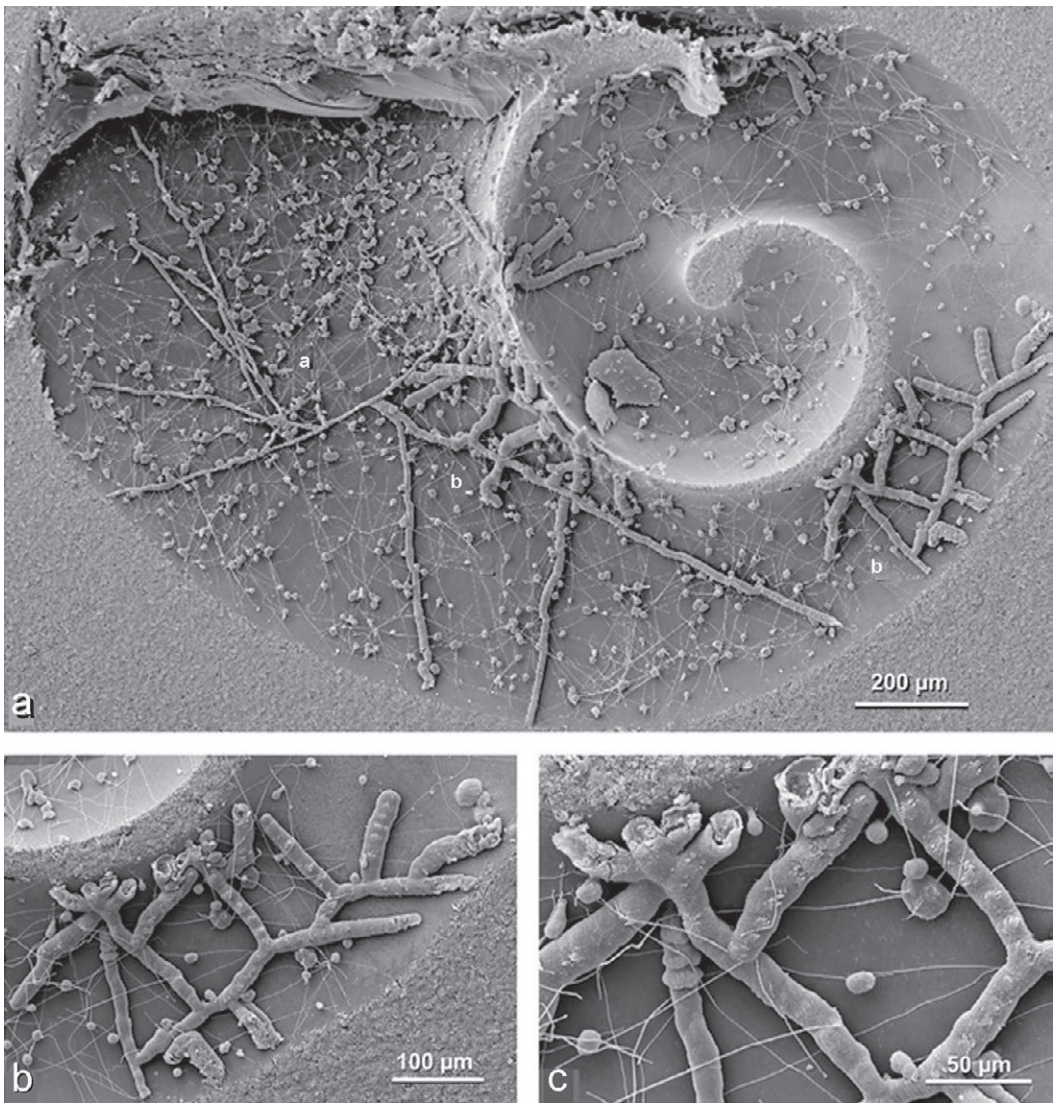

Figure 14. Tubular traces observed inside the shell of the pteropod *Limacina helicina* PHIPPS, 1774. **a.** Tubular traces associated with *Saccomorpha* ispp. along the interior surface of the shell. Photo includes new ichnospecies *Orthogonum tenue* isp. nov. shown to the left of label a (holotype) and *O. cellexpressum* isp. nov., the wider tubular trace in the region surrounding both label b's. **b.** *O. cellexpressum* isp. nov.; note the surface bumps that could have resulted from a serial arrangement of rounded cells or spores inside. Holotype. **c.** Detail of b.

that the tracemaker was adapting to the immediate microenvironment. The trace was studied in the shell of the pteropod *Limacina* (Figs. 14a, b) where it occupied most of the skeletal subsurface. The width of the branches varies from 14 to 30 μm averaging around 20 μm (20.08 μm ± 3.69 μm; n = 46). The branches are often thinner at their base. In distal and expanding parts of its system, the tubules are slightly wider and flattened, elliptical in cross section, repeatedly branched as they adhere to the interior substrate surfaces of the host's skeleton (Fig. 14a, centre and right; Figs. 14b, c). This type of branching is similar to that shown in *O. arbor*. The inward oriented surfaces of the branches show a series of bumps alternating with slight depressions about 15 μm apart, suggesting a series of cells in the interior causing the swellings along distal tubules – similar to peas in a pod.

Comment: Although highly variable regarding size, cross section, and branching pattern, the different interconnected parts seem to have been produced by the same organism. The boring activity appears to have progressed in two phases. The tubules are initially straight, narrow, ca. 10 μm wide, circular in cross section, remaining unbranched for long stretches (up to 500 μm) yielding an impression of exploratory tunnels. In a second phase, the tunnels branch, widen, flatten somewhat, and make an impression that growth slowed and differentiated a little.

4.3. Vermicular microboring morphotypes

Vermicular trace morphotypes include narrow (<15 μm), winding, infrequently branched tubules formally described as the ichnogenus *Scolecia* RADTKE 1991**,** with the type ichno-

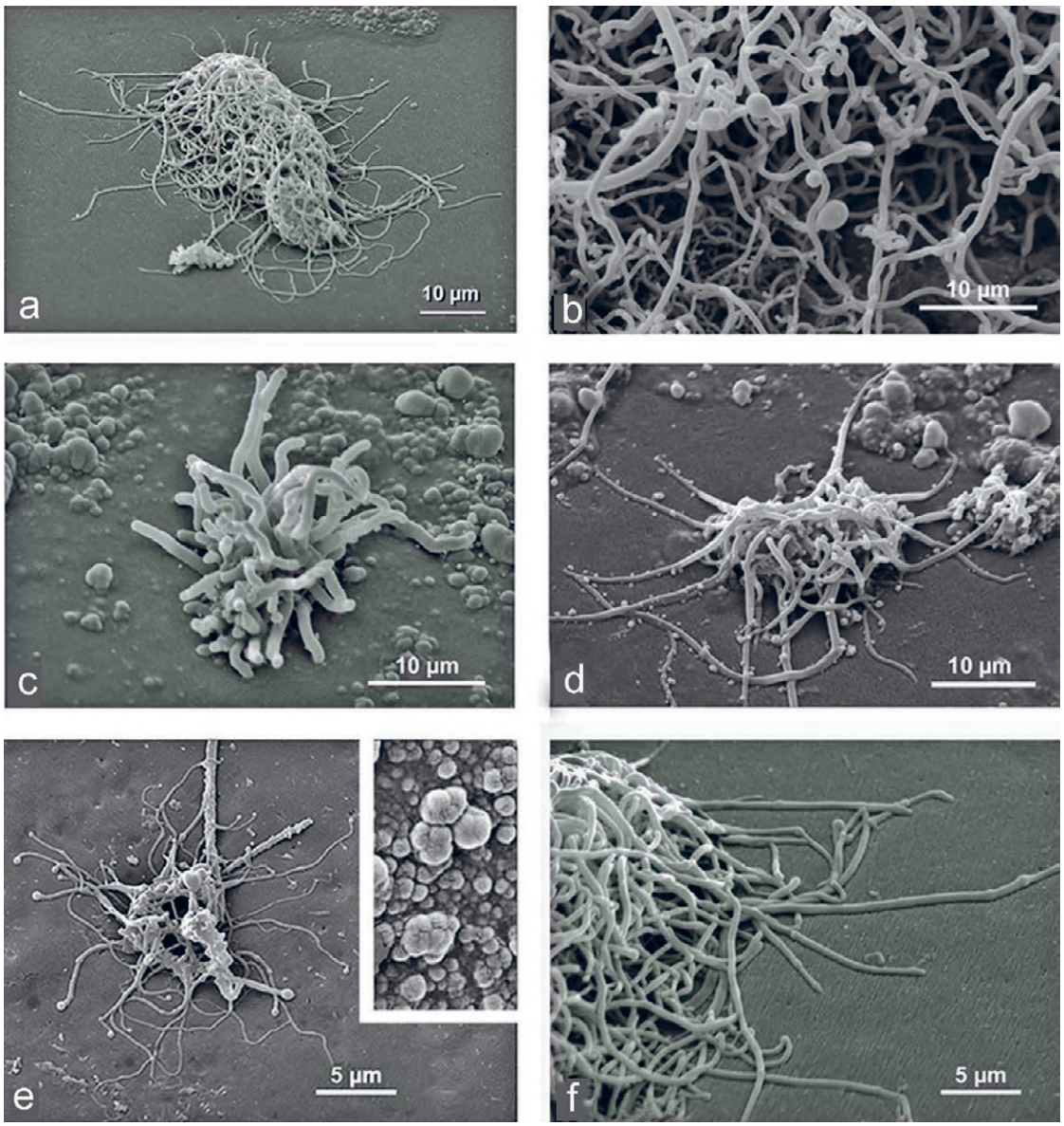

Figure 15. *Scolecia nodosa* isp. nov. and associated coccoid traces in a pteropod shell from the 1,553 m deep sediment collection Me5–158 at Port Sudan, Red Sea. **a.** Accumulation of narrow and tapered filaments of *S. nodosa* with intercalary and terminally positioned nodules. The trace was originally more widely spaced, but it collapsed following the removal of the carbonate support by acid treatment. **b.** Detail of a: showing tubular termini of *S. nodosa*, including distal curled branches with and without terminal nodules. **c.** A young colony of *S. nodosa* with diverging primary filaments next to a colony of coccoid-shaped depressions of the shell surface. **d.** *S. nodosa* colony that illustrates the characteristic tapering of filaments, with laterally positioned nodules. Holotype. **e.** A colony with filaments tapered down to a submicron size with terminal nodules. **Insert:** a representative sample of euendolithic coccoids showing the reproductive pattern of multiple fission. **f.** Margin of a collapsed colony of *S. nodosa* with tapered filament endings.

species *S. maeandria* RADTKE, 1991, from the Lutetien, Eocene of Paris Basin (RADTKE 1991, p. 70-76, pl. 7, fig. 6, pl. 8), with three additional ichnospecies: *S. filosa, S. serrata* (Trace 24) and *S. botulifera*. The present study of deep sea euendoliths yielded a new discovery: a distally tapered or nodulated vermicular trace described here as *Scolecia nodosa* isp. nov. This resulted in the slight modification of the original genus diagnosis to include distal attenuation and formation of nodules as described below (compare with HOOK, 1991, p. 134-138, as 'vermicular morphs').

Trace 20: *Scolecia nodosa* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Figs. 15a–f)

Holotype image: Fig. 15d.

Etymology: Latin *nodus* = knot, swelling.

Key feature (diagnosis): *S. nodosa* or "nodulated vermicular" boring is a euendolithic, intensely proliferating trace with long, filamentous, distally tapered microborings having a smooth surface and numerous lateral and often terminal nodules. The trace consists of tunnels (filaments in resin-casts) with diameters of about 1 μm, tapering distally down to a diameter of less than 0.1 μm (Fig. 15a). The branching of *S. nodosa* is uncommon, with an increased frequency toward the terminal parts of the filaments where the last generation of branches are tightly curled (Fig. 15b). The growth of *S. nodosa* starts in the form of a cluster of diverging round-tipped filaments (tunnels, Fig. 15c) and is later associated with nodules (Figs. 15b, d, e), which finally occur on filaments or on the filament terminals (Figs. 15d, e). However, the attenuated terminals also often remain free of nodulation (Fig. 15f). Nodulation is the most intriguing property of this trace. Nodules are either integrated into the filaments in a terminal position (Fig. 15b, e) or are laterally attached (Fig. 15d). Nodules also group independently in the vicinity of a filament (Fig. 15e, insert).

Comment: *Scolecia nodosa* isp. nov. is by dimension and surface features somewhat similar to *S. filosa* (RADTKE, 1991, pl. 8, fig. 3). It differs from *S. filosa* by nodulation and terminal attenuation (tapering). The true euendolithic nature of the organism producing this trace is evident during the carbonate dissolution process of specimen preparation. These replicas of fine tubules become dislodged during the acid treatment. They float in the solution and collapse as the solution drains or evaporates and accumulate resembling a pile of spaghetti (Figs. 15a, d, f). Only in young *S. nodosa* bunched short filaments still in contact with the substrate surface is their orientation vertical to it (Fig. 15c). The very small diameter tubules are similar in size to finely etched grooves that are incorporated into the substrate surface. The resin-cast tubules remain in place after acid treatment, as we have observed for the finest branches of the complex trace *Saccomorpha papilio* (see Trace 8 above) and for substrate-bound traces of *S. urbimetra* isp. nov. (see Trace 25 below).

There are two possible explanations of the extensive agglomerations of coccoid shapes that have been regularly observed in the vicinity of this trace (Figs. 15c, d, and e-insert). One is that they represent sporulation and the onset of daughter colonies. Alternatively, there could have been host-parasite interactions. These coccoids vary in size as if they are organized into colonies – reminiscent of cyanobacteria that display reproduction by multiple fission; however, the fact that these traces are attached to hard grounds in the aphotic deep sea rules out cyanobacteria which, except for very few taxa, are light-dependent. The morphology and size suggest that the casts could belong to organotrophic bacteria with a cell division pattern similar to that of cyanobacteria. Whether there is any relationship between these coccoid-like units and the ones attached as nodules to the filaments of *S. nodosa* is not known. Given that we have not seen them anywhere else, it is likely there is some relationship between them.

Close association of ultra-fine *Scolecia*-type filamentous traces with complex and tubular deep sea traces are suggestive of submicroscopic parasitic predation involving other members of the endolithic community. Several additional morphotypes of such fine tubular structures were observed as resin-replicates by high magnification and resolution SEM microscopy. Two of the morphotypes were sufficiently regular and frequent to be described as new trace ichnospecies within the filamentous ichnogenus *Scolecia* RADTKE, 1991: *Scolecia hirudo* isp. nov. and *S. acus* isp. nov., both represent micrometre-sized borings associated with larger traces, suggestive of host-parasite relationships.

Trace 21: *Scolecia hirudo* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Figs. 16a, c, g)

1991 HOOK, p. 163, figs. 5-12C

Holotype images: Figs. 16 g.

Etymology: Latin *hirudo* = leach.

Key feature (diagnosis): *S. hirudo* consists of ultra-fine, filamentous traces that are up to 20 μm long, only a fraction of a micrometer wide, terminally tapered to submicron dimensions, associated with much larger sporangial cavities of *Saccomorpha* ispp. Some of these ultra-fine tunnels are straight or mildly bent, attached to the *Saccomorpha* hyphal tunnels (Fig. 16a), or distributed over the sporangial swellings of *Saccomorpha* ispp, either as repeatedly branched (Fig. 16c) or as densely curled and tapered (Fig. 16g).

Comment: Ultra-fine tubular traces require further investigation. No relationships among the observed morphologically different properties of the traces of *S. hirudo* and the traces they were attached to could be established, and the biological identity, reproduction and dissemination all remain unknown. In addition to these flexible and curved ultrafine microborings, several different types of needle-like ultrafine structures were also found associated with larger deep sea euendolithic traces.

Trace 22: *Scolecia acus* isp. nov. HOOK, CAMPBELL, RADTKE & GOLUBIC

(Figs. 16b, d, e)

1991 'needle morph' – HOOK, p. 135, 163; figs. 5-16

Holotype image: Fig. 16b.

Etymology: Latin *acus* = needle.

Key feature (diagnosis): *S. acus* in its simplest form refers to a short, straight ultrafine tubular, ca. 4 μm long and 0.1 to 0.2 μm wide needle-like structure, with a minor, slightly detached and curved terminal swelling (Fig. 16b). These were

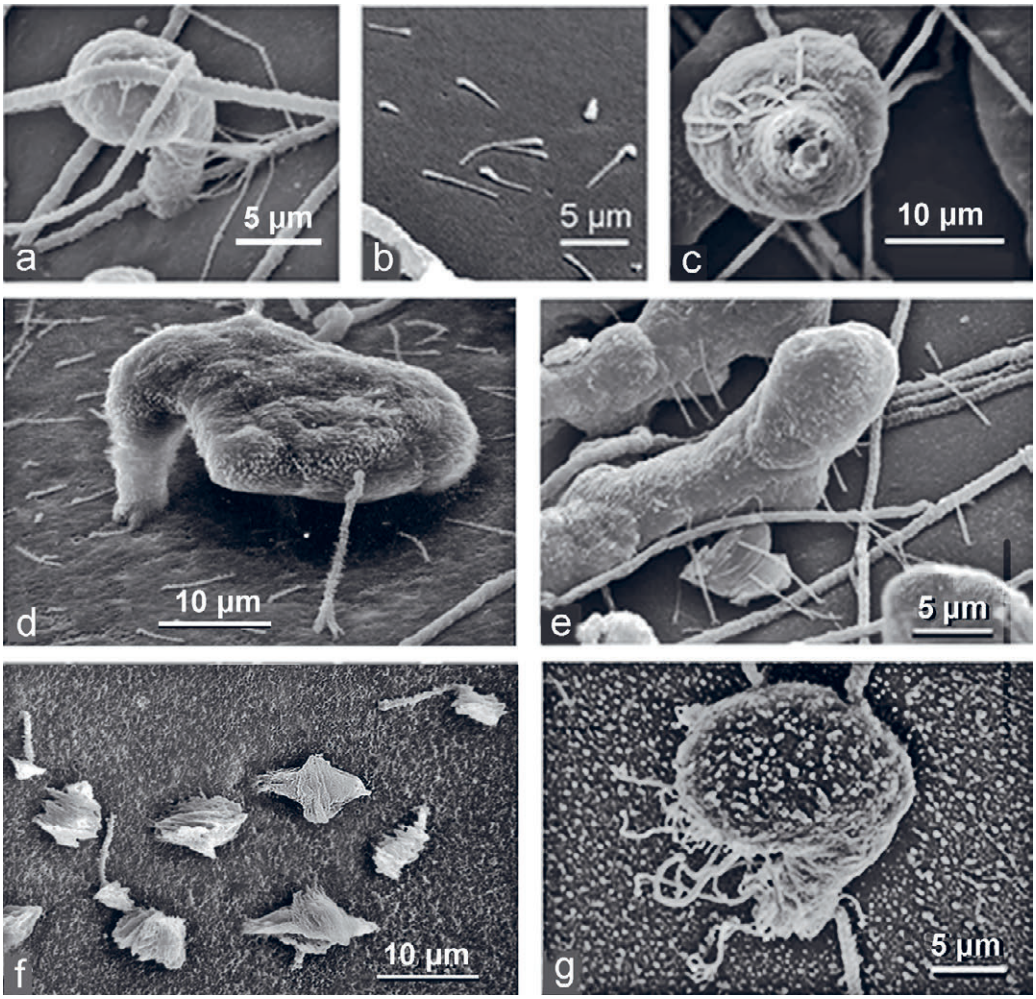

Figure 16. *Scolecia hirudo* isp. nov. (a, c, g) and *S. acus* isp. nov. (b, d, e, f). Both ichnotaxa have tiny micrometre-sized borings associated with larger traces, suggesting host-parasite relationships. **a.** Ultrafine filaments probably of *S. hirudo*, attached to hyphal tunnels at the base of a sporangial swelling of *Saccomorpha curvata* isp. nov. **b.** Submicron size pinhead-shaped traces of *S. acus,* each with a terminal swelling, scattered on the interior shell surface. Holotype. **c.** Branched ultrafine filaments of *S. hirudo* adhering to a detached sporangial swelling of *S. clava*. **d.** Inclined needle-shaped tubule similar but larger than *S. acus* leaning on *S. curvata* sporangial swelling, forked at the contact with the shell surface, and surrounded by smaller pinhead-type needles (as in b.) scattered over the inner substrate surface. **e.** *S. acus* comprised of numerous ultrafine inclined rods, forked at the base, connecting tubular traces with the substrate surface. **f.** *S. stellaris* isp. nov traces consist of scattered isodiametric holes with crystalline outlines, attached to ultrafine up to 10 µm long tubules. Holotype. **g.** Ultrafine tapered and wound filamentous *S. hirudo* borings curled at their tips, associated with the sporangial swelling of *Saccomorpha clava*. Holotype.

originally termed "pinheads" (HOOK, 1991). They are loosely distributed and adhere to the interior substrate surface (Fig. 16d, bottom). It is not clear whether these very small objects are depicted in their original positions, or whether they were displaced and redeposited in the process of dissolution of carbonate, and/or by surface tension forces exerted during evaporation in preparation for scanning. The second type of ultrafine needle boring morphology, observed *in situ*, refers to needles that provide connections between larger endolithic traces and the internal substrate surface. *S. acus* is often connected with larger swellings and tubular microboring traces by its pointed end and attached to the substrate surface by a forked end at the opposing terminus. Two sizes were observed, the larger ca. 13 µm long and < 1 µm wide (Fig. 16d, right), and numerous smaller ones, similar in size to the above described "pinheads" (Fig. 16e).

The third type, consisting of ultrafine needles was observed to be attached to relatively large isodiametric depressions with crystalline outlines, described as Trace 23.

Trace 23: *Scolecia stellaris* isp. nov. HOOK, CAMPBELL, RADTKE & GOLUBIC

(Fig. 16f)

1991 'starburst morph' – HOOK, p.137, 171; figs. 5-16b

Holotype image: Fig. 16f.

Etymology: Latin stellaris = star. From the original description of 'starburst' in Hook (1991).

Key feature (diagnosis): These short (<10 µm long) and 0.3–0.5 µm wide filaments are polarly attached to crystal-shaped casts. They appear to be scattered on the interior of the substrate surface.

Scolecia stellaris, in its initial stages, (see small tubes with triangular heads), is similar to the pinhead boring in 16b, d, and is likely a further developmental state. The triangular head widens into a larger angular, crystal-like swelling.

Detailed observations reveal a certain degree of serration outlining even the finest *Scolecia* tubules (e.g., Fig. 16d). This morphology reflects the chemical interaction between the mi-

croborer and mineral substrate, which characterizes *Scolecia* traces that all have serrated outlines (discussed below).

Comment: Vermicular traces with serrated crystal-shaped outlines, described as *Scolecia serrata* RADTKE, 1991 were frequently observed in deep sea samples. We note that whenever *Scolecia* displays a serrated surface, it exhibits three distinct morphotypes: two planar and one three-dimensional. The serrated surface is the key characteristic of this group of traces. Accordingly, the name and description *S. serrata* RADTKE, 1991 is retained and modified for that euendolithic borer, having a three-dimensional display when it penetrates into the interior of the substrate. The traces that differ in relation to the substrate, i.e., that are also integrated into the substrate's surface, represent different behavioural patterns, and are described as a separate ichnospecies: *Scolecia urbimetra* isp. nov.

Trace 24: *Scolecia serrata* RADTKE, 1991

(Figs. 2d(2), 17a, b, c & d (left side))

1991 'vermicular morph' – HOOK, p. 134, 161; fig. 5-11

1991 *Scolecia serrata* isp. nov. – RADTKE, 1991, p. 74. pl. 8, fig. 4

S. serrata was described as a very narrow, tightly wound and intertwined, infrequently branched vermicular boring trace, with a serrate outline (RADTKE, 1991, p. 74. Pl. 8, fig. 4), found in the interior of mollusc (pteropod) shells. The tunnels are 2 to 4 µm in diameter, seen as tightly wound filaments when cast in resin (Figs. 17a, b, c, d left side). The serration stems from etching or the complete removal of crystallites comprising the shell interior, via microbial biocorrosion of the host shell (Fig.17b). These submicron-size etched grooves are replicated in resin as submicron size serrations on the filament.

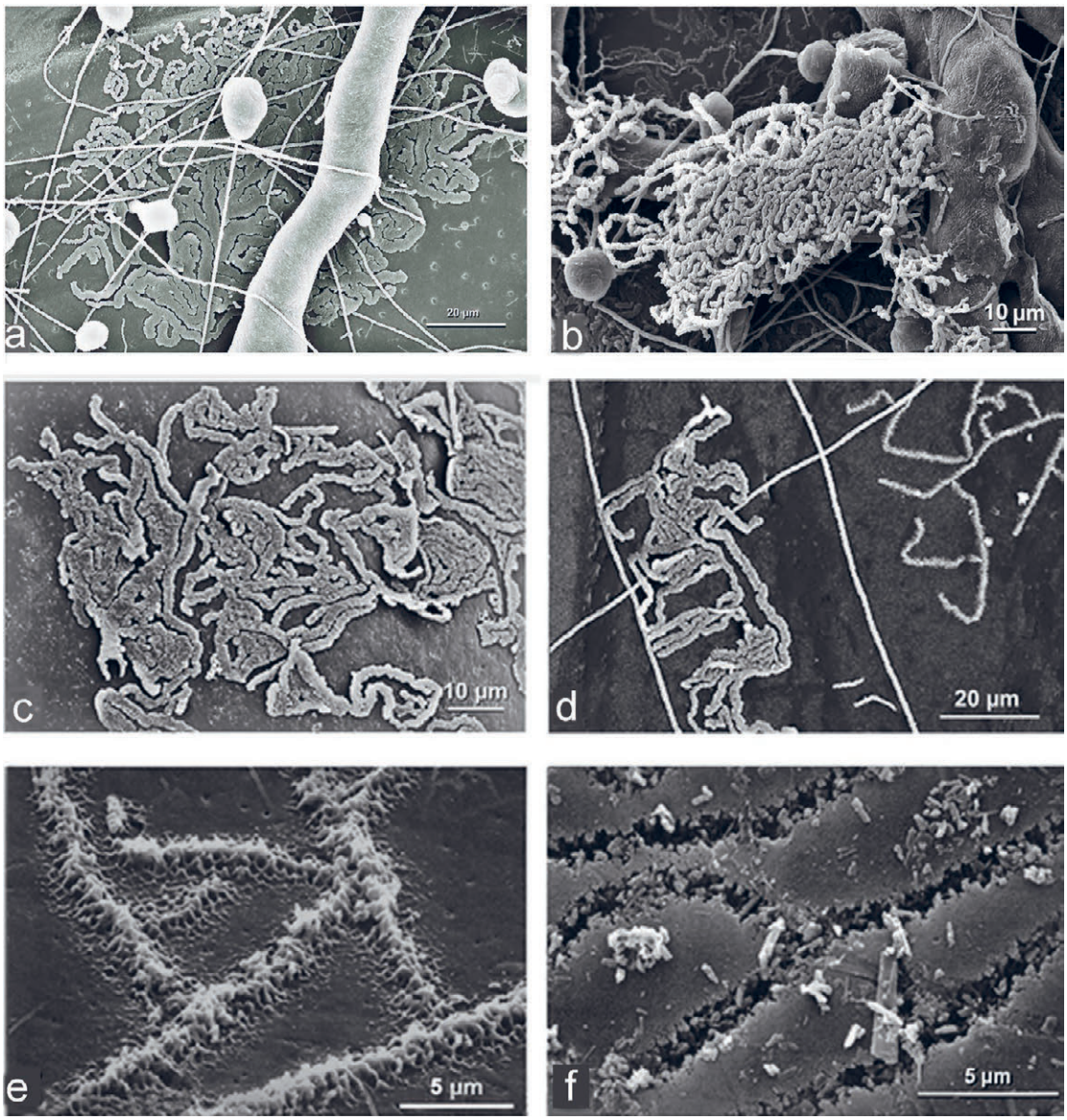

Figure 17. Vermicular traces with serrated surface outlines: *Scolecia serrata* RADTKE, 1991 (a-c, d left), (see also HOOK, 1991, fig. 5-11.) and *S. urbimetra* isp. nov. (d-right, e, f) (see HOOK, 1991, fig. 5-13.). **a.** Very densely packed tunnels of *Scolecia serrata* RADTKE, 1991, located close to the substrate surface overlain by *Orthogonum* and *Saccomorpha*. **b.** A cluster of *Scolecia serrata* with serrated outlines close to the shell surface. It is euendolithic on the margins of the cluster. The centre of the cluster is incorporated in (appears interwoven in) the substrate surface. Also note how flat it is. **c.** The trace *S. serrata,* tightly wound covering the surface of a pteropod shell. **d.** *S. serrata* (left) and *S. urbimetra* isp. nov. (right) on the surface of the same pteropod shell; note the difference in size and spacing. **e.** Detail of the trace *S. urbimetra* shown in d (right). **f.** Direct SEM image of the pteropod shell surface bio-corroded by *S. urbimetra*. The biocorrosion produces trenches outlined by the removal of aragonite crystallites. Figs. e and f are at the same magnification.

Comment: The dimensions above, and in the original description involve "serration", i. e. substrate crystallites removed lateral to a much thinner vermiculate microborer. The minimum width ranges from 0.5 to 1.2 μm, with a maximum width, including serration up to 3.8 μm (See also Radtke and Golubic 2005, Fig. 4D). The 2-dimensional traces, which are integrated in the substrate also appear as surface etching.

Trace 25: *Scolecia urbimetra* isp. nov. HOOK, RADTKE, CAMPBELL & GOLUBIC

(Figs. 2d(3), 17d upper right, e, f)

1991 'city map' morph – HOOK,, p. 136, 165; fig. 5-13

Holotype image: 17d upper right.

Etymology: Latin *urbs* = city, *metro* = measure.

Key feature (diagnosis): *S. urbimetra* morphotype is composed of a shallow, regularly spaced, and branched trace, reminiscent of a city map (Figs. 2d (upper right), 17e, f), which is integrated into the substrate surface. The replicas show a serrated outline of the network of grooves that are more sparsely branching. Direct SEM of the attacked pteropod shell (Fig. 17f) illustrates that the lines created by the trace are, in fact, grooves etched into the carbonate shell, and their serrated appearance reflects the removed aragonite crystallites of the shell. These trenches are quite uniform and narrow 1.08 ± 0.25 μm (n = 123) wide. Branches occur either as alternate or opposing, with no apparent regularity, leaving large unaffected areas of the shell surface between them. The branching angle is variable, monopodial over smaller surface areas and sympodial over larger surface areas. The distances between branch points are extremely variable, ranging from 7 to 150 μm. The tracks often bend or suddenly change direction, rarely remaining straight for any distance (Fig. 17d-right).

Comment: Continuous tracks show avoidance by bending away from each other. When crowded, the filaments usually form a tight, terminal "J" shaped hook. This morphotype is rarely solitary, mostly occurring in groups of several separate networks. Tracks and branches sometimes appear disconnected, showing short, but distinct gaps. This suggests an interruption of boring in which the trace-maker bridged the gap as an epilith, and then continued its trench excavation without abandoning the trace it had started. A similar case of a surface-bound trace has been recently presented by WISSHAK et al. (2018), demonstrating the activity of an epilithic crawler that periodically sent branches into the substrate below. SEM close-up imagery was necessary to document the direction of penetration. The causative agents of *Scolecia* ispp. with serrated outline remain unknown. The consistent distinction in the shape and distribution pattern between *S. serrata* (Fig. 17d left) vs. *S. urbimetra* (Fig. 17e right) suggests strongly that biologically different microorganisms produced these traces. Compare also figures 2d-c and 13d, where *S. urbimetra* creates a unique substrate-bound etch pattern that serves as a backdrop to euendolithic traces. Both *S. sigillum* and *S. urbimetra* are microscopic grooves carved into the shell surface. The pattern observed bears resemblance to that reported for actinobacteria, particularly those involving open loop or hook-type sporulation. Marine actinobacteria have only been demonstrated and studied recently (VALLIAPPAN et al., 2014).

Trace 26: *Scolecia pluma* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Figs. 18a-c)

1991 'bottlebrush' morph - HOOK, p. 137, 167, fig. 5-14

Holotype image: Fig. 18b.

Etymology: Latin *pluma* = feather.

Key feature (diagnosis): *S. pluma* is a trace found slightly below the surface of pteropod shells. HOOK (1991) called it "bottlebrush" (Fig. 18b) owing to the rod-like central filament with perpendicular extensions. The study of the development of this trace showed that it starts as a tunnel (a resin-cast filament), less than 1 μm in diameter, which conforms to the criteria identifying it as a member of the group of *Scolecia* traces (Fig. 18b). The later development observed along the *Scolecia* tunnel is seen in resin replication as flat foil-like lateral extensions, which under light microscope appear fuzzy and golden in colour resembling feathers, which suggests the name *S. pluma*. The main axes curve horizontally, are on average 70–80 μm long and surrounded by numerous extremely fine "downy" extensions (ca 0.1–0.2 μm wide, up to 10 μm long) departing at right-angles from it, as well as penetrating deeper into the substrate (Fig. 18c). The main axis forms a submicron sized tunnel that determines the progression of the trace.

Comment: In the cast preparations, the lateral processes appear flat, probably consisting of thin, tapering resin-foils replicating the intercrystal spaces, widened by lateral carbonate dissolution. This morph has not been previously reported, and the biological affiliation of the causative agent remains unknown.

4.4. Etching patterns on deep sea carbonate surfaces

Carbonate substrates are known as firm settling grounds for many sessile and mobile benthic organisms. Attachment and anchoring may affect the substrate and leave a trace of such attachments. This habit has been identified in the classification of traces under the group name *Podichnia* (MILLER III, 2007a). We encountered several forms of shallow etched areas marking the shell surfaces that are likely generated by different and unrelated mechanisms. These traces are probably left by the anchoring components of epilithic organisms but may also have other origins. These patterns are conspicuous, so we were obliged to describe them as a new ichnogenus;

Vestigichnus igen. nov. with the type ichnospecies *V. discus* isp. nov. which consists of slightly depressed areas on the substrate surface with exposed crystalline patterns of the shell mineralogy. They can be distinguished as disk-shaped and ring depressions in the substrate surface. Such traces are characteristic. They are described as Trace 27.

Trace 27: *Vestigichnus discus* isp. nov. RADTKE, HOOK, CAMPBELL & GOLUBIC

(Figs. 18d, e, g, h, i)

1991 'plaque pit' HOOK, p. 137; fig. 5-15

Holotype image: Fig. 18d.

Etymology: Latin *Vestigium* = remain, Latin *discus* = disk shaped.

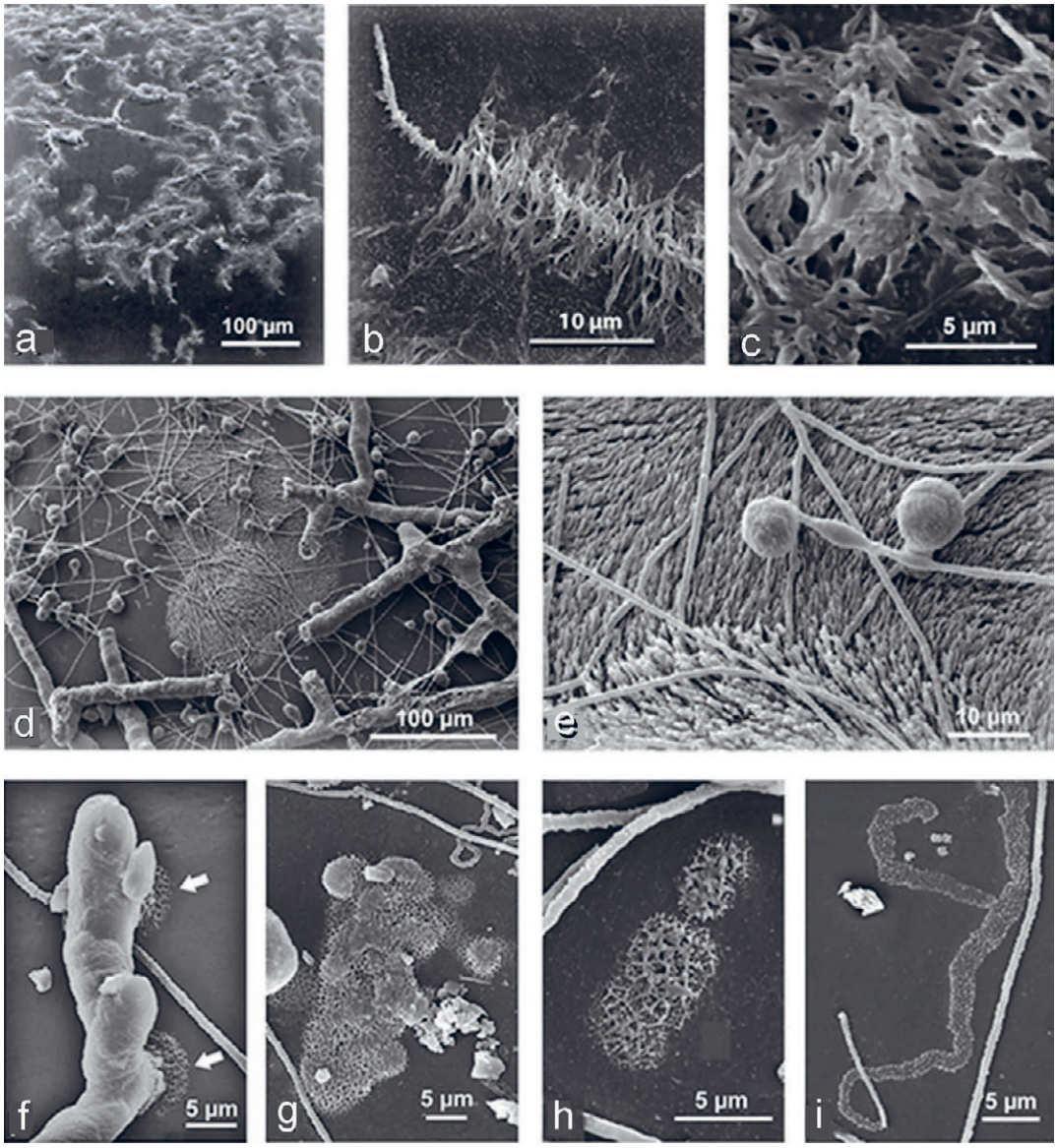

Figure 18. Etches. Etching patterns observed on the resin-replicated internal surfaces of pteropod shells are made by *Scolecia pluma* isp. nov. (a-c) (see HOOK, 1991, fig. 5-14.) *Vestigichnus discus* igen. nov. et isp. nov. (d, e, g, h, i) and *V. annulus* isp. nov (f) (arrows). **a.** *Scolecia pluma* isp. nov., a delicate feather-like euendolithic trace replicated by resin, consists of a widespread winding system of shallow traces, distributed beneath the substrate surface; composed of a filament, surrounded, and covered by foliose side branches perpendicular to the filament. **b.** Detail of a: showing the *Scolecia* filament bordered by a two-dimensional submicron diameter downy extensions. Holotype. **c.** Detail of b: view of resin-cast feathery extensions. **d.** *Vestigichnus discus* isp. nov., shown as two superimposed, slightly depressed etch-fields (centre) possibly caused by attachments of epilithic organisms (HOOK, 1991, fig. 5-16a.). A surface biocorrosion marker forming a background to deeper borings of *Orthogonum tubulare* RADTKE, 1991. **e.** Detail of d: mineral patterns by overlapping *Vestigichnus* etch fields behind hyphal tunnels and sporangial swellings of *Saccomorpha simplex* isp. nov. and *Orthogonum fusiferum* RADTKE, 1991. **f.** Resin replica of an *Orthogonum tubulare* boring with ring-shaped etch-fields (arrows; holotype) of *Vestigichnus annulus* isp. nov. around the contacts of the tubular boring with the substrate surface. **g.** Several superimposed circular etchmarks. **h.** Linear arrangement of overlapping circular etchmarks, suggesting directional displacement of an epilithic causative agent. **i.** A thin euendolithic tunnel leaving a long trail of its surface travel in the form of an elongated etching field that widens.

Key feature (diagnosis): *V. discus* or "plaque morph" (Fig. 18d, centre) consists of shallow circular lens-like depressions, up to 100 µm in diameter but only a few micrometres deep. Two superimposed well-expressed and preserved circular plaque traces with sharp etch marks expressed are illustrated in an SEM image that includes views of the resin-cast surface replicas of a pteropod shell (e.g. 18d, centre), and finer detail (Fig. 18e). The detail shows that the etch patterns conform to the mineral organization of the shell with exposed outlines of the crystal boundaries of the shell substrate.

Comment: The surface etchings in Fig. 18d form a backdrop over which deeper boring traces are superimposed, in this case *Orthogonum tubulare* RADTKE, 1991 as well as several colonies of the complex trace of *Saccomorpha* ispp., with hyphal tunnels and sporangial swellings. The detail in Fig. 18e shows two such traces and a spindle shaped swelling between two rounded sporangia of *Orthogonum fusiferum* RADTKE, 1991 (p. 66-67, pl. 6, figs. 5, 6), a trace attributed to the fungus *Ostracoblabe implexa* (BORNET & FLAHAULT, 1889; ECKBLAD & KRISTIANSEN, 1990). Comparison can also be made with other studies of endolithic fungi (MAO CHE et al.

1996, fig.6). A series of *Vestigichnus annulus* units with overlapping margins (Fig. 18g) can be understood as a time-series of epilithic settlers. A similar time-series of *Vestigichnus* units in a linear arrangement, (Fig. 18h), suggests directional movement of such a causative entity. Furthermore, a trace connected to fine tubular microborings, (Fig. 18i), documents convincingly such etch-related dynamics. It could possibly reflect epilithic growth or even "crawling" that was faster than the circular expansion of the etch-field where it overlaps with penetration of a *Scolecia*–type tunnel entering the shell's interior.

Trace 28: *Vestigichnus annulus* isp. nov. RADTKE, HOOK, GOLUBIC & CAMPBELL

(Fig. 18f – arrows)

1991 'ring pit' – HOOK, p. 137; Figs. 5-16b, d

Holotype image Fig. 18f – arrows.

Etymology: Latin *annulum* = ring.

Key feature (diagnosis): *V. annulus* or the ring-shaped morphs up to 150 µm diameter, are similar to *V. discus* plaque morphs and can be smaller or larger than the typical disk-shaped etch-fields. They consist of a depressed ring with a central area that remains elevated (not shown), or which is occupied by a different structure, e.g. a sporangial neck or similar contact of traces to the substrate surface (Fig. 4b). *Vestigichnus*-type etch fields have been observed associated with euendoliths contacting or exiting the substrate. The selected example shows a well-developed tubular euendolith *Orthogonum tubulare* RADTKE, 1991, that penetrated the substrate, parallel to its surface and generated two connections that exited the substrate, both surrounded by a halo of *V. annularis* etchings (Fig. 4b; 18f, arrows). The etching seems to have occurred over time.

Comment: Large ring pits (up to half a millimeter in diameter, not illustrated) need more research. They may represent damage left from a holdfast attachment of a stalked animal, or of a foraminifer. We were able to demonstrate similar circular depressions formed on the shell surface following the microbial destruction of periostracum (HOOK & GOLUBIC, 1993, fig. 1b). The circular depressions extend deep enough to loosen the intercrystal matter of the shell and are sufficiently extensive to be recognized as a widespread removal of carbonate. Much larger traces named *Neodendrina*, which are possibly caused by foraminifera or by attachment of algae (WISSHAK & NEUMANN, 2018, figs. 3f–i), were not observed in our collection. A much smaller, somewhat elongated ring trace has been recently identified as the attachment trace of a sessile diatom (WISSHAK et al., 2014a).

4.5. Summary of ichnotaxonomic evaluations

Some previously established ichnotaxa addressed in this study needed to be modified as required by the nomenclature and classification systems of traces – to maintain the trace identity as the expression of the behaviour of an unknown potential trace-maker. Certain excessively narrow constraints introduced in the original description of ichnogenera were modified to accommodate newly discovered ichnospecies (WISSHAK et al., 2018). A few ichnospecies, too widely conceived in their original descriptions, proved to include more than one behavioural expression, and needed to be subdivided.

Complex-compound euendolithic traces, have been recognized as products of organisms with biological complexity (MILLER III, 2007b). They consisted mostly of interconnected traces produced by vegetative vs. reproductive functions of the same trace-making organism. They have been found within the ichnogenera *Saccomorpha* RADTKE, 1991, *Polyactina* RADTKE, 1991, and *Flagrichnus* WISSHAK & PORTER, 2006.

The complex trace *Saccomorpha clava* RADTKE, 1991 is accepted as in the original description, represented by specimens considered complete with sporangial cavities and a collar around the sporangial neck. Traces that are morphologically distinct from that morphotype were described as a separate new ichnospecies. The most frequent morphologically distinct traces without a collar, are *Saccomorpha collaris* isp. nov., and *S. radiata* isp. nov. and were described as new ichnospecies after consideration of whether these forms could represent undifferentiated developmental stages of one or more microboring organisms.

The following four previously established ichnospecies categorized as complex traces have been observed in the aphotic deep sea: *S. clava* RADTKE, 1991, *S. stereodiktyon* GOLUBIC et al., 2014, *S. guttulata* WISSHAK et al., 2018, and *Polyactina araneola* RADTKE, 1991.

Eight ichnospecies novae are described and added to complex-compound ichnospecies (7 to the ichnogenus *Saccomorpha* RADTKE, 1991): *S. collaris* isp. nov., *S. curvata* isp. nov., *S. polypoda* isp. nov., *S. lobata* isp. nov., *S. radiata* isp. nov, *S. velum* isp. nov., *S. papilio* isp. nov., as well as one new ichnospecies *Flagrichnus polyfloges* isp. nov. described within the ichnogenus *Flagrichnus* WISSHAK & PORTER, 2006.

Tubular and vermicular traces consist of a single biological element, usually conforming with the outline of the trace-maker's body. Among tubular traces, trace diversity within the ichnogenus *Orthogonum* RADTKE, 1991 includes the three established, although variable ichnospecies *Orthogonum tubulare* RADTKE, 1991, *O. lineare* GLAUB, 1994, and *O. spinosum* RADTKE, 1991. We add three new ichnospecies: *O. arbor* isp. nov., *O. tenue* isp. nov., and *O. cellexpressum* isp. nov. Significant distinctions were also observed among simple vermicular i.e., worm-like filamentous traces of the ichnogenus *Scolecia* RADTKE, 1991: *S. serrata* RADTKE, 1991 is shown to include etching as well as boring.

Five new ichnospecies are presented: *S. nodosa* isp. nov., *S. hirudo* isp. nov., *S. acus* isp. nov., *S. urbimetra* isp. nov., and *S. pluma* isp. nov. The vermicular traces with serrated outlines, originally described as *Scolecia serrata* RADTKE, 1991 are now recognized to include euendolithic and/or surface etchings.

We describe one new ichnospecies with serrated outlines that are integrated (etched) into the surface of the substrate: *S. urbimetra*. This drew attention to etching patterns on the substrate surface, which resulted in the description of 1 new ichnogenus: *Vestigichnus* igen. nov. with 2 ichnospecies: *V. discus* isp. nov, and *V. annulus* isp. nov.

Table 1. Morphometrics of the ichnotaxa. The morphometric table is needed because sizes of the features of each taxon can be diagnostic. Having a condensed morphological description can help distinguish similar size ichnotaxa. It serves as an identification key.

Trace No.	Ichno-genus	Ichnospecies	Described by	Figure No.	Holo-type	Short description of trace morphology	Dimensions	
Compound traces								
	Igen. *Saccomorpha*		RADTKE 1991		N/A	Sporangial swellings Interconnected by thin uniform branched tubes	Hyphal tube Ø in μm	Swelling L x W x D in μm
1		*S. clava*	RADTKE 1991	3a – c	3b	Club-shaped swelling with connection neck lacking collar & hyphal connection	1 - 2; 1.5 ± 0.51 (38)	25 x 15 x 10
2		*S. collaris*	isp. nov. RADTKE et al.	1f, 3d – g, 4a	1f	Club-shaped swelling with a collar around the neck connection	1 - 2; 1.27 ± 0.22 (68)	40 x 30 x 30
3		*S. curvata*	isp. nov. HOOK et al.	4b	4b	Flattened and curved club-shaped swelling and neck without collar	1 - 2	25 x 15 x 6
4		*S. polypoda*	isp. nov. HOOK et al.	4c,d	4d	Isodiametric club-shaped swelling with more than one neck	1.5 - 2.2	40 x 30 x 30
5		*S. lobata*	isp. nov. HOOK et al.	4e,f	4e	Widened and flat swelling with lateral lobes, often crowding	1.5 - 2.2	50 x 50 x 35
6		*S. velum*	isp. nov. HOOK et al.	5 a – e	5e	Sail-shaped intercalary and arrow-shaped terminal swellings, no neck	1.0 - 2.5	18 x 10 x 12
7		*S. radiata*	isp. nov. RADTKE et al.	5c	5c	Central spherical swelling with neck and radiating narrow tubes	2.0 ± 0.9 (460)	25 x 20 x 20
8		*S. papilio*	isp. nov. HOOK et al.	6a – f	6c	Flat swelling parallel to substrate surface. Tube distally narrowing	Tapered 5 to < 1	< 100 x 60 x 5
9		*S. guttulata*	WISSHAK et al. 2018	2c,f; 7a – f	N/A	Spindle-shaped swellings interconnected by distally widening tubes	6-7 (4.4 ± 1.0) (100)	21.4 ± 5.5 (131)
10		*S. stereodiktyon*	GOLUBIC et al. 2014	8a – c	N/A	Cylindrical or lobed swellings terminal on trichotomous branched tubes	1.0 - 3.0	15-30; 22.4 ± 5.5 (375)
11	*Polyactina*	*araneola*	RADTKE 1991	8d – g	N/A	Central and cylindrical radiating swellings extended by tapered tubes	N/A	N/A
12	*Flagrichnus*	*polyfloges*	isp. nov. GOLUBIC et al.	9a – c	9b	Swelling appressed to substrate surface with flame-like extensions	2.0 - 3.0	40 x 30 x 40
13	*Entobia*	*micra*	WISSHAK 2008	9d,e	N/A	Thick strands of Cliona-type carbonate-carving rounded units, some open at tip	10 - 20	5 x 5 x 5
Tubular traces						Tubes of different in size and branching perpendicular to parallel to surface		
	Igen. *Orthogonum*		RADTKE 1991					
14	*Orthogonum*	*tubulare*	RADTKE 1991	10a – c; 11a – c	N/A	Tubes uniform in diameter, smooth with rounded tips	12-18 (16.5 ± 1.8) (35)	N/A
15		*O. lineare*	GLAUB 1994 – modified	12a – c	N/A	Tubes of relatively constant diameter, mostly smooth surface and rounded tips	7-12 (9.96 ± 1.7) (59)	N/A
16		*O. spinosum*	RADTKE 1991	12d – f	N/A	Tubes variable in diameter, covered by many spiny extensions.	20 to 70 (33.5 ± 7.6) (69)	N/A
17		*O. arbor*	isp. nov. HOOK et al.	13a – d, 13b	13b	Tubes start simple then branch; branches distally wider	10-12 ; 12-50	N/A
18		*O. tenue*	isp. nov. RADTKE et al.	14a – a	14a-a	Tubes consistently narrower and straighter than other described	5.4-10 (6.9 ± 1.35) (32)	N/A
19		*O. cellexpressum*	isp. nov. GOLUBIC et al.	14a – b,c	14b	Tubes distally widened and flattened with surface bumps	14 to 30 (20.1 ± 3.69) (46)	N/A
Vermicular traces						Tubes thin and winding, rarely branched, often constricted or tapered		
	Igen. *Scolecia*		Radtke 1991					
							prox. dist.	
20		*S. nodosa*	isp. nov. RADTKE et al.	15a – f	15d	Tubes tapered, smooth, with lateral and terminal globules.	1.0 to < 0.1	N/A
21		*S. hirudo*	isp. nov. RADTKE et al.	16a,c,g	16c	Tubes extremely fine. Associated with other borings like parasites	0.5 to < 0.1	N/A
22		*S. acus*	isp. nov. HOOK et al.	16b,d,e	16b,f	Extremely fine tubule with terminal swelling like "pinhead"	0.1-0.2 wide by 3-5 long	N/A
23		*S. stellaris*	isp. nov. HOOK et al.	16f	16f	Extremely fine tubules attached to crystal-shaped spaces (bodies)	0.5 to < 0.1	N/A
24		*S. serrata*	RADTKE 1991	17a,b,c	18b	Tubes tightly wound with serrated margins inside the substrate	1-2 (-4)	N/A
25		*S. urbimetra*	isp. nov. HOOK et al.	17e – right, f, g	17f, g	Surface grooves regularly spaced, thinner; branches at 45 - 90 degrees	1 - 2; 1.08 ± 0.25	N/A
26		*S. pluma*	isp. nov. RADTKE et al.	18a,b,c	18b	Shallow grooves produced by lateral, tapering foils along the substrate surface	10-12, <1	N/A
Surface Etch Marks								
	Igen. *Vestigichnus*							
27		*V. discus*	isp. nov. RADTKE et al.	18d,e,g	18d	Shallow circular depressions with etchmarks of the mineral surface	Var. up to 150	N/A
28		*V. annulus*	isp. nov. RADTKE et al.	18d	18f, arrows	Ring-shaped etchmarks around substrate surface etching of possible epiliths	Var. up to 150	N/A

Traces with serrated outlines form a group that includes transitions between euendolithic microborings in the substrate interior and the etch-marks carved into the external surfaces of carbonate substrates. Such substrate surface integration was also recorded for the peripheral filament network of the complex trace *Saccomorpha papilio* isp, nov. Etch marks are shallow traces in the host's shell surface. Note the rough surface on the cast of *S. papilio* isp in Fig. 6d. When cast in resin, etched regions tend to remain attached to the resin block following carbonate dissolution and are not dislodged during specimen preparation as are the casts of finer tunnels from the substrate interior. The traces described here as *Vestigichnus discus* igen. nov. isp. nov. represent etch marks that were probably produced by epilithic organisms acting on the substrate surface from the outside, although some, such as *V. annulus* isp. nov. was observed also to be associated with euendoliths when the latter contacts the substrate surface from within the substrate.

5. CONCLUSIONS

This study presents a photomicrographically-supported review of light-independent euendolithic trace morphotypes distributed in Holocene and older sediments of the aphotic deep sea zone of modern oceans. A total of seven ichnogenera and twenty-eight ichnospecies were studied. A final list is summarized in the morphometrics table of new and modified ichnotaxa.

The value of microboring traces as palaeo-environmental and palaeo-bathymetric indicators depends on the distinction between the traces of phototrophs and organotrophs, thus on information which concerns their biological affiliations, as well as our knowledge about their depth distribution. Based on trace morphology alone, this distinction is difficult because of the morphological similarities between light-dependent and light-independent microboring organisms, caused by convergent evolution due to their similar endolithic mode of life (GOLUBIC et al., 2016). Both light-dependent and light-independent euendolithic microorganisms evolved adaptations relevant to the structural barriers and constraints posed by the substrate they penetrate. This detailed comprehensive assessment of the deep sea traces, which are all light-independent, was motivated by the need to provide sufficient morphological detail to distinguish them from traces of light-dependent microboring organisms, because only the latter serve in palaeo-bathymetry.

We could establish that the excavations by non-clionid microborers of the interior of the bored substrate may be an order of magnitude greater than the damage observed on the substrate surface. This should be verified in future work given the implications for carbon cycling of this discovery.

In the present contribution, we have briefly addressed the question of energy and carbon sources of deep sea light-independent bioeroders. The observed orientation of euendolithic traces showed that organotrophic microbial euendoliths exploited the organic matter that the host organisms incorporated when constructing their skeletons (PRICE et al.,1976; SONG et al., 2019), including proteins that participate in the organization of carbonate crystallites of the host's shell (ALBECK et al., 1993; MARIN et al., 2005). A few euendolithic taxa might also have been able to exploit organic matter arriving to the benthos via the water column – but boring commenced only after sedimentation onto the benthos.

We distinguished between the true euendolithic habit into the interior of the substrate and shallow etchmarks integrated in the substrate surface, as some produced patterns of extremely fine traces, which by comparison with the works of others and our knowledge of modern taxa, may be caused by foraminiferal, thraustochytrids or actinomycete food-collecting systems. Boring sponges, some microscopic in size (WISSHAK, 2008), consume microorganisms that are in suspension. The organotrophic euendoliths, in various settings and depths (MAO-CHE et al., 1996; GOLUBIC et al., 2005, 2014; WISSHAK, 2008), may be indirectly supported by a wide range of primary producers in the oceans, including phototrophy of the phytoplankton (UCHMAN, 2007), and chemolithotrophy in the abyssal seeps and vents (GOLUBIC et al., 1984b; REYSENBACH & CADY, 2001; GLEASON et al., 2017, 2019).

The present study is limited by reliance on trace morphology in the sand-sized fraction of the deep sea sediment. Hard grounds in the deep sea that have been shown to harbour some unique taxa (SMITH & DEMOUPOLOS, 2003), need to be included in future studies with a greater variety of substrates to be examined along depth profiles. Knowing the biological identity of traces that reflect the maker's complete life cycle, can make distinctions among and interpretations of traces more reliable (CAMPBELL, 1980).

When interpreting traces as ichnotaxa and describing ichnospecies, this work takes the viewpoint that traces are expressions of the behaviour of the organisms that produced them. The nomenclature and classification of traces requires separating the tunnels from the biological identity and classification of trace-making organisms. However, the interpretation of traces requires them to be related to the physiological properties of their biological producers as they behave in modern environments (SEILACHER, 1967). Behaviour is just one of many biological properties of an organism (a member of a biological species), that may change during its growth, development, and physiological state (vegetative vs. reproductive) and produce different traces, documenting instantaneously a permanent change to the substrate it penetrates, leaving holes having sub-micron fidelity that can persist for eons. The microbial boring interactions of trace-makers, their shape and orientation, including features such as anastomosis and avoidance, are indicative of sensing mechanisms that must have a genetic background and control. However, the nature and extent of genetic control of such adaptations remains unknown. The difficulty of finding live deep sea trace-makers in situ and extracting them from the substrate in sufficient quantity to analyze genetically has been a main constraint for the genetic study of all types of endoliths including live ones, in addition to the difficulty of culturing them given their small size and relatively planar presentation. This limitation is only compounded in the oligotrophic deep sea where euendoliths are typically more sparsely settled than in the euphotic zone and no sampling technique of the ultrathin surface layer of newly deposited deep sea sediment is presently

available for the genetic study of deep sea euendoliths that are likely most active there. Our results underline the importance of relating the biological diversity of microboring organisms to the traces they produce using molecular tools that have been available for decades (e.g., WOESE et al., 1990; AMANN et al., 1995) and have improved over time (AVERILL et al., 2021). The results obtained from examination of fossil endoliths from deposits in the deep aphotic zones of the world oceans lead us to conclude that the traces can eventually be related to their makers.

We also predict that it will be possible to identify many ancient fossil endolithic trace assemblages as well as their modern counterparts as demonstrated in CAMPBELL (1980), using careful morphometric analysis that encompasses populations of multiple ichnotaxa as the basis for the assertion that they were deposited in the aphotic depths of ancient seas.

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REFERENCES

ADAM, Z.R., SKIDMORE M.L., MOGK, D.W. & BUTTERFIELD, N.J. (2017): A Laurantian record of the earliest fossil eukaryotes.– Geology, 45/5, 387–390. doi: 10.1130/G38749.1

ALBECK, S., AIZENBERG, J., ADDADI, L. & WEINER, S. (1993): Interaction of various skeletal intracrystalline components with calcite crystals.– Journal of the American Chemical Society, 115, 11691–11697. doi: 10.1021/ja00078a005

AL-THUKAIR, A.A. & GOLUBIC, S. (1991a): Five new *Hyella* species from the Arabian Gulf.– Algological Studies, 64, 167–197.

AL-THUKAIR, A.A. & GOLUBIC, S. (1991b): New endolithic cyanobacteria from the Arabian Gulf. I. *Hyella immanis* sp. nov.– Journal of Phycology 27, 766–780. doi: 10.1111/j.0022-3646.1991.00766.x

AL-THUKAIR, A.A., GOLUBIC, S. & ROSEN, G. (1994): New euendolithic cyanobacteria from the Bahama Bank and the Arabian Gulf: *Hyella racemus* sp. nov.– Journal of Phycology, 30, 764–769. doi: 10.1111/j.0022-3646.1994.00764.x

AMANN, R.I., LUDWIG, W. & SCHLEIFER, K.H. (1995): Phylogenetic identification and in situ detection of individual microbial cells without cultivation.– Microbiological Review 59/1, 143–169. doi: 10.1128/mr.59.1.143-169.1995

AVERILL, C., WERBIN, Z.E., ATHERTON, K.F., BHATNAGAR, J.M. & DIETZE, M.C. (2021): Soil microbiome predictability increases with spatial and taxonomic scale.– Nature Ecology and Evolution, 5, 747–756. doi: https://doi.org/10.1038/s41559-021-01445-9

BACHMANN, E. (1915): Kalkoesende Algen.– Berichte der Deutschen Botanischen Gesellschaft, 33, 45-57.

BATTERS, E.A.L. (1892): On *Conchocelis*, a new genus of perforating algae.– Phycological Memoirs, 1, 25–28.

BATHURST, R.G.C. (1966): Boring algae, micrite envelopes, and lithification of molluscan biosparites.– Journal of Geology, 5, 15–32.

BAUCON, A., BORDY, E., BRUSTUR, T., BUATOIS, L.A., CUNNINGHAM, T., DE, C., DUFFIN, C., FELLETTI, F., GAILLARD, C., HU, B., HU, L., JENSEN, S., KNAUST, D., LOCKLEY, M., LOWE, P., MAYOR, A., MAYORAL, ED., MIKULAS. R., MUTTONI, G., DE CARVALHO, C.N. & ZHANG, W.-T. (2012): A History of Ideas in Ichnology.– In: BROMLEY, D. & KNAUST, D. (eds.): Trace Fossils as Indicators of Sedimentary Environments. Developments in Sedimentology, 64, 3–43. doi: 10.1016/B978-0-444-53813-0.00001-0

BEECH, I.B. & GAYLARDE, C.C. (1999): Recent advances in the study of biocorrosion: an overview.– Revista de Microbiologia, 30/3, 177–190. do: 10.1590/S0001-37141999000300001

BENGTSON, S., SALLSTEDT, T., BELIVANOVA, V. & WHITEHOUSE, M. (2017) Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae.– PLoS Biology, 15/3, e2000735. doi: 10.1371/journal.pbio.2000735

BENTIS, C.J., KAUFMAN, L. & GOLUBIC, S. (2000): Endolithic fungi in reef-building corals (Order: Scleractinia) are common, cosmopolitan, and

potentially pathogenic.– Biological Bulletin, 198, 254–260. doi: 10.2307/1542528

BERTLING, M. (2007): What's in a Name? Nomenclature, Systematics, Ichnotaxonomy.– In: MILLER III, V. (ed.): Trace Fossils. Elsevier, Amsterdam, 81–91. doi: 10.1016/B978-044452949-7/50131-5

BERTLING, M., BRADDY, S.J., BROMLEY, R.G., DEMATHIEU, R., GENISE, J., MIKUÁŠ, J.K., NIELSEN, J.K., NIELSEN, K.S.S, RINDSBERG, K., SCHLIRF, M. & UCHMAN, A. (2006): Names for trace fossils: a uniform approach.– Lethaia, 39, 265–286. doi: 10.18261/let.55.3.3

BERTLING, M., BUATOIS, L., KNAUST, D., LAING, B., MÁNGANO, M.G., MEYER, N., MIKULÁŠ, R., MINTER, N.J., NEUMANN, C., RINDSBERG, A.K., UCHMAN, A. & WISSHAK, M. (2022): Names for trace fossils 2.0: theory and practice in ichnotaxonomy.–Lethaia 55: 1-19. doi: 10.18261/let.55.3.3

BOEKSCHOTEN, G. J. (1966): Shell borings of sessile epibiontic organisms as paleoecological guides (with examples from the Dutch coast).– Palaeogeography, Palaeoclimatology, Palaeoecology, 2, 333–379. doi: 10.1016/0031-0182(66)90023-X

BORNET, E. (1891): Note sur l'*Ostracoblabe implexa* Bornet and Flahault.– Journal de Botanique, 5, 397–400.

BORNET, E. & FLAHAULT, C. (1888): Note sur deux noveaux genres d'algues perforantes.–Journal de Botanique, 2, 161–165.

BORNET, E. & FLAHAULT, C. (1889): Sur quelques plantes vivant dans le test calcaire des mollusques.– Bulletin de la Société botanique de France, 36, 147–179.

BOUDAGHER-FADEL, M.K. & PRICE, G.D. (2010): American Miogypsinidae: An analysis of their phylogeny and biostratigraphy.– Micropaleontology, 56/6, 567-586

BRETT, C.E., BOUCOT, A.J. & JONES, B. (1993): Absolute depths of Silurian benthic assemblages.– Lethaia, 26, 25–40. doi: 10.1111/j.1502-3931.1993.tb01507.x

BRETT, C.E., BAIRD, G.C. & SPEYER, S.E. (1997): Fossil Lagerstätten: stratigraphic record of paleontological and taphonomic events.– In: BRETT, C.E. & BAIRD, G.C. (eds.): Paleontological Events: Stratigraphic Paleontological and Evolutionary Implications. Columbia University Press, New York, 3-40.

BROMLEY, R.G. (1990): Trace fossils: Biology and taphonomy.– Special Topics Paleontology Series. Unwin Hyman, London, 310 p.

BROMLEY, R.G. & NIELSEN, K.S.S. (2015): Bioerosional ichnotaxa and the fossilization barrier.– Annales Societatis Geologorum Poloniae, 85, 4453–4455. doi: 10.14241/asgp.2015.033

BUDD, D.A. & PERKINS, R.D. (1980): Bathymetric zonation and palaeoecological significance of microborings in Puerto Rican shelf and slope sediments.– Journal of Sedimentary Petrology, 50, 881–904. doi: 10.1306/212F7B17-2B24-11D7-8648000102C1865D

BUNDSCHUH, M. (2000): Silurische Mikrobohrspuren. Ihre Beschreibung und Verteilung in verschiedenen Faziesräumen (Schweden, Litauen, Großbritannien und USA).– Unpubl. Ph.D. Thesis, FB Geowissenschaften, J.W.-Goethe-Universität Frankfurt a.M., 129 p.

BUTTERFIELD, N.J. (2015): Early evolution of the eukaryote.– Palaeontology, 58, 5–17. doi: 10.1111/pala.12139

CAMPBELL, S.E. (1980): *Palaeoconchocelis starmachii*, a carbonate boring microfossil from the Upper Silurian of Poland (425 million years old): implications for the evolution of the Bangiaceae (Rhodophyta).– Phycologia, 9/1, 25–36. doi: 10.2216/i0031-8884-19-1-25.1

CAMPBELL, S.E. (1982a): Precambrian endoliths discovered.– Nature, 299, 429–431. doi:10.1038/299429a0

CAMPBELL, S.E. (1982b): The modern distribution and geological history of calcium carbonate boring microorganisms.– In: WESTBROEK, P. & JONG, E.W. (eds.): Biomineralization and Biological Metal Accumulation. D. Reidel Publ. Co., Dordrecht, 99–104. doi: 10.1007/978-94-009-7944-4_8

CAMPBELL, S.E. & COLE, K. (1984): Developmental studies on cultured endolithic Conchocelis (Rhodophyta).– Hydrobiologia, 116, 201–208. doi: 10.1007/BF00027666

CAMPBELL, S.E. & HOFFMAN, E.J. (1979): Endoliths and their microborings: how close is the fit?.– 2nd International Symposium on Fossil Algae. Abstract with Program.

CAMPBELL, S.E., KAZMIERCZAK, J. & GOLUBIC, S. (1979): *Palaeoconchocelis starmachii* n. gen, n. sp., a Silurian endolithic rhodophyte (Bangiaceae).– Acta Palaeontologica Polonica, 25, 405–408.

CAMPBELL, S.E., DROBNE, K. & CIMERMAN, F. (1983): Microborings in foraminiferal tests: an ecological and paleoecological cross-reference.– Rapports et Proces-Verbaux des Reunions Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée Monaco, 28/3, 245–246.

CHAZOTTES, V., LE CAMPION-ALSUMARD, T. & PEYROT-CLAUSADE, M. (1995): Bioerosion rates on coral reefs: interactions between macroborers, microborers, and grazers (Moorea, French Polynesia).– Palaeogeography, Palaeoclimatology, Palaeoecology, 113, 189–198. doi: 10.1016/0031-0182(95)00043-L

CHAZOTTES, V., CABIOCH, G., GOLUBIC, S. & RADTKE, G. (2009): Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia – Implications for palaeodepth reconstructions in Holocene corals.– Palaeogeography, Palaeoclimatology, Palaeoecology, 80, 456–468. doi: 10.1016/j.palaeo.2009.06.033

CLEMENTS, K.D., GERMAN, D.P., PICHE, J., TRIBOLLET, A. & CHOAT, J.H. (2016): Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. The Linnean Society of London.– Biological Journal of the Linnean Society, 120, 729–751. doi: 10.1111/bij.12914

COURADEAU, E., ROUSH, D., SCOTT GUIDA, B. & GARCIA-PICHEL, F. (2017): Diversity and mineral substrate preference in endolithic microbial communities from marine intertidal outcrops (Isla de Mona, Puerto Rico).– Biogeosciences, 14, 311–324. doi: 10.5194/bg-2016-254.

CRIMES, T.P. & HARPER, J.C. (eds.)(1970): Trace Fossils.– Seel House Press, Liverpool, 547 p.

DIELS, L. (1914): Die Algenvegetation der Südtiroler Dolomitriffe.– Berichte der Deutschen botanischen Gesellschaft, 32, 507–531.

ECKBLAD, F-E. & KRISTIANSEN, G. (1990): *Ostracoblabe implexa*, a taxonomic reappraisal.– Mycological Research, 94, 706–708. doi: 10.1016/S0953-7562(09)80673-4

ERCEGOVIĆ, A. (1925): Litofitska vegetacija vapnenaca i dolomita u Hrvatskoj (La vegetation lithophytes sur les calcaires et les Dolomites en Croatie).– Acta Botanica Instituti Botanici Regalis Universitatis Zagrebiensis, 1, 64–114.

ERCEGOVIĆ, A. (1932): Ekološke i sociološke studije o litofitskim cijanoficejama sa jugoslavenske obale Jadrana (Études écologieques et sociologiques des cyanophycées lithophytes de la côte yougoslave del'Adriatique).– Bulletin international de l'Academie Yougoslavie des sciences at des arts, 244, 129–220.

FALKOWSKI, P.G., KATZ, M.E., KNOLL, A.H., QUIGG, A., RAVEN, J.A., SCHOFIELD, O. & TAYLOR, F.J.R. (2004): The Evolution of Modern Eukaryotic Phytoplankton.– Science, 305, 354–360. doi: 10.1126/science.1095964

FÄRBER, C., WISSHAK, M., PYKO, I., BELLOU, N. & FREIWALD, A. (2015): Effects of water depth, seasonal exposure, and substrate orientation on microbial bioerosion in the Ionian Sea (Eastern Mediterranean).– PLoS ONE, 10/4, e0126495. doi: 10.1371/journal.pone.0126495

FINE, M. & LOYA, Y. (2002): Endolithic algae: an alternative source of photoassimilates during coral bleaching.– Proceedings of the Royal Society, London, 269,1205–1210. doi: 10.1098/rspb.2002.1983

FRÉMY, P. (1930): Les Myxophycées de l´Afrique équatoriale francaise.– Archives de Botanique, 2, 1–508.

FRÉMY, P. (1934): Cyanophyceées des cotes d'Europe.– Memoires de la Societe Nationale des Sciences Naturelles et Mathematiques De Cherbourg, 41, 1–234.

FREMY, P. (1945): Contribution à la physiologie des thallophytes marins perforant et cariant, des roches calcaires et des coquilles.– Annales de l'Institut océanographique, 22, 107–144.

FREY, R.W. (1975): The Study of Trace Fossils.– Springer-Verlag, Heidelberg.

FRIEDMANN, E.I. (1971): Light and scanning electron microscopy of the endolithic desert algal habitat.– Phycologia, 10, 411–428.

GARCIA-PICHEL, F., RAMIREZ-REINAT, E. & GAO, Q. (2010): Microbial excavation of solid carbonates powered by P-type ATPase-mediated transcellular Ca^{2+} transport.– Proceedings of the National Academy of Sciences USA, 107, 21749–21754. doi: 10.1073/pnas.1011884108

GARRAFFONI, A. R. S. & FREITAS, A.V.C. (2017): Photos belong in the taxonomic Code.- Science, 355, 6327. doi: 10.1126/science.aam7686

GERDES, G., CLAES, M., DUNAJTSCHIK-PIEWAK, K., RIEGE, H., KRUMBEIN, W. & REINECK, H.-E. (1993): Contribution of microbial mats to sedimentary surface structures.–Facies, 29, 61–74. doi: 10.1007/BF02536918

GLAUB, I. (1994): Mikrobohrspuren in ausgewählten Ablagerungsräumen der europäischen Jura und der Unterkreide (Klassifikation und Palökologie).– Courier Forschungs Institut Senckenberg, 174, 292 p.

GLAUB, I., GOLUBIC, S., GEKTIDIS, M., RADTKE, G. & VOGEL, K. (2007): Microborings and microbial endoliths: Geological Implications.– In: MILLER, W. (ed.): Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam, 368–381. doi: 10.1016/B978-044452949-7/50147-9

GLEASON, F.H., GADD, G.M., PITT, J.I. & LARKUM, A.W.D. (2017): The roles of endolithic fungi in bioerosion and disease in marine ecosystems. I. General concepts. Mycology. 1–11. (Published online). II. Potential facultatively parasitic anamorphic ascomycetes can cause disease in corals and molluscs.– Mycology, 8/3, 216–227. doi: 10.1080/21501203.2017.1352049

GLEASON, F.H., LARKUM, A.W.D., RAVEN, J.A., MANOHAR, C.S. & LILJE, O. (2019): Ecological implications of recently discovered and poorly studied sources of energy for the growth of true fungi especially in extreme environments.– Fungal Ecology, 39, 380–387. doi: 10.1016/j.funeco.2018.12.011

GOLUBIC, S. (1969): Distribution, taxonomy, and boring patterns of marine endolithic algae.–American Zoologist, 9, 747–751.

GOLUBIC, S. (1990): Shell boring microorganisms.– In: BOUCOT, A. (ed.): The Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam, 347–352.

GOLUBIC, S. & KNOLL, A.H. (1993): Fossil prokaryotes.– In: LIPPS, J.H. (ed.): Fossil Prokaryotes and protists. Blackwell, 51–76.

GOLUBIC, S. & SCHNEIDER, J. (2003): Microbial endoliths as internal biofilms.– In: KRUMBEIN, W.E, DORNIEDEN, T. & VOLKMANN, M. (eds.): Fossil and Recent Biofilms. Kluwer Academic Publishers, Dordtrecht, 249–263.

GOLUBIC, S., BRENT, G. & LE CAMPION, T. (1970): Scanning electron microscopy of endolithic algae and fungi using a multipurpose casting-embedding technique.– Lethaia, 3, 203–209.

GOLUBIC, S., PERKINS, R.D. & LUKAS, K.J. (1975): Boring microorganisms and microborings in carbonate substrates.– In: FREY R.W. (ed.): The Study of Trace Fossils. Springer-Verlag, Heidelberg, 229–259.

GOLUBIC, S., FRIEDMANN, I. & SCHNEIDER, J. (1981): The lithobiontic ecological niche, with special reference to microorganisms.– Journal of Sedimentary Petrology, 51, 475–478.

GOLUBIC, S., CAMPBELL, S.E. & SPAETH, C. (1983): Kunsharzausgüsse fossiler Mikroben-Bohrgänge (Resin-casting of fossil microbial borings).– Der Präparator, Bochum, 29, 197–200.

GOLUBIC, S., CAMPBELL, S.E., DROBNE, K., CAMERON, B., BALSAM, W.L., CIMERMAN, F. & DUBOIS, L. (1984a): Microbial endoliths: a benthic overprint in the sedimentary record, and a paleobathymetric cross-reference with foraminifera.– Journal of Paleontology, 58, 351–361.

GOLUBIC, S., HOOK, J.E., SIKES, E. & CURRAY, J. (1984b): Biological communities at the Florida escarpment resemble hydrothermal vent taxa.– Science, 226, 965–967. doi: 10.1126/science.226.4677.965

GOLUBIC, S., RADTKE, G. & LE CAMPION-ALSUMARD, T. (2005): Endolithic fungi in marine ecosystems.– Trends in Microbiology, 13, 229–235. doi: 10.1016/j.tim.2005.03.007

GOLUBIC, S., RADTKE, G. & LE CAMPION-ALSUMARD, T. (2007): Endolithic fungi.– In: GANGULI, B.N. & DESHMUKH, S.K. (eds.): Fungi: Multifaceted Microbes. Anamaya Publishers, New Delhi, 38-48.

GOLUBIC, S., RADTKE, G., CAMPBELL, S.E., LEE S.-J., VOGEL, K. & WISSHAK, M. (2014): The complex fungal microboring trace *Saccomorpha stereodiktyon* isp. nov. reveals growth strategy of its maker.– Ichnos, 21, 100–110. doi: 10.1080/10420940.2014.888301

GOLUBIC, S., PIETRINI, A.M. & RICCI, S. (2015): Euendolithic activity of the cyanobacterium *Chroococcus lithophilus* Erc. in biodeterioration of the Pyramid of Caius Cestius, Rome, Italy.– International Biodeterioration and Biodegradation, 100, 7–16. doi: 10.1016/j.ibiod.2015.01.019

GOLUBIC, S., CAMPBELL, S.E., LEE S-J. & RADTKE, G. (2016): Depth distribution and convergent evolution of microboring organisms.– Paläontologische Zeitschrift, 90/2, 315-326. doi: 10.1007/s12542-016-0308-6

GOLUBIC, S., SCHNEIDER, J., LE CAMPION-ALSUMARD, T., CAMPBELL, S.E., HOOK, J.E. & RADTKE, G. (2019): Approaching microbial bioerosion.– Facies, 65, 1–18. doi: 10.1007/s10347-019-0568-1

GRANGE, J.S., RYBARCZYK, H. & TRIBOLLET, A. (2015): The three steps of the carbonate biogenic dissolution process by microborers in coral reefs (New Caledonia).– Environmental Science Pollution Research, 22,13625–13637. doi:10.1007/s11356-014-4069-z

GREEN, J.W., KNOLL, A.H. & SWETT, K. (1988): Microfossils from oolites and pisolites of the upper Proterozoic Eleonore Bay Group, Central East Greenland.– Journal of Paleontology, 62, 835–852. doi: 10.1017/s0022336000030109

GUIDA, B.S. & GARCIA-PICHEL, F. (2016): Extreme cellular adaptations and cell differentiation required by a cyanobacterium for carbonate excavations.– Proceedings of National Academy of Science USA, 113/2, 5712–5717. doi: 10.1073/pnas.1524687113

HAMILTON, W.A. (2003) Microbially influenced corrosion as a model system for the study of metal microbe interactions: a unifying electron transfer hypothesis.– Biofouling, 19/1, 65–76. doi: 10.1080/0892701021000041078

HASSENRÜCK, C., JANTZEN, C., FÖRSTERRA, G., HÄUSSERMANN, V. & WILLENZ, P. (2013): Rates of apical septal extension of *Desmophyllum dianthus:* effect of association with endolithic photo-autotrophs.– Marine Biology, 160, 2919–2927. doi.: 10.1007/s00227-013-2281

HÖHNK, W. (1969): Űber den pilzlichen Befall kalkiger Hartteile von Meerestieren.– Deutsche Wissenschaftliche Komission für Meeresforschung, Hamburg, 20/2, 129–140.

HOFMANN, K. (1996) Die mikro-endolithischen Spurenfossilien der borealen Oberkreide Nordwest-Europas.– Geologisches Jahrbuch A, 136, 1-153.

HOOK, J.E. (1991): Microborings from the deep Atlantic (Bermuda Pedestal; Blake Plateau) and Gulf of Mexico (Florida Escarpment): Borers and the ecological and diagenetic fate of the microborings.– Unpubl. Ph.D. Thesis. Boston University Graduate School, 207 p.

HOOK, J.E. & GOLUBIC, S. (1988): Mussel periostracum from deep-sea redox communities as a microbial habitat: the scalloping periostracum borer.– Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology, 9, 347–364. doi: 10.1111/j.1439-0485.1988.tb00212.x

HOOK, J.E. & GOLUBIC, S. (1990): Mussel periostracum from deep-sea redox communities as a microbial habitat 2: Pit borers.– Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology, 11, 239–254. doi: 10.1111/j.1439-0485.1990.tb00242.x

HOOK, J.E. & GOLUBIC, S. (1992): Mussel periostracum from deep-sea redox communities as a microbial habitat 3: Secondary inhabitants.– Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology, 13, 119–131. doi: 10.1111/j.1439-0485.1992.tb00344.x

HOOK, J.E. & GOLUBIC, S. (1993): Microbial shell destruction in deep-sea mussels, Florida Escarpment.– Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology, 14, 81–89. doi: 10.1111/j.1439-0485.1993.tb00366.x

HOOK, J.E., GOLUBIC, S. & MILLIMAN, J.D. (1984): Micritic cement in microborings is not necessarily a shallow-water indicator.– Journal of Sedimentary Petrology, 54, 425–431. doi: 10.1306/212F8431-2B24-11D7-8648000102C1865D

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN)(1999): International Code of Zoological Nomenclature.

Fourth edition.– International Trust for Zoological Nomenclature, London, 306 p. doi: 10.5962/bhl.title.50608

JAVAUX, E.J. & KNOLL, A.H. (2016): Micropaleontology of the lower Mesoproterozoic Roper Group, Australia, and implications for early eukaryotic evolution.– Journal of Paleontology, 91/2, 99–229. doi: 10.1017/jpa.2016.124

KAZMIERCZAK, J. & GOLUBIC, S. (1976): Oldest organic remains of boring algae from Polish Upper Silurian.– Nature, 261, 404–406.

KNOLL, A.H., GREEN, J.W., GOLUBIC, S. & SWETT, K. (1986): Peritidal assemblages from the Late Proterozoic Limestone-Dolomite Series, central East Greenland.– Geological Society of America, Annual Meeting 1986, Abstracts and Program, 17, 631.

KNOLL, A.H. & GOLUBIC, S. (1992): Proterozoic and living cyanobacteria.– In: SCHIDLOWSKI M., GOLUBIC, S., KIMBERLEY, M.M, MCKIRDY, D.M & TRUDINGER, P.A. (eds.): Early Organic Evolution, Implications for Mineral and Energy Resources. Springer-Verlag, Berlin, 450–462.

KOBAYASHI, I. & SAMATA, T. (2006): Bivalve shell structure and organic matrix.– Materials Science and Engineering, 26/4, 692–698. doi.: 10.1016/j.msec.2005.09.101

KOHLMEYER, J. (1969): The Role of Marine Fungi in the Penetration of Calcareous Substances.– American Zoologist, 9, 741–746.

KOŁODZIEJ, B., GOLUBIC, S., BUCUR, I.I., RADTKE, G. & TRIBOLLET, A. (2012): Early Cretaceous record of microboring organisms in skeletons of growing corals.– Lethaia, 45, 34–45. doi: 10.1111/j.1502-3931.2011.00291.x

KRAUSE, S., LIEBETRAU, V., NEHRKE, G., DAMM, T., BÜSSE, S., LEIPE, T., VOGTS, A., GORB, S.N. & EISENHAUER, A. (2019): Endolithic algae affect modern coral carbonate morphology and chemistry.– Frontiers of Earth Science, 7, 304. doi: 10.3389/feart.2019.00304

KRUMBEIN, W.E. (2010): Gunflint Chert microbiota revisited – neither stromatolites, nor Cyanobacteria.– In: SECKBACH, J. & OREN, A. (eds.): Microbial Mats. Cellular Origin, Life in Extreme Habitats and Astrobiology, vol 14. Springer, Dordrecht. doi: 10.1007/978-90-481-3799-2_4

KRUMBEIN, W.E., PATERSON, D.M. & ZAVARZIN, G.A. (eds)(2003): Fossil and Recent Biofilms: A Natural History of Life on Earth.– Kluwer Academic Publishers, Dordrecht. doi: 10.1007/978-94-017-0193-8

KÜHL, M. & REVSBECH, N.P. (2001): Biogeochemical sensors for boundary layer studies.– In: BOUDREAU, B.P. & JØRGENSEN, B.B (eds.): The Benthic Boundary Layer, 189–210. doi: 10.1093/oso/9780195118810.003.0008

KÜHL, M., FENCHEL, T. & KAZMIERCZAK, J. (2003): Growth, structure and calcification potential of an artificial cyanobacterial mat.– In: KRUMBEIN, W.E., PATERSON, D.M. & ZAVARZIN, G.A. (eds) (2003): Fossil and Recent Biofilms: A Natural History of Life on Earth,. Kluwer Academic Publishers, Dordrecht 77–102. doi: 10.1007/978-94-017-0193-8_5

LE CAMPION-ALSUMARD, T. (1969): Contribution sur l'étude des cyanophycées lithophytes des étages supralittoral et médiolittoral (Région de Marseille).– Tethys, 1, 119–171.

LE CAMPION-ALSUMARD, T., CAMPBELL, S.E. & GOLUBIC, S. (1982): Endoliths and the depth of the photic zone; discussion.– Journal of Sedimentary Petrology, 52, 1333–1334. doi: 10.1306/212F8134-2B24-11D7-8648000102C1865D

LE CAMPION-ALSUMARD, T., GOLUBIC, S. & HUTCHINGS, P. (1995a): Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia).– Marine Ecology Progress Series, 117, 149–157. doi: 10.3354/meps117149

LE CAMPION-ALSUMARD, T., GOLUBIC, S. & PRIESS, K. (1995b): Fungi in corals: symbiosis or disease? Interaction between polyps and fungi causes pearl-like skeleton biomineralization.– Marine Ecology Progress Series, 117, 137–147. doi: 10.3354/meps117137

LORON, C.C., FRANCOIS, C., RAINBIRD, R.H., TURNER, E.C., BORENSZTAIN, S. & JAVAUX, E.J. (2019a): Early fungi from the Proterozoic era in Arctic Canada.– Nature, 570, 232–235. doi: 10.1038/s41586-019-1217-0

LORON, C.C, RAINBIRD, R.H., TURNER, E.C., WILDER GREENMAN, J. & JAVAUX, E.J. (2019b): Organic-walled microfossils from the late Mesoproterozoic to early Neoproterozoic lower Shaler Supergroup (Arctic Canada): Diversity and biostratigraphic significance.– Precambrian Research, 321, 349–374. doi: 10.1016/j.precamres.2018.12.024

LUKAS, K.J. (1974): Two species of the chlorophyte genus *Ostreobium* from skeleton of Atlantic and Caribbean reef corals.– Journal of Phycology, 10, 331–336. doi: 10.1111/j.1529-8817.1974.tb02722.x

LUKAS, K.J. (1978): Depth distribution and form among common microboring algae from the Florida continental shelf.– Geological Society of America. Annual Meeting 1978, Abstracts and Program, 10, 448.

MAO-CHE, L., LE CAMPION-ALSUMARD, T., BOURY-ESNAULT, N., PAYRI, C., GOLUBIC, S. & BEZAC, C. (1996): Biodegradation of shells of the black pearl oyster *Pinctada margaritifera* var. *cumingii*, by microborers and sponges of French Polynesia.– Marine Biology, 126, 509–519. doi: 10.1007/BF00354633

MARIN, F. & LUQUET, G. (2004): Molluscan shell proteins.– Comptes Rendus Palevol, 3, 469–492. doi : 10.1016/j.crpv.2004.07.009

MARIN, F., AMONS, R., GUICHARD, N., STIGTER, M., HECKER, A., LUQUET, G., LAYROLLE, P., ALCARAZ, G., RIONDET, C. & WESTBROEK, P. (2005): Caspartin and Calprismin, two proteins of the shell calcitic prisme of the Mediterranean fan mussel *Pinna nobilis*.– Journal of Biological Chemistry, 280/40, 33895–33908. doi: 10.1074/jbc.M506526200

MARIN, F., LUQUET, G., MARIE, B. & MEDAKOVIC, D. (2007): Molluscan shell proteins: primary structure, origin, and evolution.– Current Topics in Developmental Biology, 80, 209–276. doi: 10.1016/S0070-2153(07)80006-8

MASSÉ, A, TRIBOLLET, A., MEZIANE, T., BOURGUET-KONDRACKI, M.L., YÉPRÉMIAN, C., SÈVE, C., THINEY, N., LONGEON, A., COUTÉ, A. & DOMART-COULON, I. (2020): Functional diversity of microboring *Ostreobium* algae isolated from corals.– Environmental Microbiology, 22/1, 4825–4846. doi.: 10.1111/1462-2920.15256

MAY, J.A. & PERKINS, R.D. (1979): Endolithic infestation of carbonate substrates below the sediment-water interface.– Journal of Sedimentary Petrology, 49, 357–378. doi: 10.1306/212F7748-2B24-11D7-8648000102C1865D

MEYER, N., WISSHAK, M. & FREIWALD, A. (2020): Ichnodiversity and bathymetric range of microbioerosion traces in polar barnacles of Svalbard.– Polar Research, 39. doi: 10.33265/polar.v39.3766

MILLER III, W. (2007a): Complex Trace Fossils.– In: MILLER III, W. (ed.): Trace Fossils: Concepts, Problems, Prospects,. Elsevier, Amsterdam 458–465. doi: 10.1016/B978-044452949-7/50153-4

MILLER III, W. (ed.)(2007b): Trace Fossils: Concepts, Problems, Prospects.– Elsevier, Amsterdam, 632 p.

MIURA, A. (1961): A new species of *Porphyra* and its *Conchocelis*-phase in nature.– Journal of the Tokyo University Fisheries, 47, 305–311.

MURRAY, J.W. (1973): Distribution and Ecology of Living Benthic Foraminiferids.– Heinemann, London,. 274 p.

MURRAY, J.W. (1991): Ecology and Palaeoecology of Benthic Foraminifera.– Logman Scientific & Technical, London, 408 p.

NADSON, G.A. (1900): Die perforierenden (kalkbohrenden) Algen und ihre Bedeutung in der Natur.– Scripta Botanica Horti Universitatis Petropolis,18, 1–40.

NADSON, G.A. (1927): Les algues perforantes de la Mer Noire.– Comptes rendus l'Académie des Science, 184, 896.

NEUMANN, C. (1966): Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*.– Limnology and Oceanography, 11, 92–108.

PALINSKA, K.A., ABED, R.M.M., VOGT, J.C., RADTKE, G. & GOLUBIC, S. (2017): Microbial endoliths Adriatic limestone coast: Morphological vs. molecular diversity.– Geomicrobiology, 34, 903–915. doi: 10.1080/01490451.2017.1297512

PAULL, C.K., HECKER, B., COMMEAU, R., FREEMAN-LYNDE, R.P., NEUMANN, C., CORSO,W.P., GOLUBIC, S., HOOK, J.E., SIKES, E. & CURRAY, J. (1984): Biological communities at the Florida escarpment

resemble hydrothermal vent taxa.– Science, 226, 965–967. doi: 10.1126/science.226.4677.965.

PERNICE, M., RAINA, J-B., RÄDECKER, N., CÁRDENAS, A., POGOREUTZ, C. & VOOLSTRA, C.R. (2020): Down to the bone: the role of overlooked endolithic microbiomes in reef coral health.– International society for microbial ecology journal, 14/2, 325–334. doi: 10.1038/s41396-019-0548-z

PICA, D., TRIBOLLET, A., GOLUBIC, S., BO, M., GIOIA DI CAMILLO, C., BAVESTRELLO, G. & PUCE, S. (2016): Microboring organisms in living stylasterid corals (Cnidaria, Hydrozoa).– Marine Biology Research, 12/6, 573–582. doi: 10.1080/17451000.2016.1169298

PLOTNICK, R.E. (2012): Behavioral biology of trace fossils.– Paleobiology, 38/3, 459–473. doi: 10.1666/11008.1

PORTER, C.L. & ZEBROWSKI, G. (1937): Lime-loving molds from Australian sands.– Mycologia, 29, 252–257.

POULICEK, M. & JASPAR VERSALI, M.F. (1984): Biodegradation de la trame organique des coquilles de mollusques en milieu marin: action des microorganismes endoliths.– Société Royale des Sciences de Liège, Bulletin, 53, 114–126.

PRICE, T.J., THAYER, G.W., LACROIX, M.W. & MONTGOMERY, G.P. (1976): The organic content of shells and soft tissues of selected estuarine gastropods and pelecypods.– Proceedings of National Shellfish Association, 65, 26–31.

PRIESS, K., LE CAMPION-ALSUMARD, T., GOLUBIC, S., GADEL, F. & TOMASSIN, B.A. (2000): Fungi in corals: black bands and density-banding of *Porites lutea* and *P. lobata* skeleton.– Marine Biology, 136, 19–27. doi: 10.1007/s002270050003

RADTKE, G. (1991): Die mikroendolitischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung.– Courier Forschungsinstitut Senckenberg, 138, 1–185.

RADTKE, G. (1992): Microendolithic trace fossils of Paris basin as facies indicators.– Proceeding 7th International Coral Reef Symposium, 1, 419–426.

RADTKE, G. (1993): The distribution of microborings in molluscan shells from Recent reef environments at Lee Stocking Island, Bahamas.– Facies, 29, 81–92. doi: 10.1007/BF02536921

RADTKE, G. & GOLUBIC, S. (2005): Microborings in mollusk shells, Bay of Safaga, Egypt: Morphometry and ichnology.– Facies, 51, 118–134. doi: 10.1007/s10347-005-0016-02

RADTKE, G. & GOLUBIC, S. (2011): Microbial euendolithic assemblages and microborings in intertidal and shallow marine habitats: insights in cyanobacterial speciation.– In: REITNER, J., QUERIC, W. & ARP, G. (eds.): Advances in Stromatolite Geobiology – Lecture Notes in Earth Sciences, 131, 213–244. Springer, Berlin. doi: 10.1007/978-3- 642-10415-2_16

RADTKE, G., LE CAMPION-ALSUMARD, T. & GOLUBIC, S. (1996): Microbial assemblages of the bioerosional "notch" along tropical limestone coasts.– Algological Studies, 83, 469–482. doi: 10.1127/algol_stud/83/1996/469

RADTKE, G., HOFMANN, K. & GOLUBIC, S. (1997): A bibliographic overview of micro- and macroscopic bioerosion.– Courier Forschungsinstitut Senckenberg, 201, 307–340

RADTKE, G., GLAUB, I., VOGEL, K. & GOLUBIC, S. (2010): A new dichotomous microboring: *Abeliella bellafurca* isp. nov., distribution, variability and biological origin.– Ichnos, 17, 25–33. doi: 10.1080/10420940903358628

RADTKE, G., SCHÄFER, P., BLASCHKE, H. & GOLUBIC, S. (2011): Microborings from shallow marine habitats on both sides of the Panama Isthmus.– Annale des Naturhistorischen Museums, Wien, Series A, 113, 245–265. https://www.semanticscholar.org/paper/Microborings

RADTKE, G., CAMPBELL, S.E. & GOLUBIC, S. (2016): *Conchocelichnus seilacheri* igen. and isp. nov., a complex microboring trace of Bangialean rhodophytes.– Ichnos, 23/3–4, 228–236. doi.: 10.1080/10420940.2016.1199428

REID, R.P., FOSTER, J.S., RADTKE, G. & GOLUBIC, S. (2011): Modern marinestromatolites of Little Darby Island, Exuma Archipelago, Bahamas: Environmental setting, accretion mechanisms and role of euendoliths. In: REITNER, J., QUERIC, W. & ARP, G. (eds.): Advances in Stromatolite Geobiology – Lecture Notes in Earth Sciences, 131, 77-89. Springer, Berlin. doi: 10.1007/978-3-642-10415-2_4

REYSENBACH, A-L. & CADY, S.L. (2001): Microbiology of ancient and modern hydrothermal systems.– Trends in Microbiology, 9, 79–86. doi: 10.1016/s0966-842x(00)01921-1

RIOULT, M. & DANGEARD, L. (1967): Importance des cryptogames perforantes marines en geologie.– Le Botaniste, 50, 389–413.

ROUSH, L. & GARCIA-PICHEL, F. (2020): Succession and colonization dynamics of endolithic phototrophs within intertidal carbonates.–Microorganisms, 2020, 8/2, 214. doi: 10.3390/microorganisms8020214

SAMATA, T., HAYASHI, N., KONO, M., HASEGAWA, K., HORITA, C. & AKERA, S. (1999): A new matrix protein family related to the nacreous layer formation of *Pinctada fucata*.–Federation of European Biochemical Society Letters, 462, 225–229. doi: 10.1016/s0014-5793(99)01387-3

SANCHEZ-BARACALDO, P., RAVEN, J., PISANI, D. & KNOLL, A. (2017): Early photosynthetic eukaryotes inhabited low salinity habitats.– Proceedings of the National Academy of Sciences USA, 114, E7737-E7745. doi: 10.1073/pnas.1620089114

SARASHINA, I. & ENDO, K. (2001): The complete primary structure of Molluscan Shell Protein 1 (MSP-1), an acidic glycoprotein in the shell matrix of the scallop *Patinopecten yessoensis*.– Marine Biotechnology, 3, 362–369. doi: 10.1007/s10126-001-0013-6

SCHAUER, R., BIENHOLD, C., RAMETTE, A. & HARDER, J. (2010): Bacterial diversity and biogeography in deep-sea surface sediments of the South Atlantic Ocean.– The International Society for Microbial Ecology Journal, 4, 159–170. doi: 10.1038/ismej.2009.106

SCHMIDT, M. (1990): Mikrobohrspuren in Fossilien der triassischen Hallstätter Kalke und ihre bathymetrische Bedeutung.– Facies, 23, 109–119. doi: 10.1007/BF02536709

SCHNEIDER J. (1976): Biological and inorganic factors in the destruction of limestone coasts.– Contributions to Sedimentology, 6, 1–112.

SCHNEIDER, J. & LE CAMPION-ALSUMARD, T. (1999): Construction and destruction of carbonates by marine and freshwater cyanobacteria.– European Journal of Phycology, 34, 417–426. doi: 10.1080/09670269910001736472

SCHNEIDER, J. & TORUNSKI, H. (1983): Biokarst on limestone coasts, morphogenesis and sediment production.– Marine Ecology, 4, 45–63.

SCHÖNBERG, C.H.L. (2008): A history of sponge erosion: from past myths and hypotheses to recent approaches.– In: WISSHAK, M. & TAPANILA, L. (eds.): Current Developments in Bioerosion, 165–202. Springer-Verlag, New York. doi: 10.1007/978-3-540-77598-0_9

SCHÖNBERG, C.L, GLEASON, F.H., MEYER, N. & WISSHAK, M. (2019): Close encounters in the substrate: when macroborers meet microborers.– Facies 65,25. doi: 10.1007/s10347-019-0567-2

SCHOPF, J.W. & KLEIN C. (eds.)(1992): The Proterozoic Biosphere: A Multidisciplinary study.– Cambridge University Press, 1374 p. doi: 10.1017/CBO9780511601064

SEILACHER, A. (1967): Fossil behavior.– Scientific American, 217, 72–80.

SEILACHER, A. (2007): Trace Fossil Analysis.– Springer-Verlag, New York, 226 p.

SMITH, C.R. & DEMOUPOLOS, A.W.J. (2003): Ecology of the Pacific Ocean floor.– In: TYLER, P.A. (ed.): Ecosystems of the World, 179–218. Elsevier, Amsterdam.

SONG, X., LIU, Z., WANG, L. & & SONG L. (2019): Recent advances of shell matrix proteins and cellular orchestration in marine Molluscan shell Biomineralization.– Frontiers in Marine Science, 10. https://doi.org/10.3389/fmars.2019.00041

SPERO, H.J. (1988): Ultrastructural examination of chamber morphogenesis and biomineralization in the planktonic foraminifer *Orbulina universa*.– Marine Biology, 99, 9–20. doi: 10.1007/BF00644972

SWINCHATT, J.P. (1969): Algal boring: A possible depth indicator in carbonate rocks and sediments.– Geological Society of America, Bulletin, 80, 1391–1396.

TRIBOLLET, A. (2008a): Dissolution of dead corals by euendolithic microorganisms across the northern Great Barrier Reef (Australia).– Microbial Ecology, 55/4, 569–580. doi: 10.1007/s00248-007-9302-6

TRIBOLLET, A. (2008b): The boring microflora in modern coral reef ecosystems: a review of its roles.– In: WISSHAK, M. & TAPANILA, L. (eds.): Current Developments in Bioerosion. Springer-Verlag, New York, 67–94. doi: 10.1007/978-3-540-77598-0_4

TRIBOLLET, A. & GOLUBIC, S. (2005): Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia.– Coral Reefs, 24, 422–434. doi: 10.1007/s00338-005-0003-7

TRIBOLLET, A., GOLUBIC, S., RADTKE, G. & REITNER, J. (2011a): On microbiocorrosion.– In: REITNER, J., QUERIC, W. & ARP, G. (eds.): Advances in Stromatolite Geobiology – Lecture Notes in Earth Sciences, 131, 265-276. Springer, Berlin.

TRIBOLLET, A., RADTKE, G. & GOLUBIC, S. (2011b): Bioerosion.– In: REITNER, J. & THIEL, V. (eds.): Encyclopedia of Geobiology. Lecture Notes in Earth Sciences Series, 117–134. Springer-Verlag, New York. doi: 10.1007/978-1-4020-9212-1_25

TRIBOLLET, A., CHAUVIN, A. & CUET, P. (2019): Carbonate dissolution by reef microbial borers: a biogeochemical process producing alkalinity under different pCO_2 conditions.– Facies, 65, 9. doi: 10.1007/s10347-018-0548-x

TSENG, C.K. & CHANG, T.J. (1955): Studies on Porphyra III, sexual reproduction of Porphyra.– Acta Botanica Sinica, 4, 153–166.

UCHMAN, A. (2007): Deep-sea ichnology: Development of major concepts.– In: MILLER III, W. (ed.): Trace Fossils: Concepts, Problems, Prospects. Elsevier, Amsterdam, 248-267. doi: 10.1080/09853111.2015.1065306

VALLIAPPAN, K., SUN, W. & LI., Z. (2014): Marine actinobacteria associated with marine organisms and their potentials in producing pharmaceutical natural products.– Applied Microbiology and Biotechnoogy, 98, 7365–7377. doi: 10.1007/s00253-014-5954-6

VALLON, L.H., RINDSBERG, A.K. & BROMLEY, R.G. (2016): An updated classification of animal behavior preserved in substrates.– Geodinamica Acta, 28, 5–20. doi: 10.1080/09853111.2015.1065306

VOGEL, K. & BRETT, C.E. (2009): Record of microendoliths in different facies of the Upper Ordovician in the Cincinnati Arch region USA: The early history of light-related microendolithic zonation.– Palaeogeography, Palaeoclimatology, Palaeoecology, 281, 1–24. doi: 10.1016/j.palaeo.2009.06.032

VOGEL, K., GOLUBIC, S. & BRETT, C.E. (1987): Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, USA.– Lethaia, 20, 263–290. doi: 10.1111/j.1502-3931.1987.tb02047.x

VOGEL, K., GEKTIDIS, M., GOLUBIC, S., KIENE, W.E. & RADTKE, G. (2000): Experimental studies on microbial bioerosion at Lee Stoking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions.– Lethaia, 33, 190–204. doi: 10.1080/00241160025100053

WALKER, M., JOHNSEN, S., RASMUSSEN, S.O., POPP, T., STEFFENSEN, J.-P., GIBBARD, P., HOEK, W., LOWE, J., ANDREWS, J., BJÖRK, S., CWYNAR, L.C., HUGHEN, K., KERSHAW, P., KROMER, B., LITT, T., LOWE, D.J., NAKAGAWA, T., NEWNHAM, R. & SCHWANDER, J. (2009): Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records.- Journal of Quaternary Science 24, 3–17. https://doi.org/10.1002/jqs.1227

WIERZCHOS, J., CASERO, M.C., ARTIEDA, O. & ASCASO, C. (2018): Endolithic microbial habitats as refuges for life in polyextreme environment of the Atakama Desert.– Current Opinion in Microbiology, 43, 124–139. doi: 10.1016/j.mib.2018.01.003

WISSHAK, M. (2006): High-latitude bioerosion: The Kosterfjord Experiment.– Lecture Notes in Earth Sciences, 109, 1–202. Springer, Heidelberg. doi: 10.1007/978-3-540-36849-6.

WISSHAK, M. (2008): Two new dwarf *Entobia* ichnospecies in a diverse aphotic ichnocoenosis (Pleistocene / Rhodes, Greece).– In: WISSHAK, M. & TAPANILA, L. (eds.): Current Developments in Bioerosion. Springer-Verlag, Heidelberg, 213–233. doi: 10.1007/978-3-540-77598-0_11

WISSHAK, M. (2012): Microbioerosion. In: BROMLEY, D. & KNAUST, D. (eds.): Trace Fossils as Indicators of Sedimentary Environments,. Developments in Sedimentology, 64, 213–243. Elsevier, Amsterdam. doi: 10.1016/B978-0-444-53813-0.00008-3

WISSHAK, M. (2019): Taming an ichnotaxonomical Pandora's box: revision dendritic and rosette microborings (ichnofamily: Dendrinidae).– European Journal of Taxonomy, 390, 1–99. doi: 10.5852/ejt.2017.390

WISSHAK, M. & NEUMANN, C. (2018): Large dendrinids meet giant clam: the bioerosion trace fossil *Neodendrina carnelia* igen. et isp. n. in a *Tridacna* shell from Pleistocene-Holocene coral reef deposits, Red Sea, Egypt.– Fossil Record, 21, 1–9. doi: 10.5194/fr-21-1-2018

WISSHAK, M. & PORTER, D. (2006): The new ichnogenus *Flagrichnus* – A paleoenvironmental indicator for cold-water settings?.– Ichnos, 13/3, 135–145. doi: 10.1080/10420940600851255

WISSHAK, M. & RÜGGEBERG, A. (2006): Colonisation and bioerosion of experimental substrates by benthic foraminiferans from euphotic to aphotic depths (Kosterfjord, SW Sweden).– Facies, 52, 1–17. doi: 10.1007/s10347-005-0033-1

WISSHAK, M. & TAPANILA, L. (eds.)(2008): Current Developments in Bioerosion.– Springer-Verlag, Berlin, 516 p. doi: 10.1007/978-3-540-77598-0_11

WISSHAK, M., GEKTIDIS, M., FREIWALD, A. & LUNDÄLV, T. (2005): Bioerosion along a Bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study.– Facies, 51, 93–117. doi: 10.1007/s10347-005-0009-1

WISSHAK, M., TRIBOLLET, A., GOLUBIC, S., JAKOBSEN, J. & FREIWALD, A. (2011): Temperate bioerosion: Ichnodiversity and biodiversity from intertidal to bathyal depths (Azores).– Geobiology, 9, 492–520. doi: 10.1111/j.1472-4669.2011.00299.x

WISSHAK, M., ALEXANDRAKIS, E. & HOPPENRATH, M. (2014a): The diatom attachment scar *Ophthalmichnus lyolithon* igen. et isp. n.– Ichnos, 21, 111–118. doi: 10.1080/10420940.2014.907572

WISSHAK, M., SCHÖNBERG, C.H.L., FORM, A. & FREIWALD, A. (2014b): Sponge bioerosion accelerated by ocean acidification across species and latitudes?.– Helgoland Marine Research, 68, 253–262. doi: 10.1007/s10152-014-0385-4

WISSHAK, M., MEYER, N., RADTKE, G. & GOLUBIC, S. (2018): *Saccomorpha guttulata,* a new marine fungal microbioerosion trace fossil from cool- to cold-water settings.–Paläontologische Zeitschrift, 92, 3, 525–533. doi: 10.1007/s12542-018-0407-7

WISSHAK, M., KNAUST, D. & BERTLING, M. (2019): Bioerosion ichnotaxa: review and annotated list.– Facies, 65, 24. doi: 10.1007/s10347-019-0561-8

WOESE, C.R., KANDLER, O. & WHEELIS, M.L. (1990): Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eucarya.– Proceedings of National Academy of Sciences USA, 87, 4576–4579. doi: 10.1073/pnas.87.12.4576

ZEBROWSKI, G. (1936): New genera of Cladochytriaceae.– Annals of the Missouri Botanical Garden, 23, 553–564.

ZEFF, N.L. & PERKINS, R.D. (1979): Microbial alteration of Bahamian deep-sea carbonates.– Sedimentology, 26, 175–201. doi: 10.1111/j.1365-3091.1979.tb00350.x

ZHANG, Y. & GOLUBIC, S. (1987): Endolithic microfossils (Cyanophyta) from early Proterozoic stromatolites, Hebei, China.– Acta Micropalaeontologica Sinica, 4, 1–12.

ZHANG, X-G & PRATT, B.R. (2008): Microborings in Early Cambrian phosphatic and phosphatized fossils.– Palaeogeography, Palaeoclimatology, Palaeoecology, 267, 185–195. doi: 10.1016/j.palaeo.2008.06.015