

Depth distribution and convergent evolution of microboring organisms

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Abstract Traces of microbial euendoliths have been recognized as convenient indicators of ancient depositional depths, particularly in ranges that lack physical evidence of actions of waves and currents. The paleobathymetric indication value is sought in recognizing the distinction between traces made by phototrophic microorganisms, which are expected to be restricted to the illuminated portions of the ocean, and organotrophic ones, which are light-independent and may occur at any depth. Our findings show that unrelated organisms often use similar solutions to solve similar problems, resulting in convergent evolution of body shapes and their functions, also expressed in the traces of phototrophic and organotrophic, which limits their recognition and indication value. The relationship between microboring organisms and their traces can only be studied in modern environmental settings, followed by comparisons with traces in the fossil record. Examples of convergent evolution between phototrophic and organotrophic euendoliths that resulted in similar morphological features of their trace morphologies are illustrated ways to improve the distinction between light-independent and light-dependent microboring forms are discussed.

Keywords Bioerosion · Convergent morphologie · Evolution · Euendoliths · Microborings · Paleobathymetry

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Kurzfassung Spuren von mikrobiellen Euendolithen wurden schon früh als Indikatoren für fossile Ablagerungsbereiche erkannt, speziell für Bereiche, wo physikalische Nachweise für Wellen oder Strömungen fehlen. Der paläobathymetrische Anzeigewert zeigt sich in der Erkennung und Unterscheidung von Spuren phototropher Mikroorganismen in durchlichteten Meeresbereichen, und organotrophen Mikroorganismen, die lichtunabhängig sind und daher uneingeschränkt in jeder Tiefe vorkommen können. Nichtverwandte Organismen jedoch weisen ähnliche Lösungen bei ähnlichen Verhältnissen auf, was auf einer konvergenten Evolution von Körperform und Funktion beruht. Es gibt stichhaltige Belege für konvergente Evolution zwischen phototrophen und organotrophen Euendolithen, die zu ähnlichen morphologischen Merkmalen führen und daher die Bestimmung erschweren. In vorliegendem Beitrag zeigen wir Beispiele für konvergente Morphologien bei Spurenfossilien und diskutieren Wege und Möglichkeiten, um Unterschiede zwischen lichtabhängigen und lichtunabhängigen Mikrobohrern besser erkennen zu können. Konvergenzerscheinungen zwischen phototrophen und organotrophen Bohrorganismen und deren Spuren wurden sowohl in verzweigten als auch unverzweigten, in geraden als auch gewundenen Filamenten verschiedenen Durchmesser sowie in sackartigen Schwellungen beobachtet. Die Beziehungen zwischen Mikrobohrern und deren Spuren können nur unter Rezenten Umweltbedingungen erkannt werden, um diese dann mit fossilen Spuren zu vergleichen. Die Unterschiede sind teils diffizil und nur in feinen Nuancen, aber bei genauer Beobachtung erkennbar. Aus diesem Grund sind detaillierte und präzise qualitative wie auch quantitative Beschreibungen von Spuren notwendig. Hierfür ist eine gewisse Menge von Bildmaterial erforderlich.

Schlüsselwörter Bioerosion · Konvergente Morphologie · Evolution · Euendolithen · Mikrobohrspuren · Paläobathymetrie

Introduction

Traces of organismal activities preserved in sediments contain information about diversity, behavior, development, and distribution of their makers, as well as of their interaction with the sediment matrix. The study of traces gave rise to ichnology, a branch of paleontology with separate rules for trace classification and nomenclature (Bertling et al. 2006; Miller 2007a; Knaust and Bromley 2012), which also apply to microborings, the traces of euendoliths (Golubic et al. 1981). Microbial euendoliths are specialized microorganisms able to penetrate rocky substrates. They leave traces that often conform closely to the outlines of the body of microorganisms that made them (Campbell and Hoffman 1979). They occupy a number of ecological niches in contemporary marine environments from the coastal zone reached by tides and waves (Le Campion-Alsumard 1966, 1975; Golubic 1969; Golubic et al. 1975; Perkins and Tsentas 1976) to the abyssal depths (Zeff and Perkins 1979; Golubic et al. 1984; Hook and Golubic 1993).

The microbial boring activity, when integrated in marine ecosystems through food webs of invertebrate and vertebrate grazers (Schneider 1976; Schneider and Torunski 1983; Bruggemann et al. 1994), contributes significantly to marine bioerosion (Tribollet et al. 2011a, b; Wisshak 2012), affecting especially shallow tropical waters (Vogel et al. 2000) and coral reefs (Tribollet 2008; Chazottes et al. 2009; Tribollet and Golubic 2005, 2011). Microbial euendoliths tolerate fluctuating salinities (Brandes et al. 2015). They are common in marine environments, but less common in freshwater environments (Radtke 1998; Schneider and Le Campion Alsumard 1999; Tribollet et al. 2008). Recent experimental evidence suggests that the microbial bioerosion may accelerate with the increase in partial pressure of the atmospheric CO₂ and the corresponding sea water acidification (Tribollet et al. 2009; Wisshak et al. 2012).

Microboring traces have high preservation potential, acting as “instant fossils” (Golubic et al. 2014). Fossil euendoliths and their traces are known from the mid-Proterozoic to Recent (Campbell 1982, 1983; Zhang and Golubic 1987), and most of them changed very little in shape over extended geological time (Knoll et al. 1975, 1986; Green et al. 1988; Knoll and Golubic 1992), including complete modern looking trace assemblages (Wisshak et al. 2008). Fossil microboring traces were

recorded throughout the Phanerozoic (Vogel et al. 1987; Radtke 1991, 1992; Hofmann and Vogel 1992; Schmidt 1992; Glaub 1994; Hofmann 1996; Balog 1997; Vogel and Marincovich 2004; Vogel and Brett 2009) and described using ichnological nomenclature (reviewed by Glaub et al. 2007).

Microbial boring activities in shallow warm seas combined with carbonate precipitation were recognized as the main cause of micritic envelopes formation around carbonate grains (Bathurst 1966). Bathurst (1967) also recognized the potential to use the microborings as indicators of the depositional depth of ancient sediments (see also Hook et al. 1984). The boring behavior of microbial euendoliths and the boring patterns produced are often so specific that they could be applied in taxonomic description and characterization of biotaxa (e.g. Zebrowski 1936; Golubic and Le Campion-Alsumard 1973; Pohowsky 1978).

A palaeobathymetric indication based on depth distribution of identified shapes of microborings was suggested by Boekschoten (1966), Swinchatt (1969), Golubic (1972), and more recently by Vogel et al. (2000). The introduction of scanning electron microscopy of resin-cast microborings in modern (Golubic et al. 1970) and fossil carbonates (Golubic et al. 1983; Wisshak 2012) improved the visualization of their shapes at resolution, as well as the 3-dimensional display of microborings inside bored substrates.

Although carbonate microboring activity is most intensive in shallow tropical waters, the destruction of shells and other skeletal carbonates by microboring organisms occurs at all depths (Golubic et al. 1975; Zeff and Perkins 1979; Golubic et al. 2005) and in a wide range of latitudes (Wisshak et al. 2005, 2011; Tribollet and Golubic 2011). The carbonate boring habit evolved among light-dependent, phototrophic microorganisms, as well as among light-independent organotrophic ones. Phototrophic euendoliths inhabit illuminated, euphotic ranges in the ocean (and inland waters), whereas the organotrophic members of the group may grow at any depth, provided that suitable organic nutrients are available. Chemolithotrophy among euendoliths has never been registered.

Both phototrophic and organotrophic euendoliths evolved adaptive strategies to grow and survive in their peculiar habitats. Differences in these adaptations characterize distinct ecological niches—the similarities illustrate solutions to common problems. Similar morphological properties may have resulted from convergent evolution that occurred independently in phototrophic and organotrophic euendoliths. These and similar convergences limit their value as environmental indicators.

The present contribution illustrates some similar morphological features shared by phototrophic and organotrophic microborers. We investigate similarities between

borings of shallow marine (supratidal, intertidal, and subtidal) assemblages of phototrophic microbial euendoliths and those formed by organotrophs in shell fragments exposed at the surface of deep sea sediments.

Convergent evolution of euendolith behavior and morphology

There are many examples of convergent evolution among plants and animals, resulting in similar morphological properties and behavior in unrelated organisms. These are known and recognized among macroorganisms. They have been less commonly studied in microorganisms (e.g. Golubic and Marčenko 1965). The application of microboring traces as paleoecological, specifically paleobathymetric indicators requires the recognition of the organism that made the trace and an understanding of its energy requirements-based on the assessment of the trace morphology alone. The paleo-depth estimation rests on the distinction between traces formed by light-dependent microorganisms from those formed by light-independent microorganisms.

Both, euendolithic microorganisms and their borehole traces coexist in modern environmental settings where their specific relations and diversity can be learned. We extract and identify the resident microborers in modern environmental settings, comparing them with the traces they make. Then we compare them with the traces encountered in the fossil record. Once modern euendoliths and their traces have been correlated with the environmental conditions under which they thrive, this information can be used in reconstruction of ancient environmental conditions and facies descriptions. In paleoenvironmental reconstruction, the procedure and information flows in the opposite direction, starting with the morphology of borehole traces, their diversity and associations, then we compare them with the modern counterpart with known resident euendolithic microorganisms.

The taxonomy and biology of microorganisms that penetrate rocks are poorly known, and the studies are in progress. This is particularly true for the organotrophs, which mostly remain undescribed. For this reason, the organotrophic euendoliths are best studied in deep sea sediment collections where similar traces of phototrophic euendoliths are certainly excluded. This principle was applied in the following illustrations. Size is important in comparing natural populations of microorganisms as well as their traces and we carried out the comparisons at the same scale whenever possible. Studies of populations of microorganisms and their traces in the field may require morphometric and statistical evaluations (e.g. Radtke and Golubic 2005, 2011).

Similarities and distinctions in boring patterns

The interaction between euendoliths and the substrate they penetrate starts with their entry. Coastal limestone rocks across the intertidal and supratidal wave-spray zones are densely populated and perforated by uniformly distributed populations of euendolithic cyanobacteria (Fig. 1), which appear to be well adapted to these harsh conditions (Le Campion-Alsumard 1966; Radtke and Golubic 2011). The perforations are most frequently perpendicular to the rock surface. They may also be truncated by grazers (Fig. 1a), mostly gastropods in the upper ranges and by polyplacophores, echinoderms, and fishes in the lower ranges (Schneider and Torunski 1983; Bruggemann et al. 1994; Radtke et al. 1996). The translucent resin replicas of microborings of intertidal cyanobacterial populations of *Solentia foveolarum* Ercegovic are displayed as a continuous interior endolithic landscape (Fig. 1b) with the pigmented apical cells visible at the tips of the tunnel replicas. The SEM preparations (Fig. 1c) permit an assessment of borehole outlines in situ at different angles and in perspective, albeit at a higher resolution.

Pleurocapsalean cyanobacteria *Hyella* and *Solentia* are the most common constituents and boring agents of the intertidal and supratidal biocorrosion of limestone rocks. Their cellular arrangements differ even though they conform in the shape and orientation of their borings (Fig. 1d), thus illustrating one of the objective limitations in the use of borings to identify their makers. In this and similar cases, a single ichnotaxon, i.e. *Fascichnus* Radtke et Golubic (new name for *Fasciculus* Radtke) represents the borings of two cyanobacterial genera. The species of *Hyella* and *Solentia* are both phototrophic and similar in their intertidal distribution, and both are accompanied and attacked by fungal hyphae (Fig. 1b, note the fine cobweb-type filaments). Microboring activity in the intertidal ranges is carried out by cyanobacteria that are resistant to excessive solar irradiation, periodic water shortage, and extreme fluctuations in temperature and salinity. They are also often confronted by fungi and may form cyanolichens. In addition, grazing on coastal phototrophic euendoliths extends their activity by displacing the illuminated zone deeper into the rock thereby turning a potentially static activity into a progressing one (Schneider and Torunski 1983; Radtke et al. 1996).

Diversity of microorganisms, as well as of their traces was observed to increase from the supratidal ranges across the intertidal toward the permanently submerged subtidal environments, where the ecological conditions are less extreme and less variable. Loose carbonate grains are less affected by grazers, both in shallow subtidal waters as in abyssal depths. Their surfaces are often beset by small

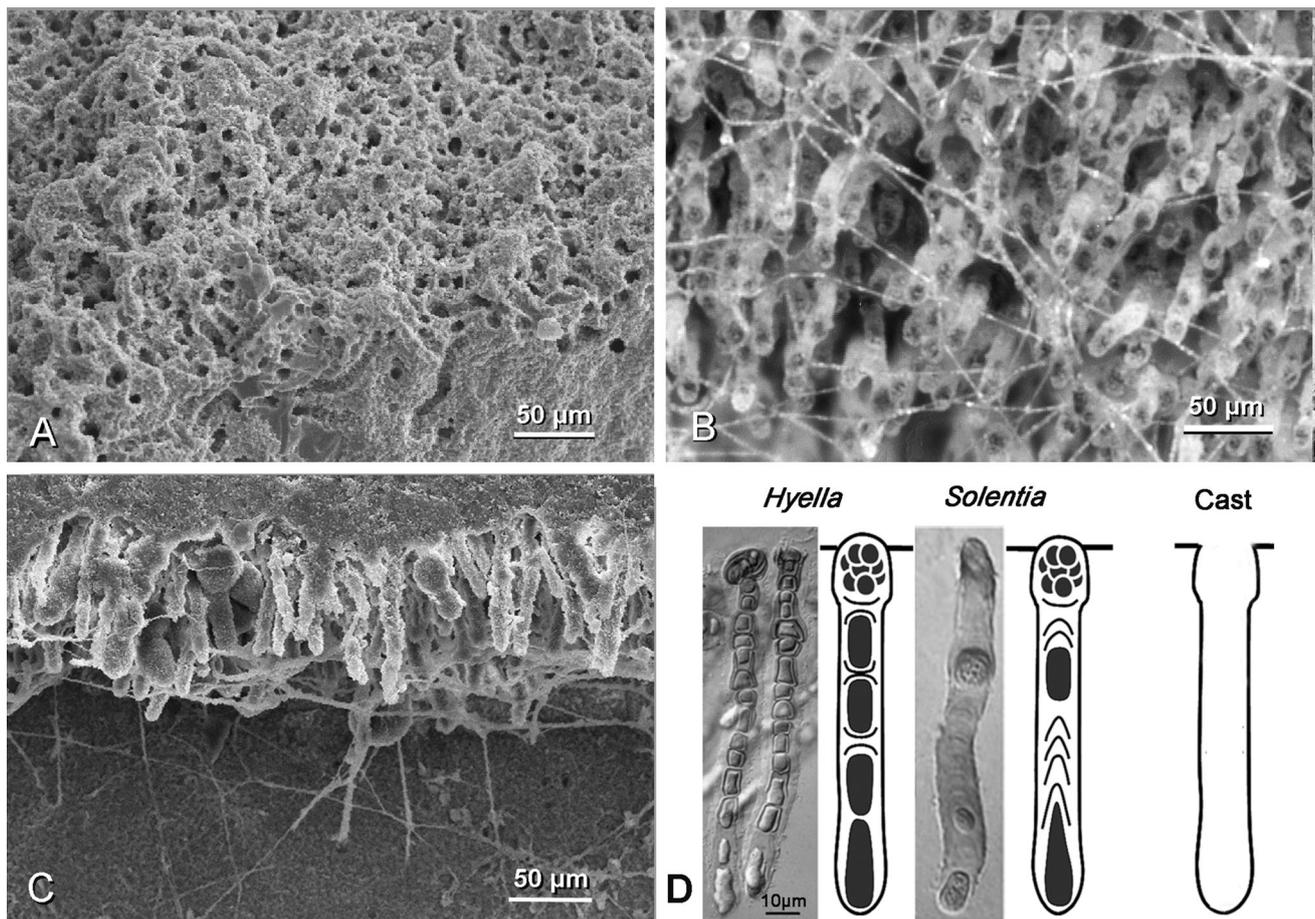


Fig. 1 Microborings produced by microbial penetration of coastal limestone, intertidal zone, Vela Luka, Island Korcula, Croatia. **a** The effect of cyanobacterial biocorrosion of the coastal limestone in the upper intertidal zone. Microborings are in part truncated by invertebrate grazing. **b** In situ borings of *Solentia foveolarum* Ercegovic replicated in transparent polymerized resin, accompanied by thin tunnels of euendolithic fungi. Note the droplet-shaped apical cells of

Solentia at the tips of gelatinous (EPS) stalks. **c** SEM image of replicated microborings in an HCl treated petrographic thin section cut perpendicular to rock surface. **d** Comparison of light photomicrographs and drawings of *Hyella* and *Solentia* showing their different cell arrangements as compared with the tunnel outlines observable by SEM

perforations, which in the interior of the grain expand to voluminous galleries, an effect also known for boring sponges. Once inside the interior of the substrate, a successful euendolith would expand from the point of entry in any direction. Tubular borings make fast progress and appear to be the favored strategy of filamentous euendoliths (Fig. 2). Most tubules extend initially parallel to the surface, whereas others venture deeper to explore the interior of the substrate. Some maintain a fairly constant diameter, while others are more variable. The predominantly horizontal distribution of branched filaments with repeated widening along the tube is characteristic of the phototroph *Phaeophila dendroides* (Crouan) and its trace *Rhopalia catenata* Radtke (Fig. 2a). This trace has a similar organotrophic counterpart in the deep sea (Fig. 2b). Both produce tunnels with irregular swellings connected by narrower, cylindrical sections. The accompanying very fine

tunnels are mostly made by fungal hyphae in shallow and deep water settings. Lateral expansion and increased coverage by filamentous borings is accomplished by branching (Fig. 2c) in some euendoliths, such as *Ostreobium quekettii* [trace *Ichnoreticulina elegans* (Radtke)] and by winding (Fig. 2d) as in the deep sea trace *Scolecia*, or by a combination of both. These strategies are employed by phototrophic and organotrophic euendoliths alike, resulting in similar morphological adaptations. A common behavior of microboring organisms is to grow parallel to the substrate surface without exiting the substrate, a strategy also shown in detail at a smaller scale by the borer's avoidance of pre-existing tunnels (e.g. Fig. 2c). Similar behavior among organotrophs was recently illustrated by Golubic et al. (2014: fig. 1g). A radiating pattern extending from the point of entry (Fig. 2b) is common to both phototrophic and organotrophic euendoliths.

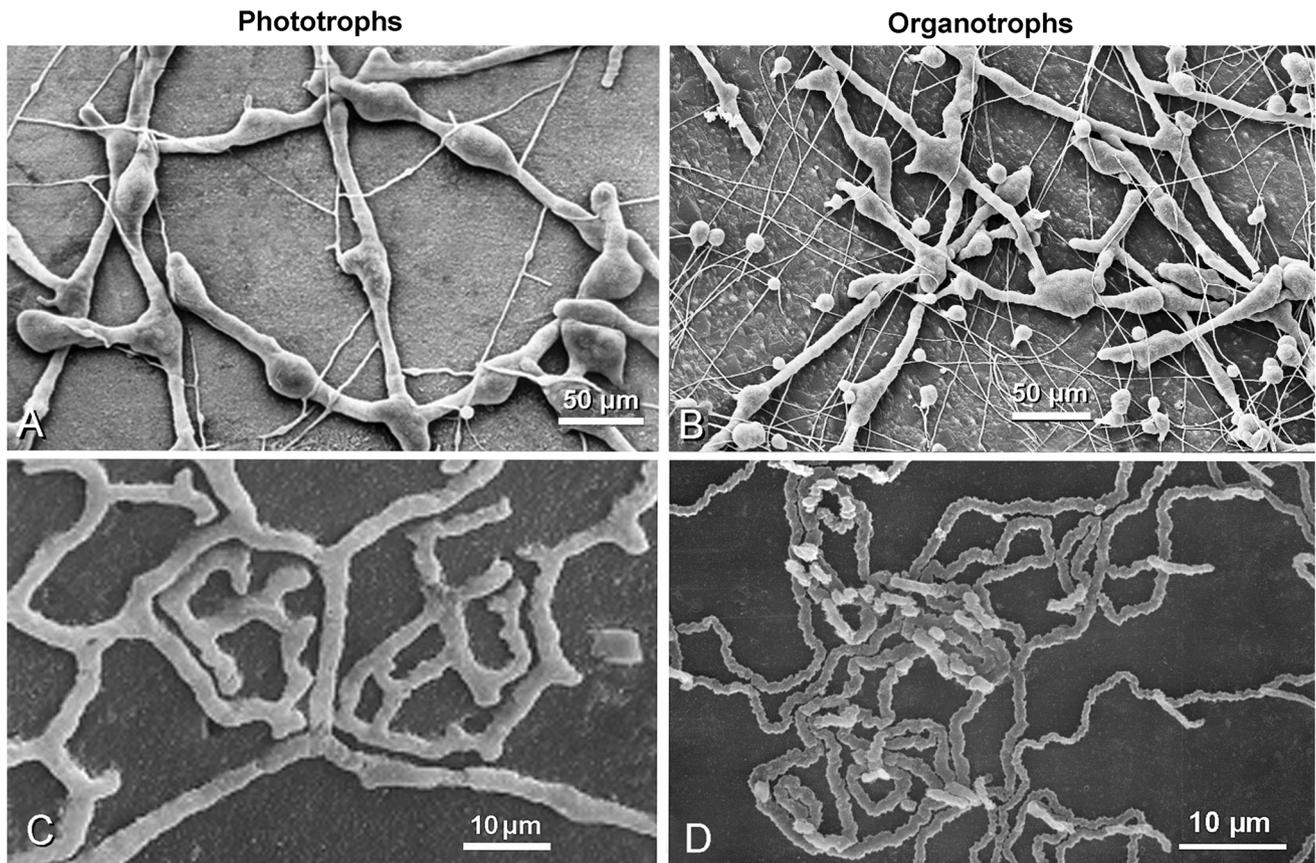


Fig. 2 SEM images of phototrophic and organotrophic euendoliths forming tunnels that spread parallel to the substrate surface. **a** Horizontal tunnels produced by the septate chlorophyte *Phaeophila engleri* Reinke with characteristic rhythmically repeated swellings. Its trace *Rhopalia catenata* Radtke is accompanied by thin tunnels produced by the euendolithic fungus *Ostracoblabe implexa* Bornet et Flahault. Lee Stocking Island, Bahamas, 1.5 m depth. **b** Predominantly horizontal tunnels with rhythmic swellings are also produced in deep sea by a common yet undescribed organotrophic microborer,

excavating a shell fragment. M.S. Meteor Me5-158, Red Sea, 1558 m depth. **c** Reticulate branching pattern of the euendolithic siphonal chlorophyte *Ostreobium quekettii* Bornet et Flahault [trace *Ichnoreticulina elegans* (Radtke)], exploiting the surface area while avoiding penetration of pre-existing tunnels. Lee Stocking Island, Bahamas, shallow subtidal. **d** Densely winding trace, *Scolecia serrata* Radtke widely distributed in bored shells in aphotic depths by an unidentified organotrophic microbial euendolith

Most euendoliths maintain periodic contacts with the substrate surface, depending on different physiologically and biologically required functions, such as the exchange of nutrients and metabolic products, or the release of spores and other propagules as a part of their reproduction. Among filamentous euendoliths that penetrate deeper into the substrate, many still maintain periodic contact with the substrate surface by repeated arching of tunnels toward the surface. This pattern was observed in phototrophic boring algae (Fig. 3a) as well as in non-phototrophic tubular borings in deep sea (Fig. 3b).

Radiating tubules from the point of the initial settlement oriented to the interior of the substrate to form dense bushes is characteristic of *Fascichnus* traces (see Radtke 1991) (Fig. 3c). These traces are produced by a variety of species of *Hyella* (see Al-Thukair and Golubic 1991a, b; Radtke and Golubic 2011). *Fascichnus* borings are

prevalent in the lower intertidal and very shallow subtidal environments (Radtke 1993). However, very similar orientation and deep penetration of borings also occurs in unidentified organotrophic euendoliths of the deep sea (Fig. 3d). Distinctly dichotomous traces described as *Abeliella* Mägdefrau were found to be produced by cyanobacteria of the genus *Hyella* (Radtke et al. 2010). The same form was recently observed among deep sea microborings (Wisshak, personal communication).

Organisms reproduce and spread most efficiently and economically by producing and releasing large numbers of small reproductive cells to be released, which would settle elsewhere and grow in new habitats. This strategy of “seeding” evolved in prokaryotes and eukaryotes organization alike, including those with phototrophic as well as with organotrophic metabolism involving a variety of euendolithic taxa. In pleurocapsalean cyanobacteria, small

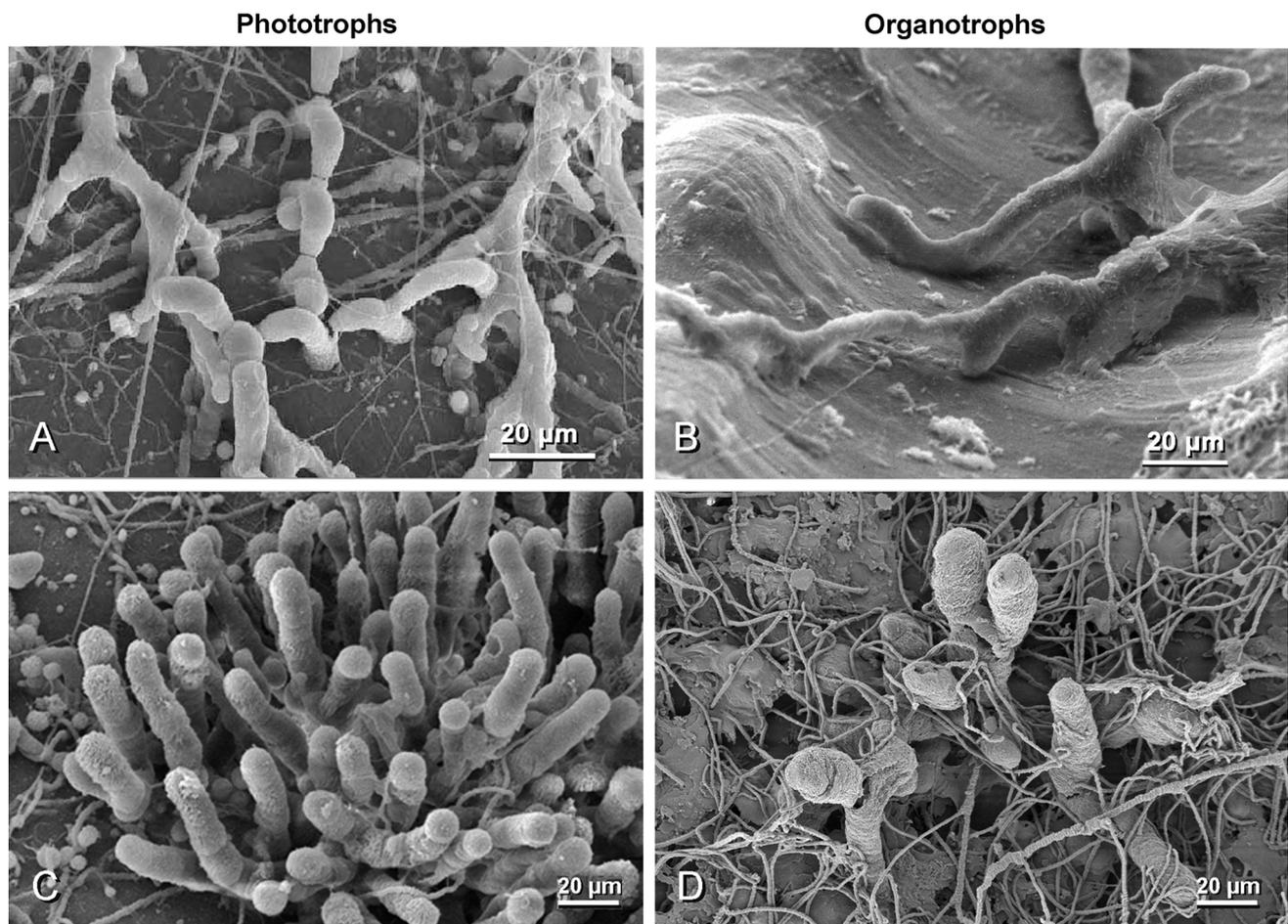


Fig. 3 Euendoliths penetrating deeper in the substrate. **a** The trace *Rhopalia* “saltator” (Radtke et al. 2011) attributed to a phototrophic euendolith maintains contact with the substrate surface by rhythmically repeated arches; Bivalve shell in shallow coastal waters of the Caribbean Sea, Panama. **b** Similar arching is shown by an organotrophic (probably fungal) euendolith in shell fragments

exposed to microboring at the surface of deep sea sediment. **c** Trace *Fascichnus frutex* (Radtke) formed by cyanobacterium *Hyella* sp. in an ooid grain at 6 m depth, Lee Stocking Island, Bahamas. **d** Deep sea equivalent boring of an unknown organotroph. M.S. Meteor, Red Sea, Me5-176, 1970 m

reproductive cells called baeocytes (Waterbury and Stanier 1978) form by multiple fission and are released into surrounding waters. They are functional equivalents to spores and gametes of eukaryotic algae and fungi. Carbonate penetrating species evolved in unrelated and remotely related groups, but facing similar problems evolved similar reproductive strategies.

The production of a large number of propagules requires storage space prior to their release, usually in the form of enlarged bag-like cavities containing sporangia, gametangia, and similar reproductive structures. These cavities usually open toward the substrate surface, where the propagules can be released. The pear-shaped boring trace *Planobola macrogota* Schmidt (Fig. 4a) is produced by the pleurocapsalean cyanobacterium *Cyanosaccus piriformis* Lukas et Golubic. *Cyanosaccus* produces baeocytes in cells that are closest to the substrate surface (Fig. 4b). The

reproductive pulses of this cyanobacterium produce populations of *Planobola* traces in different stages of growth and correspondently different sizes on surrounding substrates. Very similar club-shaped cavities regularly harbor fungal sporangia produced by *Dodgella priscus* Zebrowski the maker of the complex trace, *Saccomorpha clava* Radtke (Fig. 4c). The critical distinction between *Planobola macrogota* Schmidt and *S. clava* is that fungal sporangial cavities are always associated with narrow tunnels containing hyphae (Fig. 4c, upper right), which distribute and generate the sporangia within the substrate and are important to recognize the fungus as well as the ichnogenus referring to its complex trace.

Combinations of narrow, cylindrical, sparingly branched “exploratory” filaments (e.g. Radtke and Golubic 2005: fig. 8c) with intensely ramified side branches (Fig. 2c), ending with enlarged, irregularly shaped

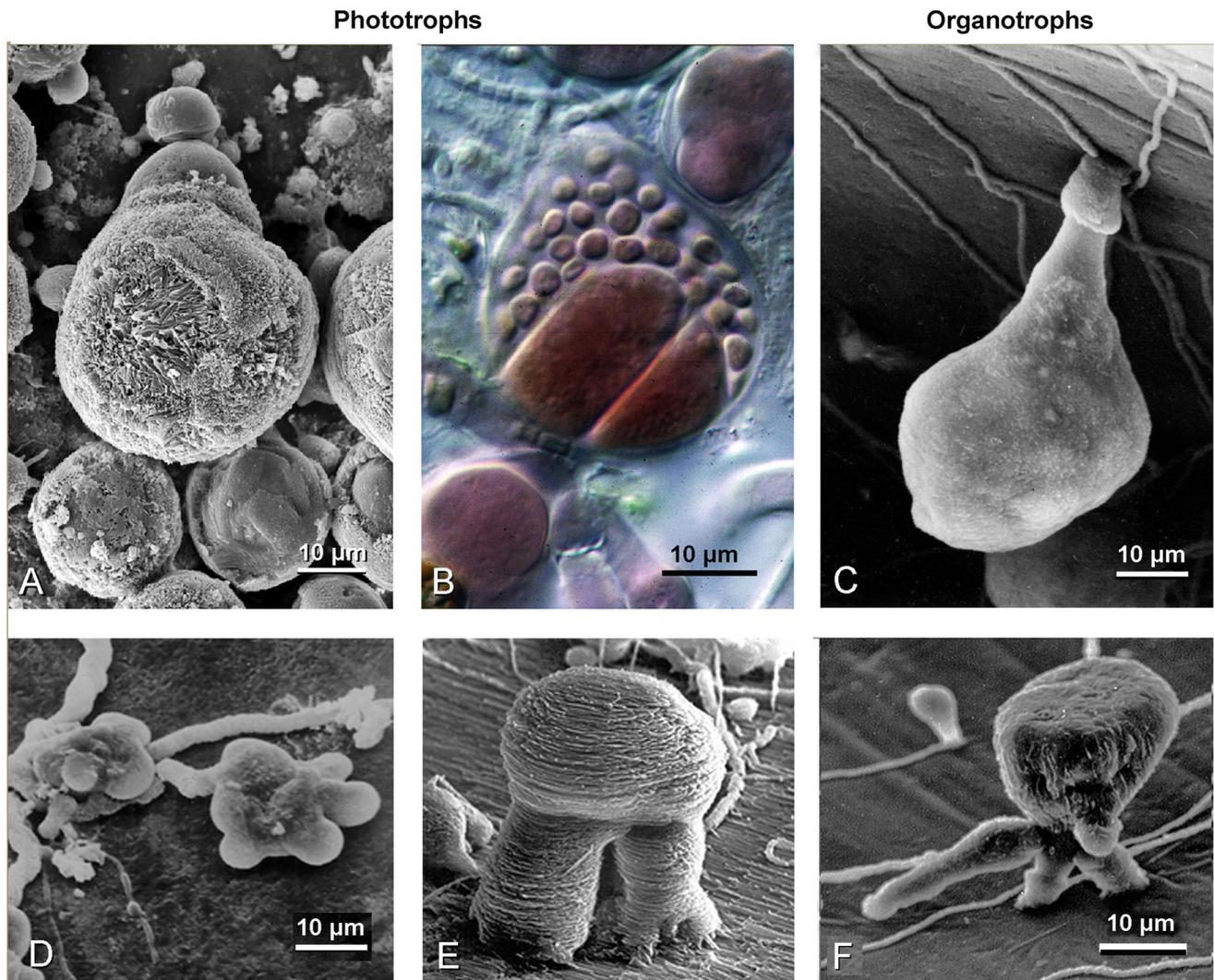


Fig. 4 Bag-like or saccomorph traces harboring reproductive structures such as sporangia or equivalents. **a** Resin replicas of *Planobola macrogota* Schmidt traces produced by the pleurocapsalean cyanobacterium shown in **b**. Note the wide range of sizes including a small bag adjacent, but separate in center top. **b** Pleurocapsalean cyanobacterium *Cyanosaccus piriformis* Lukas et Golubic in the process of producing baeocytes by multiple fission of the cell closest to the substrate surface. **c** Complex traces *Saccomorpha clava* Radtke produced by the fungus *Dodgella priscus* Zebrowski. The sporangial cavities are interconnected by thin 1–2 µm wide hyphal tunnels. The

“neck” of the cavity is close to the substrate surface where the spores are released. **d** Isodiametric bag with lobes, a part of the complex trace *Ichnoreticulina elegans* (Radtke), formed by the siphonal chlorophyte *Ostreobium quekettii* Bornet et Flahault. Lee Stocking Island, Bahamas, 6 m depth. Note a different expression of this complex trace in Fig. 2c. **e** The trace *Cavernula pediculata* Radtke produced by the euendolithic “Codiolum stage” in the life cycle of a septate chlorophytes. **f** Club-shaped cavity with several exits produced by a deep sea organotroph similar to *Dodgella*. M.S. Meteor Me5-158, Red Sea, 1558 m depth

cavities (Fig. 4d) comprise the boring patterns of the complex trace *Ichnoreticulina elegans* (Radtke) made by the siphonal chlorophyte *Ostreobium quekettii* Bornet et Flahault particularly well developed in hermatypic corals (Le Campion Alsumard et al. 1995a). A combination of tunnels and sporangial bags characterizes another complex trace *Rhopalia clavigera* Golubic et Radtke, built in the course of the endolithic growth of the septate

chlorophyte *Eugomontia sacculata* Kornmann (Golubic and Radtke 2008: fig. 3).

Other chlorophytes have euendolithic phases alternating with epilithic ones as a part of their life cycle (O’Kelly et al. 2004), as represented by euendolithic “Codiolum” stages (Fig. 4e), although similar cavities with multiple exits connects to the substrate surface may be formed by organotrophic euendoliths of fungal affinity (Fig. 4f).

The interrelationship between euendoliths and the substrate

All euendoliths, regardless of their metabolic mode, share the interaction with the bored substrate, but the mechanism of this interaction and the resulting traces and textures may differ. Some may reflect the properties of the boring microorganism, including their metabolic properties and dependency on energy sources (phototrophy vs. organotrophy), while others reveal the properties of the substrate. Microboring activity has been observed in a variety of carbonate substrates, ranging from purely inorganic, such as limestone and dolomite rocks or calcite spars (Golubic 1969; Le Campion-Alsumard 1975), to various skeletal carbonates with different amounts of incorporated organic matter.

The way by which the microbial euendoliths affect carbonate substrates involves chemical action of biocorrosion (reviewed by Tribollet et al. 2011a) that leaves distinct etch marks. A mechanism called “calcium pump” has been proposed (Garcia-Pichel 2005; Garcia-Pichel et al. 2010). The boring activity may be differently localized on particular euendoliths. In most filamentous microborers the dissolution of carbonate is concentrated at the tips of the filament, while the sides of the tunnels conform to the outlines of the filament, with no evidence of a lateral expansion of the dissolution process. Similar boring pattern occurs in coccoid cyanobacteria (order Pleurocapsales) with polarized growth promoted by directional production of exopolymer stalks (Figs. 1d, 2, 3c). These patterns suggest an effective, presumably fast boring process. Lateral expansion of carbonate dissolution away from the filament and along crystal boundaries within the substrate, which produces large etch-fields, appears to be associated with slower penetration rates and prolonged local exposure of the substrate to corrosion.

Euendolithic phototrophs are effective in removing the carbonate along their growth, but are less able to penetrate the organic substances incorporated inside skeletal carbonates. The resin replicas of tunnels made by phototrophs in limestone frequently reflect the crystalline arrangements of the rock. When penetrating bivalve shells, boring algae are often confined within single crystals due to their inability to penetrate the inter-crystalline conchiolin envelopes, which does not seem to pose any problem for euendolithic fungi apparently specialized to dissolve and possibly digest this substance (Golubic et al. 1975). It seems that the method and efficiency of microbial carbonate penetration depends on metabolic tools available to the euendolith in relation to the obstacles posed by the structure of the substrate.

The preference of euendolithic fungi to seek organic lamellae inside the bored shell is consistent with their

organotrophic metabolism. The intensity of boring activity is enhanced at such encounters leaving visible marks in the form of profuse and often dark pigmented etchfields (Mao-Che et al. 1996; Priess et al. 2000; Golubic et al. 2014). Organotrophs may consume organic compounds incorporated in the shell, but they also attack plants and animals supported or protected by such skeletal structures. For example, euendolithic fungi derived from coral skeletons regularly attack the coral animal thereby triggering the cnidarian’s defense mechanism in form of deposition of dense pearl-like carbonate cones, an apparent attempt to block the fungal attack (Le Campion-Alsumard et al. 1995b; Bentis et al. 2000). A similar response was described for the attack by foraminifera on bivalves (Beuck et al. 2008; Tribollet et al. 2011b: fig. 13).

A different set of interpretational problems relates to secondary precipitates in and around the borings. There is a good evidence that carbonate removed by euendoliths is transported (see Garcia-Pichel 2005; Garcia-Pichel et al. 2010) and becomes precipitated in the borings (Macintyre et al. 2000). This raises concerns that microbial euendoliths may be influencing the isotopic composition of coral skeleton (Nothdurft et al. 2007) in studies reconstructing past environmental conditions during a coral’s growth. Microbial bioerosion contributes to carbonate substrate porosity, which often enters the fossil record. There is a high proportion of fossil microborings remaining empty. These can be replicated with polymerizing resins and compared with similarly treated modern microborings. Other microborings remained preserved as natural casts due to differential solubility between the borehole fill and the bored matrix that may be more easily weathered away (e.g. Harris et al. 1979).

Summary of observations based on the study of modern euendolith settings

The application of microbial traces to the discipline of paleoenvironmental and paleobathymetric reconstruction requires identifying of organisms that produce them, based on studies in modern environmental settings. The preparation methods and analytical tools available are to a large extent applicable to both modern and fossil euendoliths and their traces. They complement the light microscopy of microbial euendoliths extracted from matrix by carbonate dissolution, as well as those observed in petrographic thin sections.

Euendolithic traces are three-dimensional features with a particular relation to the substrate surface. So SEM imaging of their replicas needs to observe and document them at different angles. The vertical “aerial” view of the

euendolithic landscape records the population's size and area it covers, whereas profile imaging records the depth of their penetration. Oblique views, achievable by tilting the specimen are often important to present the trace in perspective. This also includes its connection with the substrate surface. Publishing stereo-pairs was recently replaced by computer-assisted tomographic reconstruction (Beuck et al. 2007).

Size is an important property regarding the organisms, their parts and traces, as well as entire microbial populations. The microscopic size of microbial euendoliths and their borings enables population-level studies, including statistical evaluation of variability of size and shape, because entire trace assemblages may co-occur in sand-sized carbonate particles. In comparing microorganisms and microboring traces, it is a good practice to do all comparisons at the same scale.

Microbial euendoliths produce traces of various sizes and complexities: some euendoliths produce consistently simple tunnels and repetitive patterns, while others produce more than one type of trace or change their boring strategy in the course of their growth and development, producing complex traces (see Miller 2007b). Organisms with complex life cycles may involve alternation of endolithic and epilithic generations.

The distinction between simple and complex traces is a practical starting point in categorizing of microboring traces. Assemblages of simple traces may represent ichno-coenoses, if they reflect associations of different microboring organisms. In contrast, a complex trace represents associations of different morphological expressions in the course of the development of a single similarly complex biotaxon. Examples include interconnected developmental stages in the life cycle of the green alga *Eugomontia sacculata* Kornmann (Golubic and Radtke 2008), and associated hyphal tunnels and sporangia in the common euendolithic fungus *Dodgella priscus* Zebrowski (trace *Saccomorpha clava* Radtke). Complex traces produced by developmental stages separated in time include the euendolithic Conchocelis stages in the life cycle of the bangialean rhodophytes *Bangia* and *Porphyra* (Campbell and Cole 1984) and "Codiolum" stages in chlorophytes (Kornmann 1960, 1961).

Microbial euendoliths are well integrated in the marine ecosystems as a part of the food chains, involving animal grazing, which turns their activity into a progressing bio-erosional force that at a large scale results in modifying the coastal landscape by formation of biokarst and of bioerosional notches (Schneider and Torunski 1983; Radtke et al. 1996).

Most microbial euendoliths live completely immersed inside the rock, leaving only a small perforation on the substrate surface where they entered. Other organisms

penetrate the rock only with parts of their body as in the case of euendolithic rhizoids of the dasycladacean chlorophyte *Acetabularia* (Radtke et al. 1997), or the holdfasts of brachiopods (*Podichnus* Bromley et Surlyk). Some epilithic microorganisms and their products leave only grooves or shallow depression in the carbonate surface as an imprint of an extracellular product (Wisshak et al. 2014).

Modern microborings are not always occupied by resident euendoliths. The highest proportion of microborings with resident euendoliths was observed in supratidal and upper intertidal ranges. Their frequency declined toward the low intertidal and subtidal ranges. Deep-sea carbonate substrates contain predominantly empty borings. A large proportion of fossil microborings also remained empty or incompletely filled.

Microboring activity can be cumulative. Substrates are often colonized and bored repeatedly by different generations of euendoliths, with or without intermittent calcareous precipitates, so that different boring patterns superimposed over the preceding ones result in formation of constructive (Bathurst 1966) or destructive (Alexandersson 1972) micritic envelope.

In our survey of morphological similarities that may have resulted from convergent evolution in unrelated organisms and in different marine settings, we call for attention to subtle distinctions between them, as a requirement in descriptions of microbial traces. The distinctions may be expressed by shape, size, and proportions, as well as by orientation of the borings, but should exclude the imprints that reflect the substrate texture and the presence of precipitates. A system developed on the basis of modern traces with recognition of the microorganisms that made them, including their environmental requirements and responses is important if microboring traces are to be reliable paleoecological and paleobathymetric indicators.

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