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ORIGINAL ARTICLE

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Microendoliths of the Shallow Euphotic Zone in open and shaded habitats at 30°N – Eilat, Israel – paleoecological implications

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Abstract This study examines microendolithic community patterns in experimental carbonate blocks in shallow waters between 0 m and 30 m adjacent to Eilat, Israel. We set up two different habitats per depth: one in full light and one shaded. After 6 months of exposure we observed 23 species of which five are unknown to science and herein described as forms. Differences in community patterns between open and shaded habitats were clearly visible at 0 m, indistinct between 6 m and 15 m and indiscernible at 30 m. Three modern producers of key ichnotaxa were confirmed in our experiments within their paleobathymetrical range: *Hyella balani* (*Fascichnus acinosus*), *Conchocelis* (*Palaeoconchocelis starmachii*), and *Ostreobium queketti* (*Ichnoreticulina elegans*). For *Fascichnus dactylus* we found six possible producers. We dismiss *Scolecia filosa*, *Eurygonum nodosum* and *Rhopalia catenata* as potential key ichnotaxa because of the broad bathymetrical range of their producers.

Keywords Bioerosion · Paleo-bathymetry · Key-ichno taxa · Microendolith · Eilat · Red Sea · Shallow Euphotic Zone

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Introduction

The microbenthos of a reef slope shows a depth-related shift in community patterns (Budd and Perkins 1980; Perry and Macdonald 2002). Organisms settle depending on their physiological requirements for nutrition, light, temperature, and other physical parameters, and with increasing depth, these factors change. While it is fairly comfortable to measure the linear change of physical parameters in modern marine environments, in fossil basins the question of from which paleo-depth a fossil carbonate has originated is often difficult to answer. One promising group for paleobathymetrical indications is microbial rock-inhabiting organisms.

Modern microbial endolithic organisms, called "microendoliths" hereafter, have diameters of less than 100 μm, can be separated in phototrophic (cyanobacteria and alga) and heterotrophic (mainly bacteria and fungi) species, and colonize carbonates from marine as well as freshwater and terrestrial habitats (Golubic et al. 1975, 2005). The limiting factor for photoautotrophic species distribution is light that is reflected in the reduction of species diversity with increasing depth of water (Golubic et al. 1975; May et al. 1982).

Comparable patterns of microendolithic bathymetric distribution were found in the Mediterranean Sea (Schneider 1976; Le Campion-Alsumard 1978), East Atlantic Ocean and the Caribbean (Golubic et al. 1975; Budd and Perkins 1980; Gektidis 1997), Pacific Ocean (Hutchings 1986; Chazottes et al. 1995, 2002; Gektidis 1999b; Vogel et al. 1999, 2000), the NE-Atlantic (Wisshak et al. 2005) and the Red Sea (Potts 1980; Radtke and Golubic 2005). In all of the above-mentioned studies, cyanobacteria preferred supra- to intertidal habitats; a mixed community of cyanobacteria, chlorophyta and *Conchocelis* colonized shallow waters and heterotrophic fungi and bacteria dominated in deep, aphotic waters.

While most studies use microendolithic organisms for taxonomic identification, some authors base their analysis on traces (ichnotaxa) these organisms leave (Günther 1990;

Radtke 1993; Perry and Macdonald 2002). In a stabile substrate like carbonates, microendolithic ichnotaxa represent exact imprints of their producers and exhibit a remarkable constancy through time (Green et al. 1988; Golubic and Seong-Joo 1999). Single traces follow an independent ichnotaxonomy (Bertling et al. 2006) and as trace communities (ichnocoenoses) they can be used as paleo-depth indicators in fossil basins (Vogel et al. 1987; Radtke 1991; Glaub 1994; Balog 1996; Hofmann 1996; Plewes 1996; Bundschuh 2000; Vogel and Marincovich 2004). Five photic zones are distinguished on the basis of depth-specific ichnocoenoses (after Glaub 1994; Glaub et al. 2001): The Shallow Euphotic Zones (SEZs) II and III, the Deep Euphotic Zone (DEZ), the Dysphotic Zone (DZ) and the Aphotic Zone (AZ). These zones are viewed as indicative for paleophotic zones rather than absolute paleo-depths (Perry and Macdonald 2002). Factors that potentially obscure this system and provoke false paleobathymetrical conclusions are therefore in the focus of modern studies.

Due to the three-dimensional structure of the reef framework, light is not a constant factor at each depth (Vermeij and Bak 2002). The experimental design of the present study was chosen to assess the pattern of microendolithic distribution in habitats with different light conditions but situated at the same depth of water. We demonstrate that differences between these habitats have to be taken into account but do not present an insuperable obstacle for bathymetric and consequently paleobathymetrical interpretations.

Location

This study was conducted at 0–30 m depth on coral reefs adjacent to the Interuniversity Institute for Marine Science (IUI) at Eilat, Gulf of Aqaba, northern Red Sea (29.5°N, 35°E). Stony corals at this site form small patch reefs interspersed with coarse sand. Scattered beach rock also occurs in shallow water at this site, and stony corals grow directly attached to these formations. In the Gulf of Aqaba, the maximum water depth is 1,830 m, salinity is 41‰, oxygen levels are 4.8–5.0 mg l^{-1} throughout the water column, and mean monthly temperatures range from 21.5°C in winter to 24.5°C in summer. Tides are semidiurnal and have a mean range at spring tide between 50 and 70 cm (Potts 1980). The water masses of Eilat are highly translucent and the Shallow Euphotic Zone in open and shaded habitats extends down to approximately 50 m (Goffredo and Chadwick-Furman 2000).

Experimental design

Carbonate substrates cut into 1-cm^3 cubes were deployed in the Shallow Euphotic Zone at depths of 0, 6, 15, and 30 m on the reef slope. The selected substrates consisted of dense micrite (Solnhofen limestone), translucent calcite spar, and *Tridacna* mollusk shells. Twelve substrates (six micrites, three spars, and three shells) were deployed at each depth and habitat. Thus, a total of 96 substrates were investigated (24 cubes per depth in four depths). Small blocks of calcite, micrite and mollusk shells have successfully been used for microendolithic analyses before, which make our study well comparable to others (i.e., Golubic et al. 1975; Kiene et al. 1995; Wisshak et al. 2005).

The carbonate cubes were interspersed randomly on three PVC-plates per depth within each of the two habitats (six plates total per depth and 24 plates all together), and cubes were attached to the plates using Aquamend Underwater Epoxy. The plates were fastened with a heavy weight at the sea floor with the cubes oriented toward the water surface.

Two types of habitat were examined at each depth. Open habitats were areas on the reef slope directly exposed to light from the surface. Shaded habitats consisted of shallow caves, small holes, and reef crevices that were partially shaded from direct sunlight.

For the 0-m experiments, we used the poles of the landing stage on the boat pier of the IUI. The open habitat experiment was fastened at one of the exposed poles. For the shaded habitat, a position at one of the inner poles under the pier was used. The experiments were positioned right below the water surface at low tide, which ensured a continuous submersion of the substrates for most of the time. In contrast to all other depths, the PVC-plates at 0 m depth could not be positioned parallel to the water surface. They were attached to the poles at an angle of approximately 45°.

Preparation of substrates

Shell substrates yield the best results for scanning electron microscopy (SEM) because resin casts of microborings have smooth and undisturbed surfaces (Golubic et al. 1975). Calcite spar is translucent and allows rapid identification of species under the light microscope. The orientation of different microendolithic colonies can be viewed directly in situ. Micrite is known to be a very attractive substrate for microendoliths and is usually densely bored (Gektidis 1997). With micrite, great care was taken to isolate the microendoliths from their surrounding substrate to ensure a successive and intact transfer of all endolithic material onto glass slides. First, the upper layer of carbonate containing an epilithic carpet of fleshy algae was mechanically removed from the substrate cube under optical control, using a low power microscope (Zeiss Stemi SV 11). Then, the cleaned carbonate cube was exposed for 5–10 s to Perenyi solution (30 ml 0.5% chromic acid, 40 ml 10% nitric acid, 30 ml 90% ethanol), which dissolves calcium carbonate in order to loosen the incrusting epiliths. After all the epiliths were removed, the substrate was rinsed with a pressurized jet of water from a spray-bottle and re-exposed to diluted Perenyi solution (1:10) for about 1 min. The impact of the acid freed the microendolithic algae from their surrounding substrate. The now exposed microendolithic carpet was flushed by a jet of water into a small glass bowl (1 cm in diameter). It was then transferred to a drop of water on a glass slide using slightly opened pincers, prepared for microscopy and viewed under a Nomarski

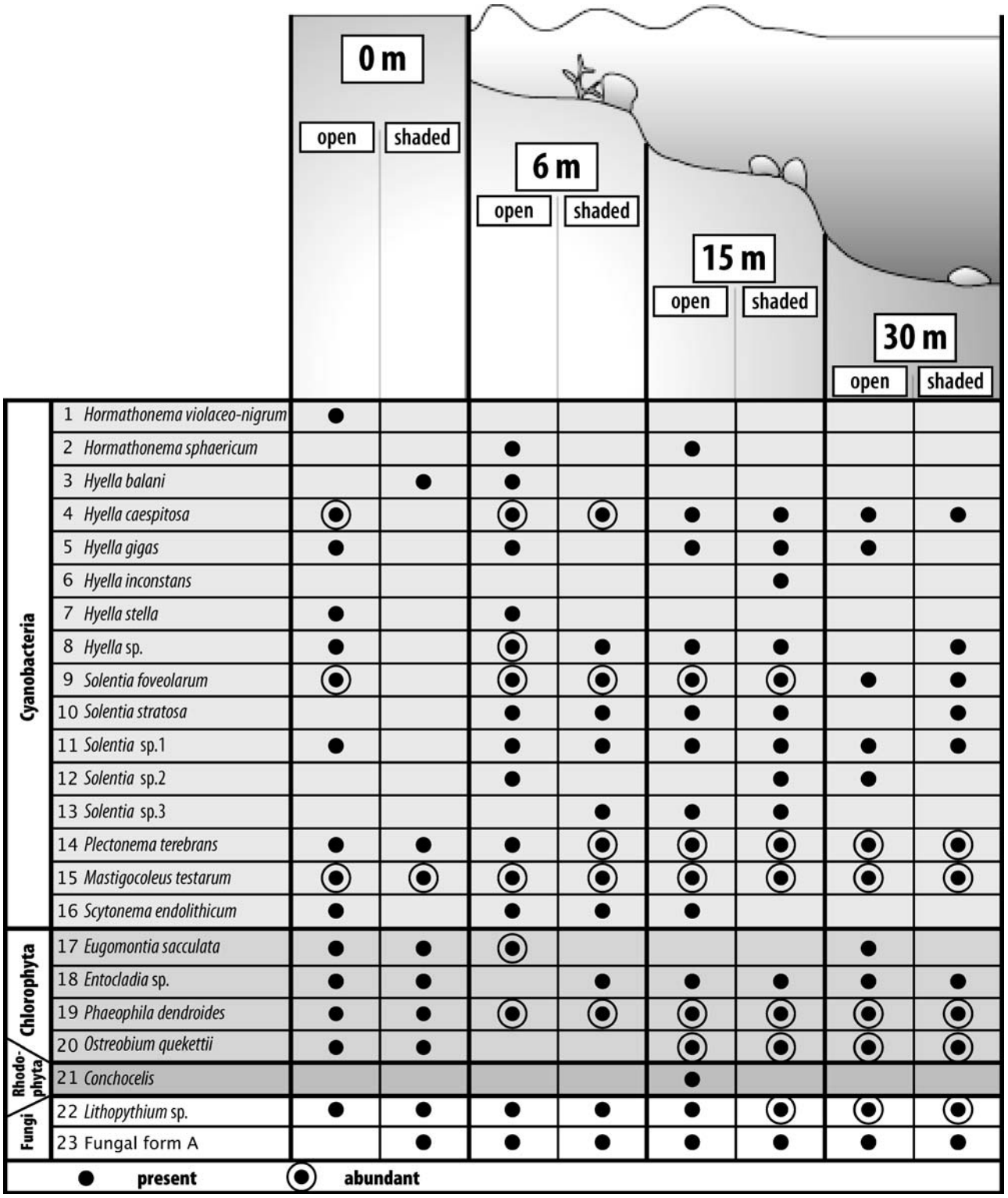


Fig. 1 Distribution and taxonomic diversity of microendoliths in experimental carbonate substrates along a bathymetric gradient on the coral reef slope at Eilat, northern Red Sea

microscope (Zeiss Axioskop). The extraction was repeated until no more colonies were visible. This procedure ensured the preservation of the original orientation of the microendoliths in the carbonate substrate. All species that were identified in one substrate comprised the biocoenosis of this substrate.

A non-quantitative comparison of the abundance of extracted microendoliths was performed among the six mi-

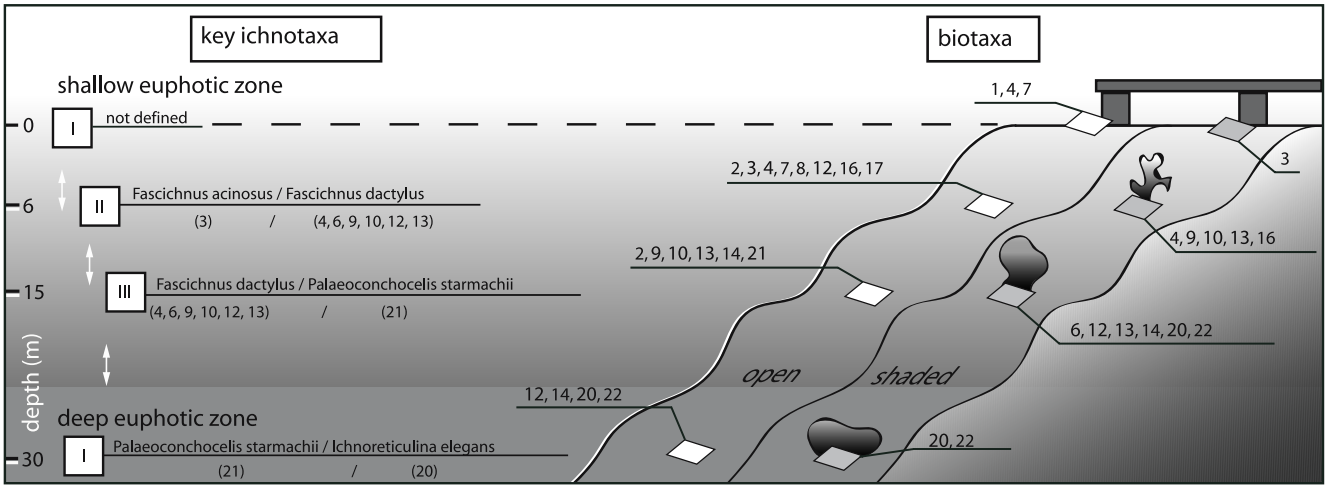


Fig. 2 Illustration of the Shallow Euphotic Zones from I to III, and the Deep Euphotic Zone on the basis of fossil key ichnotaxa. *White arrows* indicate that boundaries between the zones are subject to variations. On the *right side*, a bathymetric profile shows the occurrence of the dominant microendoliths of this study at each depth and habitat (*numbers* for taxa are taken from Fig. 1). Possible producers of key-ichnotaxa are shown in *bold numbers*

crite cubes per depth. Only the micrite cubes were used for the estimation of abundance, because controlled and successive dissolution of this carbonate substrate ensured comparable results between the cubes. In contrast, calcite spars easily break and splinter during processing, which results in a loss of carbonate and microendoliths. Species are rated here as "present" or "abundant." "Present" species occurred in 1–3 and "abundant" species in >3 cubes of micrite.

For SEM observations, the shell-substrates were freed from organic material in a bath of hydrogen peroxide. They were then impregnated with a high viscosus resin that filled the boreholes. After the resin dried, the surrounding carbonate was dissolved with 10% HCl (Golubic et al. 1970). The resulting three-dimensional resin cast of the boring trace community was sputtered with gold and then viewed under the SEM. All traces identified in one cast formed the trace community of this substrate.

Taxonomic identification

The following publications were used for the identification of microendoliths: Al-Thukair and Golubic (1991a,b, 1996), Bornet and Flahault (1889), Ercegovic (1927, 1929, 1930, 1932), Geitler (1932), Kornmann (1959) and Le Campion-Alsumard and Golubic (1985a,b).

For the taxonomic identification of extracted microendoliths on a morphometrical basis, we ensured measurements (>20) of cell diameters, ramifications (angles), tube diameters, distances between cells and between ramifications, distance between the apical cell and the proximate vegetative cell, and, if in existence, observation of reproductive cells, heterocysts or other specialized cells and the preparation of casts.

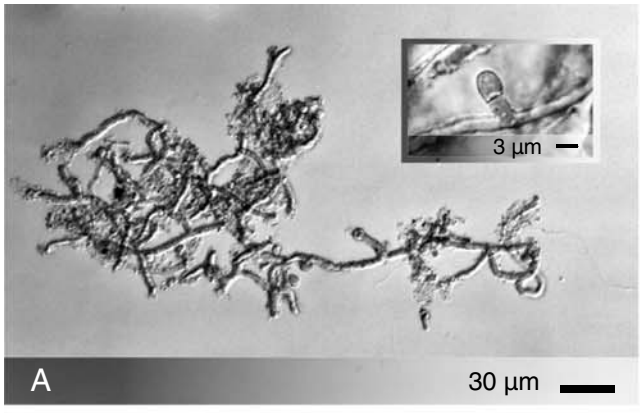
Results

Microendolithic distribution

Twenty-three types of microendoliths were found in our experimental substrates. Figure 1 summarizes their distribution along the reef slope down to 30 m. We found the following cyanobacteria: *Hormathonema violaceo-nigrum*; *Hormathonema sphaericum* (Fig. 4A); *Hyella balani* (Fig. 3E); *Hyella caespitosa*; *Hyella gigas*; *Hyella inconstans* (Fig. 3F); *Hyella stella*; *Solentia foveolarum* (Fig. 4C); *Solentia stratosa* (Fig. 4D); *Plectonema terebrans* (Fig. 3G); *Mastigocoleus testarum* (Fig. 3A); *Scytonema endolithicum* (Fig. 4B); four chlorophyta: *Eugomontia sacculata* (Fig. 5G); *Entocladia* sp. (Fig. 5A); *Phaeophila dendroides* (Fig. 5C); *Ostreobium quekettii* (Fig. 5E); one rhodophyte: *Conchocelis* (Fig. 5H); and one microendolithic species of fungal origin: *Lithopythium* sp. (Fig. 6F).

The following microendolithic organisms did not match published descriptions of species, and are therefore listed as forms: Four cyanobacteria named *Hyella* sp. (Fig. 3C); *Solentia* sp. 1 (Fig. 4E, F); *Solentia* sp. 2 (Fig. 4G); *Solentia* sp. 3 (Fig. 4H); and one heterotroph named fungal form A (Fig. 6A–E).

Fig. 3 **A** *Mastigocoleus testarum* (phylum: Cyanobacteria; order: Stigonematales) extracted from micrite with detail (*scale* is 3 µm) of a heterocyst. **B** SEM-cast of *Eurygonum nodosum*. The assumed producer of this trace is *Mastigocoleus testarum*. **C** Branched thallus of *Hyella* sp. (phylum: Cyanobacteria; order: Pleurocapsales) in situ in a calcite spar. **D** SEM-cast of *Fascichnus* sp. The assumed producer of this trace is *Hyella* sp. **E** Small colony of *Hyella balani* (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite. **F** Colony of *Hyella inconstans* (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite. **G** Colony of *Plectonema terebrans* (phylum: Cyanobacteria; order: Nostocales) extracted from micrite. **H** SEM-cast of *Scolecia filosa*. The assumed producer of this trace is *Plectonema terebrans* ▶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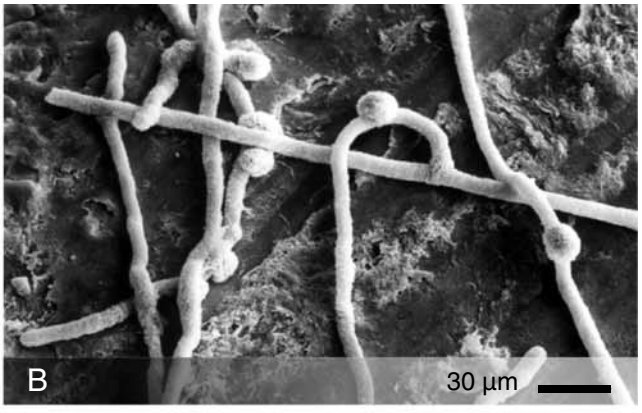
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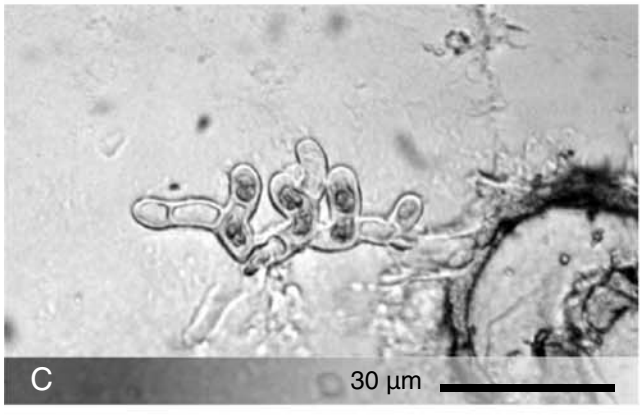
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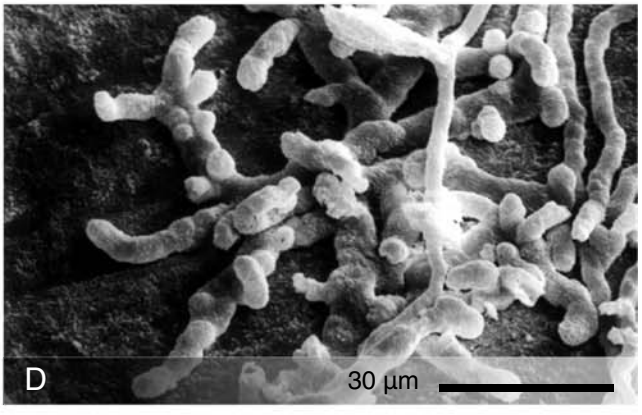
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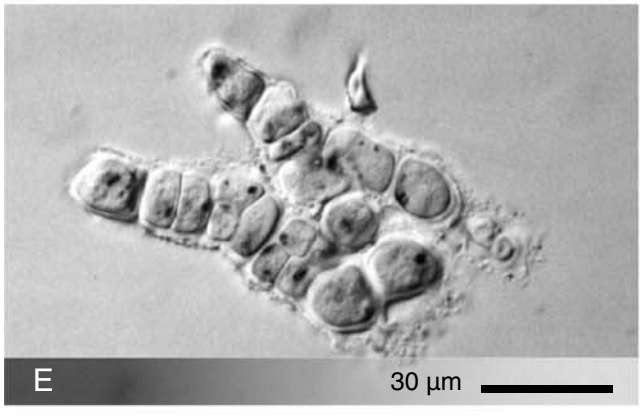
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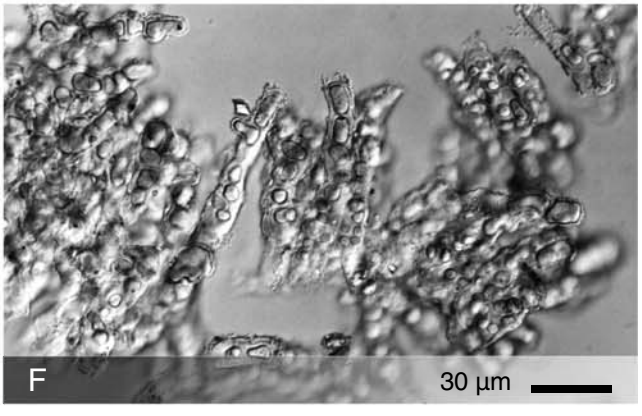
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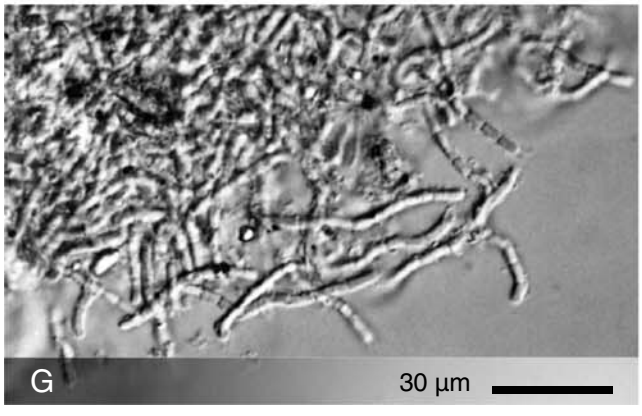
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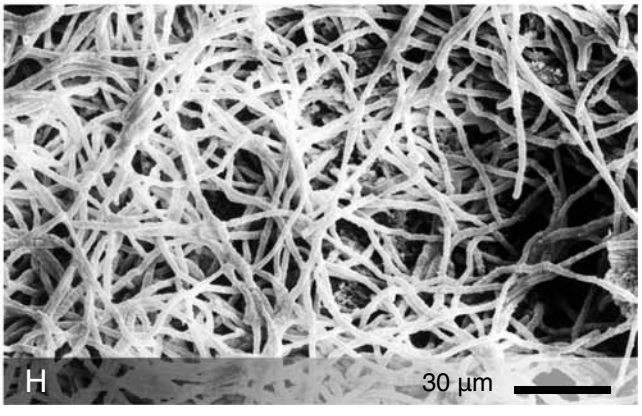
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Description of forms

Hyella sp.

This species grows in small colonies with many branchings. Dimensions of vegetative cells range from 7.5 to 11.6 μm in length and 4.1 to 5.8 μm in width ($n = 28$). Apical cells are often smaller than subapical cells and range from 5.2 to 6.6 μm in length and 5 μm in width ($n = 22$). Diameters of thalli range from 6.5 to 7.5 μm ($n = 23$). Thalli are organized in single rows of cells. Distances between the cells ranges up to 1.3 μm. Baeocytes were not observed.

Solentia sp. 1

This species grows in dense colonies from which long "exploratory" filaments extrude. Dimensions of vegetative cells range from 30 to 92 μm in length and 4.4 to 10 μm in width ($n = 23$). Apical cells are elongated, slightly bended at their tip, and their dimensions range from 39 to 65 μm in length and 6.9 to 9.2 μm in width ($n = 19$). The distance from apical to subapical cells can reach up to 69.7 μm ($n = 19$). Thalli are organized in single rows of cells and range between 9.2 and 11.5 μm in diameter ($n = 23$). The typical layers of mucus that usually form beneath the apical cell in all other known species of *Solentia* were not observed. Instead, a horizontal layering of mucus exists inside the thallus. We assume that the apical cell does not restrict mucus secretion to its basal part like most other *Solentia* species do, but instead secretes along its whole axis with exception of its terminal part where the boring activity takes place. This enhances pressure inside the tube of the thallus. The apical cell is pressed forward and simultaneously squeezed at its sides. As a result, apical and subapical cells display an elongated morphology with cells up to 23 times longer than they are wide. Baeocytes were not observed.

The dimensions and habitus of this form are comparable to *Solentia intricata* Ercegovic (1927). However, the length of apical cells exceeds *Solentia intricata* by a factor of two. The horizontal layering of mucus is not reported from *Solentia intricata*.

Solentia sp. 2

This species grows in dense colonies with thick filaments. Vegetative cells are round to oval-shaped and range from 16.6 to 18.7 μm in length and 14.3 to 18.7 μm in width ($n = 25$). Apical cells are more often oval-shaped than round and have diameters ranging from 30 to 42.8 μm in length and 15.4 to 20 μm in width ($n = 20$). The distance from apical to the subapical cell can reach up to 115 μm ($n = 12$). Thalli are organized in single rows of cells and range between 18.75 and 37.5 μm in diameter ($n = 25$). Baeocytes were not observed.

Solentia sp. 3

This species grows in small colonies from which long filaments extrude. Vegetative cells have diameters between 8.6 and 13.1 μm in length and 5.7 and 7.9 μm in width ($n = 22$). Apical cells range from 15 to 21.8 μm in length and 6.8 to 9.5 μm in width ($n = 20$). The distance from apical to subapical cell reaches up to 88.2 μm ($n = 14$). Thalli are organized in single rows of cells and range between 8.3 and 10.9 μm in diameter ($n = 22$). Baeocytes were not observed.

Fungal form A

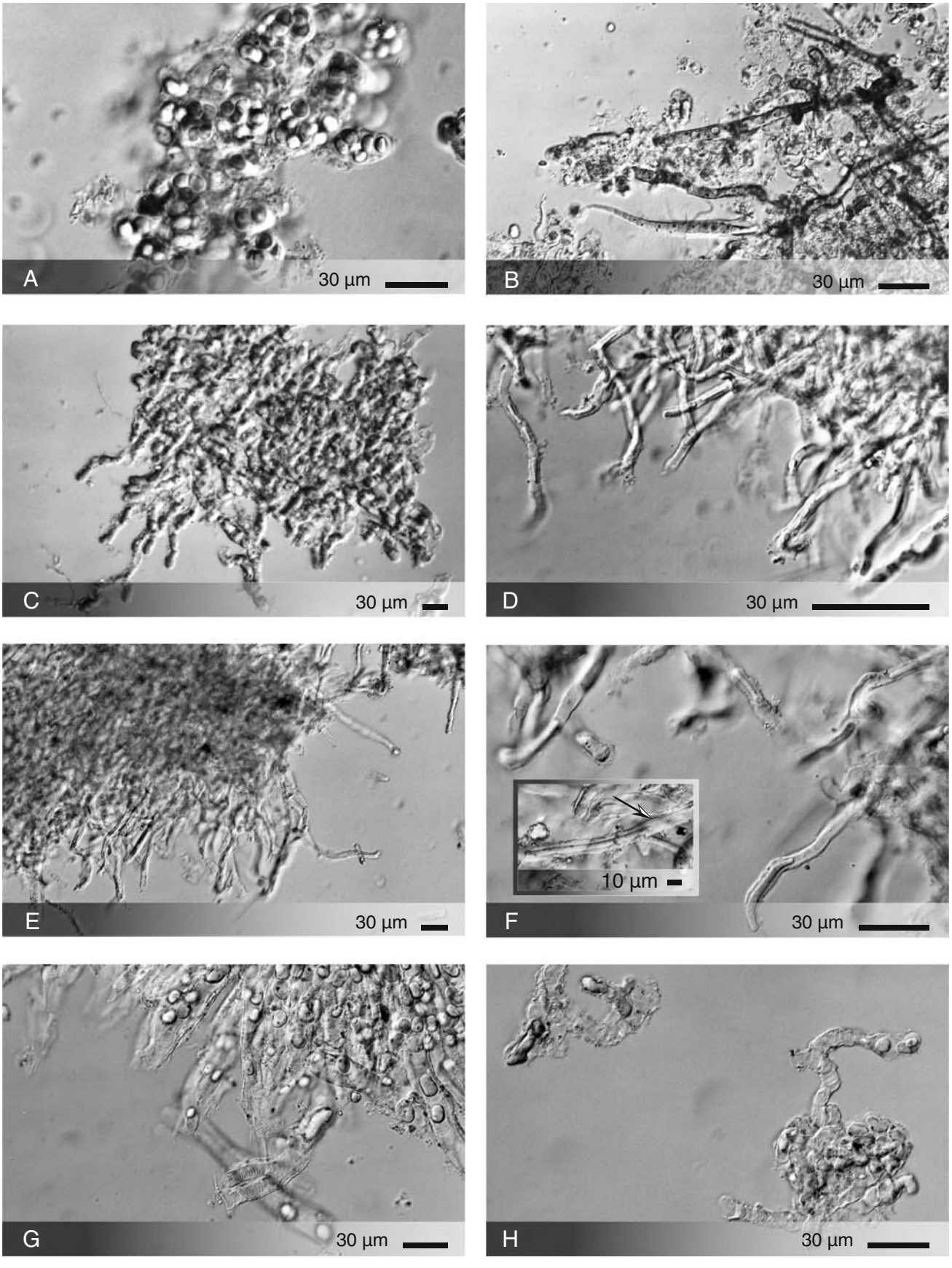
This form builds extended, branched networks. Hyphae have diameters between 1.1 and 2.1 μm ($n = 25$). We observed intercalar as well as terminal swellings. Swellings are organized in one or numerous bulbs. Bulbs are either lined up like beads (Fig. 6E, F) or branch from a central part to form a tree-like swelling (Fig. 6C). The mode of branching remains unknown.

Microendolithic community structure

The taxonomic composition of the microendolithic community varied with depth on the reef slope (Fig. 1). The intertidal community (0 m depth) consisted of 11 types of cyanobacteria, four chlorophyta, and two heterotrophs. The mid-slope community at 6–15 m was comprised of 15 types of cyanobacteria, four chlorophyta, one *Conchocelis*, and two heterotrophs. The deep-slope community at 30 m was less diverse, with nine cyanobacteria, four chlorophyta, and two heterotrophs. *Mastigocoleus testarum* and *Phaeophila dendroides* were abundant in all substrates. *Mastigocoleus testarum* was more common than all other microendoliths at Eilat. The abundance of *Lithopythium* sp. increased substantially in the deepest habitats.

The differences between microendolithic biocoenoses of open and shaded habitats decreased down the reef slope. At 0 m, eight species (all cyanobacteria) were found exclusively in the open but only two species (one cyanobacterium and one heterotroph) in the shaded habitat. At 6 m, six species (five cyanobacteria and one chlorophyte) were restricted to the open habitat and two species (one cyanobac-

Fig. 4 **A** Colony of *Hormathonema sphaericum* (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite. **B** Network of *Scytonema endolithicum* (phylum: Cyanobacteria; order: Hormogonales) extracted from micrite. **C** Colony of *Solentia foveolarum* (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite with its typical habitus of distant apical cells. **D** Thalli of *Solentia stratosa* (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite. **E**, **F** Colonies of *Solentia* sp. 1 (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite. In the *detail-box* (**F**; *scale* is 10 μm) the *arrow* points to the layering of the sheath. **G** Thalli of *Solentia* sp. 2 (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite **H** Small colony of *Solentia* sp. 3 (phylum: Cyanobacteria; order: Pleurocapsales) extracted from micrite ▶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terium and one chlorophyte) to the shaded habitat. The open and shaded habitats at 15 and 30 m differed in one species only.

Figure 2 compares the microendolithic taxa of this study with key ichnotaxa from the system of photic zonation (Glaub et al. 2002). Fossil carbonates are attributed to the SEZ II, if an ichnocoenosis contains the traces *Fascichnus acinosus* and *Fascichnus dactylus*. The assumed producer of *Fascichnus acinosus* is *Hyella balani,* which was found in carbonates from 0 m shaded habitat and 6 m open habitat. The assumed producer of *Fascichnus dactylus* is *Hyella caespitosa,* which was found in all habitats except 0 m shaded.

The SEZ III is defined by *Fascichnus dactylus* and *Palaeoconchocelis starmachii*. The assumed producer of *Palaeoconchocelis starmachii* is *Conchocelis,* which was found once in an open habitat at 15 m.

The DEZ is defined by *Palaeoconchocelis starmachii* and *Ichnoreticulina elegans*. The assumed producer of *Ichnoreticulina elegans* is *Ostreobium quekettii*, which was found in all habitats except 6 m.

Discussion and conclusions

The Shallow Euphotic Zone of Eilat supports a microendolithic biocoenosis that is well comparable to other tropical coral reef habitats (i.e., Golubic et al. 1975; Hoffman 1985; Mao Che et al. 1996). Eilat near the northern most limit of tropical coral reef distribution does not support a specialized or endemic population of microendoliths.

Our findings are consistent with results from a study that was conducted further south at Safaga Bay (Radtke and Golubic 2005) and a study that took place 20 years earlier at Eilat (Potts 1980). Table 1 gives an overview of species that were found at comparable depths in all three studies.

Variations in species composition between the three studies result from the different experimental designs. Radtke and Golubic (2005) collected shells from different habitats. As additional taxa, they reported four more species of *Hyella* (*H. salutans*, *H. pyxis*, *H. reptans* and *H. gelatinosa*), *Cyanosaccus*, *Codiolum* stages, *Phaeophila tenuis* and the *Acetabularia* rhizoid. They show a picture that might have emerged in our experiments if we had expanded our exposure-time to two or more years. With time, more and more microendolithic as well as epilithic biomass builds up and changes conditions in the substrate. A shift in species composition usually follows (Gektidis 1999a; Vogel et al. 2000). Potts (1980) had focused his study on cyanobacteria in the intertidal zone and collected fragments with unknown exposure-times as well. He reports the occurrence of one additional species, *Kyrtuthrix dalmatica*.

The stability and predictability of microendolithic zonation along a modern reef slope provides the basis for actuopaleontolgical interpretations. Neither geographical variations nor succession of time have an effect on the fundamental pattern of microendolithic depth distribution as it was presented by Golubic (1969) and as it was found for the Euphotic Zone in our experiments: Cyanobacteria prefer supra- and intertidal habitats (i.e., Schneider 1976; Schneider and Torunski 1983; Radtke et al. 1996), shallow waters are inhabited by all known microendolithic taxa in more or less equal proportions (i.e., Perkins and Tsentas 1976; May et al. 1982; Chazottes et al. 1995; Perry and Macdonald 2002), and where light gets scarce, low light specialists among the phototrophs plus heterotrophs populate the dysphotic benthos (Zeff and Perkins 1979; Bentis et al. 2000; Golubic et al. 2005). Only heterotrophic microendoliths are able to explore the aphotic benthic zones of the oceans (i.e., Hook and Golubic 1993; Freiwald et al. 1997).

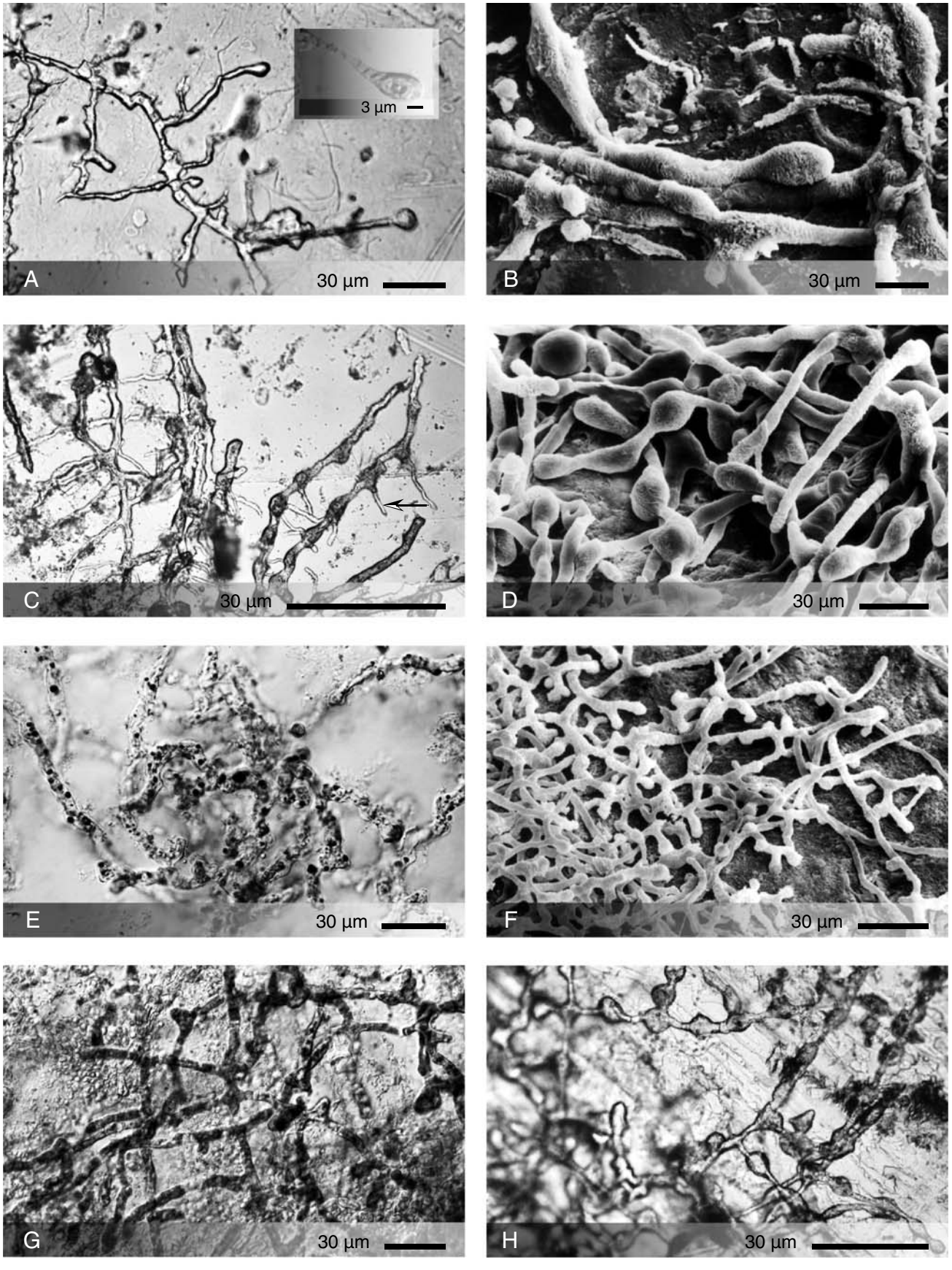
This pattern, however, provides only four zones for actuopaleontological interpretations: the intertidal, shallow-water, dysphotic, and aphotic zone. The desire for paleontologists to enhance the resolution of the method is expressed in their search for key-ichnotaxa and their modern producers that show narrow depth ranges, respectively. So far, key-ichnotaxa from fossil environments allow the division of the Shallow Euphotic Zone into three parts from which the upper part is not defined (Fig. 2). Figure 2 also displays how results from this study fit into this profile. We focused on microendoliths of the Shallow Euphotic Zone and searched for key-taxa with two characteristics: First, a need for specific light conditions resulting in a narrow depth-range, and second, a distinctive morphology reflected in its trace.

Only one taxon, found in our experiments in sufficient numbers, *Hyella balani* (*Fascichnus acinosus*), fulfilled these requirements and may prove useful for this type of analysis. *Hyella balani* occurred only in substrates from 0 m shaded and 6 m open habitats. Our results match known occurrences of this microendolith (Le Campion-Alsumard and Golubic 1985b; Schneider 1976). This stenobathic distribution pattern is coupled with a distinctive morphology of producer and trace alike.

All other candidates showed distribution patterns that either reduced their value as producers of key-ichnotaxa or ruled them out completely or were found in insufficient numbers to draw any conclusions of their occurrence, as it was the case with *Conchocelis*.

Three different species (*Hyella caespitosa*, *Hyella inconstans*, *Solentia stratosa*) and four forms (*Hyella* sp., *Solentia* sp. 1, *Solentia* sp. 2, *Solentia* sp. 3) can serve as potential producers of *Fasciculus dactylus*. Radtke and Golubic (2005) report as much as seven species of *Hyella*

Fig. 5 **A** *Entocladia* sp. in a calcite spar. The *detail-box* (*scale* is 3 μm) shows the typical club-shaped ending. **B** SEM-cast of *Rhopalia* sp. The assumed producer of this trace is *Entocladia* sp. The club-shaped endings are typical for this chlorophyte. **C** *Phaeophila dendroides* (phylum: Chlorophyta; order: Phaeophilales) in a calcite spar. *Arrow* points to a typical hair. **D** SEM-cast of *Rhopalia catenata*. The assumed producer of this trace is *Phaeophila dendroides*. **E** *Ostreobium quekettii* (phylum: Chlorophyta; order: Siphonales) extracted from micrite. **F** SEM-cast of *Ichnoreticulina elegans*. The assumed producer of this trace is *Ostreobium quekettii*. **G** *Eugomontia sacculata* (phylum: Chlorophyta; order: Chaetophorales) extracted from micrite. **H** *Conchocelis* (phylum: Rhodophyta; order: Porphyrales) in a calcite spar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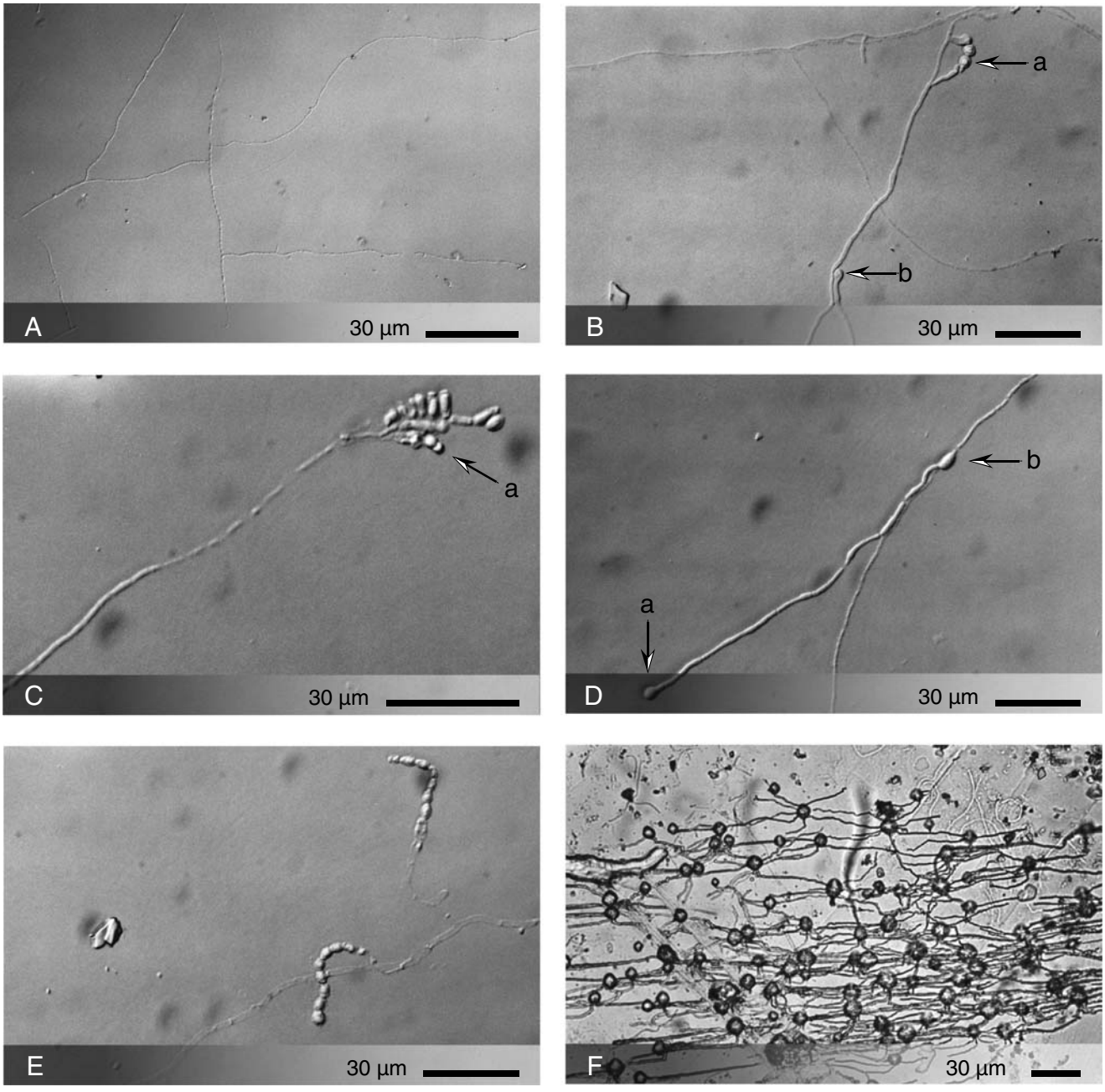

Fig. 6 **A** Fungal form A. A typical angular boring pattern is shown. **B** Fungal form A with terminal bulbous swellings: (a) chain-like terminal swellings (b) single swelling. **C** Fungal form A with terminal bulbous swelling: (a) terminal swellings with tree-like appearance. **D** Fungal form A with terminal bulbous swellings; (a) terminal swelling (b) intermediate swelling. **E** Fungal form A with chain-like terminal swellings. **F** *Lithopythium* sp. in a calcite spar

and one *Solentia* as possible producers of this trace. However, all these species are photoautotrophic and occur in the upper photic zone. As a consequence, we recommend to use *F. dactylus* as an indicator for shallow waters only, if found together with *F. acinosus*.

Hormathonema violaceo-nigrum and *H. sphaericum* are both stenobathic but the coccoid habitus of the colonies is reflected in the production of indistinct traces. They appear as unbranched balls and tips in a cast. Their value as key-ichnotaxa is therefore small.

In our experiments, *Hyella stella* provides a good candidate for a key-ichnotaxon. It is stenobathic (0 m open and 6 m open) and produces a distinctive trace, described as the body fossil *Eohyella dichotoma*. However, this microendolithic species has been reported from deeper zones as well, for example by Radtke and Golubic (2005) from 10 m (Table 1). Therefore, the narrow depth-range we found in Eilat cannot be viewed as a characteristic of *Hyella stella* and an indication as key-ichnotaxon is not supported.

Table 1 Depth ranges of microendoliths in comparison to Potts (1980) and Radtke and Golubic (2005)

Organism/locality	Eilat depth range (m)	Gulf of Elat (Potts 1980) depth range (m)	Safaga Bay (Radtke and Golubic 2005) depth range (m)
Cyanobacteria			
Hyella caespitosa	0–30	Intertidal, lithified rock	1–22, not at 17 m
Hyella inconstans	15	–	1–17, not at 10 m
Hyella stella	0–6	–	10
Plectonema terebrans	0–30	–	1–22
Mastigocoleus testarum	0–30	Lower littoral, beachrock	10–22
Solentia stratosa	6–30	Lower littoral, rocks	–
Chlorophyta		Not included	
Phaeophila dendroides	0–30		10–20, not at 17 m
Ostreobium quekettii	0–30		17–22

Mastigocoleus testarum, *Plectonema terebrans* and *Phaeophila dendroides* produce characteristic traces but they are highly tolerant to variable light conditions. They were found in all substrates and all habitats of our experiments. As a consequence, their affiliated traces *Eurygonum nodosum*, *Scolecia filosa* and *Rhopalia catenata* plus the newly described *Rhopalia spinosa* (Radtke and Golubic 2005) are irrelevant as key ichnotaxa.

Finally, *Ostreobium quekettii*, the producer of *Ichnoreticulina elegans*, is known to be a specialist for low-light conditions. As such, *Ichnoreticulina elegans* serves as key-ichnospecies for deeper zones (Fig. 2). The preference of *Ostreobium quekettii* for darker habitats was visible in our experiments as well (Fig. 1). However, its usefulness as producer of a key-ichnotaxon is reduced by its ability to inhabit living corals from shallow waters as well (Shashar and Stambler 1992; Schlichter et al. 1995). Merely in zones, where the only other microendoliths are heterotrophs, its value as an indicator for the lower limit of the photic zone is expressed.

We expected to find differences in species composition between open and shaded habitats comparable to the transitions found by Perry and Macdonald (2002) between sites with different light conditions (due to the impact of enhanced turbidity). In their study from Jamaican reef environments, the authors report that the depth range of the microendolithic assemblages was reduced in turbid waters when compared to clear-water sites. We were surprised to find little evidence for a similar trend in our experiments. We had expected to find two distinct communities per depth, one open and one shaded community. Ideally, shaded communities of one depth would comprise of the same species as open communities of the following depth. But the picture that emerged was different: with increasing depth, shading provoked a gradual decline of differentiation between both habitats. At 0 m, shading resulted in a clear separation of microendoliths into an open habitat and a shaded habitat community. This obvious differentiation, marked by the absence of more than 50% of species in the shaded habitat, quickly faded down the reef slope. At 6 m, only 33% of the species at this depth were absent in the shaded habitat. This trend continued with 15% absence at 15 m and 18% at 30 m. Conversely, a constant 10–12.5% of species from the shaded habitat community were absent in the open habitats throughout the transect. No increase or decrease was observed here.

We conclude that shading has a large impact on the intertidal community, a low impact on the upper shallow-water community, and no visible impact on the lower shallow-water community. The shaded intertidal community is characterized by the absence of approximately 60% of the cyanobacteria from this depth and its composition is comparable to an upper shallow-water community. In paleo-environments, this effect presents an obstacle for the identification of intertidal carbonates—an additional explanation why key-ichnotaxa for this zone have yet to be defined. Another reason lies in the enhanced erosion of supra- and intertidal carbonates by organisms and waves (Schneider 1976; Schneider and Le Campion-Alsumard 1999), which reduces the chances of traces in such habitats to prevail throughout earth history. Apart from the intertidal experiments, shading has not influenced the development of microendoliths in any measurable way.

Outlook

With time, the high-diversity microendolithic species exhibit in shallow waters will lead to the discovery and description of species that can serve as new key-ichnotaxa for actuo-paleontological comparisons. But if we decide to actively search for such candidates, we will have to set up more sophisticated experiments (i.e. parallel measurement of physical parameters; employment of both, shaded and open, habitats per depth, short to long exposure times, microphotography of colony-development) and standardize the use of reliable techniques for the identification of both, producer and trace, as for example the double-inclusion technique and the morphometrical analysis of microendolith and trace alike. Otherwise, only half of the story will

be found, either microendoliths without traces or traces without producers.

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