# The Distribution of Microborings in Molluscan Shells from Recent Reef Environments at Lee Stocking Island, Bahamas

Gudrun **Radtke**, Mainz

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DFG-Schwerpunkt
BIOGENE SEDIMENTATION

Riff-Evolution und Kreide-Sedimentation

## SUMMARY

The distribution of microbial borings in bivalve shells was assessed between five research sites in windward and leeward environments at the Lee Stocking Island, Bahamas. The research sites are on windward coral reefs (sites B at 2 m, F at 12 m, and C at 30 m), a tidal channel stromatolite reef (site A at 5 m), and a leeward hard ground reef (site D at 3 m). A total of 22 ichnotaxa have been recognized within 100 samples. Each site contained between 14 and 17 ichnotaxa. Although the diversity of microborings, expressed both as number of taxa and number of individuals per taxon, is similar between sites, the following ranking (in descending order) was found: B-F-A-C-D. *Rhopalia catenata* was found to dominate at site D, while *Reticulina elegans* dominated at site C, and *Fasciculus dactylus* dominated at site F. The results are in accordance with the known bathymetric distribution of the boring microorganisms.

## 1 INTRODUCTION

The processes of reef sediment production has been important in reef environments throughout geological history. As a result, detailed studies of reef destructive processes and their mechanisms should provide new information about the development of fossil and Recent reefs. The process of 'bioerosion' is a major destructive process on modern reefs and it has a long fossil history (WARME, 1975; VOGEL, 1993). Therefore, bioerosion is an important link between Recent reef processes and the geological and the paleontological evolution of reefs.

Organisms that bore $CaCO_3$ skeletons include macroscopic sponges, molluscs and worms, and a variety of microscopic thallophytes. The existence of macroboring sponges, molluscs, and worms has been well documented in modern environments (HUTCHINGS, 1986), but the fossil record indicates that macroboring organisms only became important on reefs in the Mesozoic (VOGEL, 1993). Trace fossils of microboring thallophytes, that are comparable to modern types, have existed since the Precambrian (ZHANG

& GOLUBIC, 1987; VOGEL, 1993). However, very little is known about boring thallophytes on modern reefs. To investigate the factors that control the diversity, distribution and colonization rates of microendolithic thallophytes in reef environments, experiments have been established at Lee Stocking Island, Bahamas. These experiments are exposing a variety of carbonate substrates to microborer infestation in different environments for varying lengths of time. This paper presents an inventory of borers found in dead mollusc shells collected at the experimental sites and provides a basis for comparing the results from the experimental substrates with the microendolith community in 'natural' reef substrates.

## 2 MATERIALS AND METHODS

Lee Stocking Island is located in the southern Exuma Islands chain at the eastern edge of the Great Bahama Bank and facing the Exuma Sound (Fig. 1). The bioerosion experiments have been established in six sites near the Caribbean Marine Research Center (CMRC) at Lee Stocking Island in different water depths that exhibit different environmental conditions and bottom character:

Site A: Tidal channel stromatolite reefs and ooid sand dunes, 4-5 m water depth with strong tidal currents.

Site B: Windward *Acropora palmata* reef, 2-3 m water depth with strong wave energy conditions.

Site C: Windward shelf edge reef, 30 m water depth with weak water movement.

Site D: Leeward hard ground reef, 2-3 m water depth with strong tidal currents.

Site E: Leeward, *Callianassa* burrowed, sediment bottom with *Thalassia*, 2 m water depth with weak tidal currents.

Site F: Windward reef, 10 to 12 m water depth with moderate water movement.

A total of 100 molluscan shells of dead bivalves (*Cardium*, *Laevicardium, Pecten, Periglypta listeri, Tellina magna, Lima,*

Address: Dr. G. Radtke, Landesamt für Denkmalpflege, Am Obstmarkt 13, D-55126 Mainz-Finthen
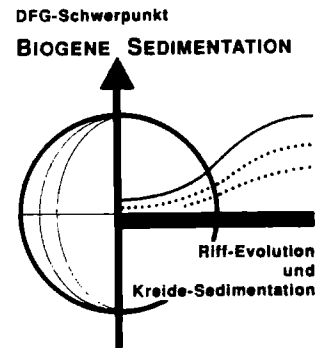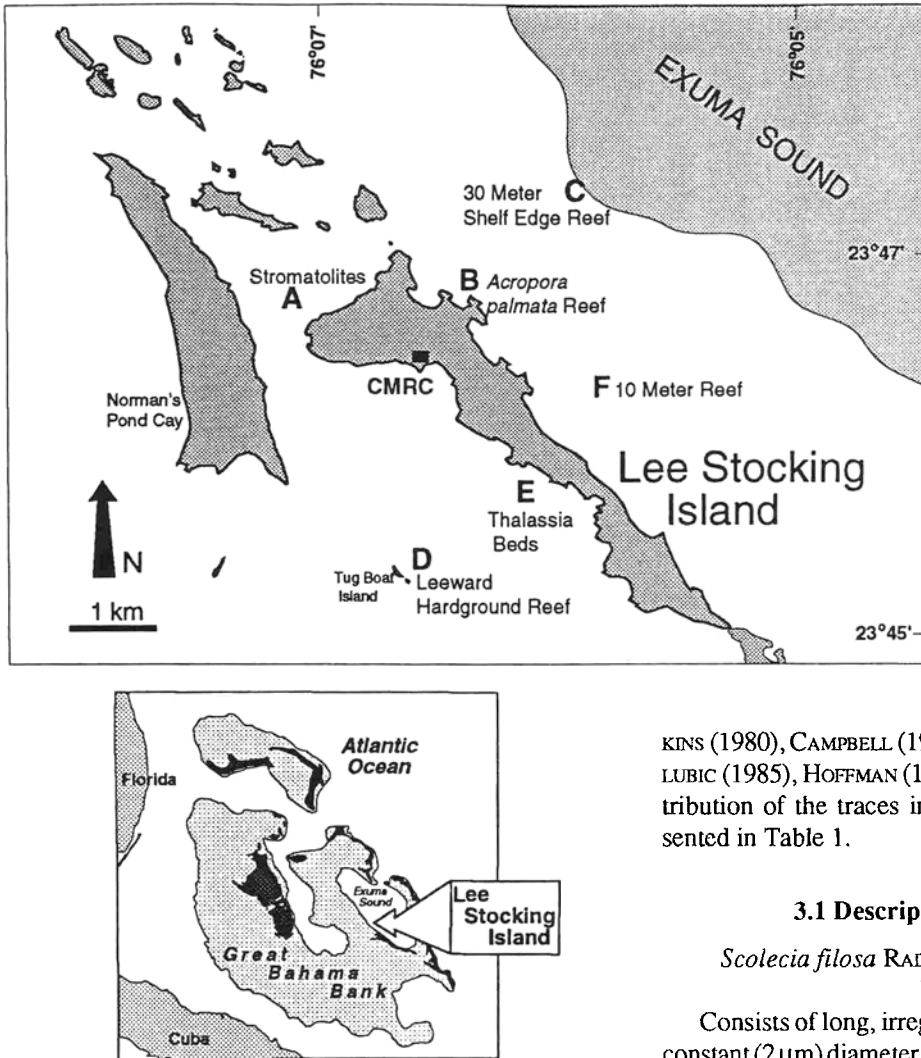
Fig. 1. Map of the sample localities (sites A to F) near the Caribbean Marine Research Center (CMRC) at Lee Stocking Island, Bahamas.

*Macoma constricta* and other indeterminate bivalve shells) were collected from the sites in October 1991, February 1992, and October 1992. No collections were made at site E because of the lack of shell material caused by extensive *Callianassa* bioturbation that makes this site unfavorable for bivalves. Shells were initially examined under a dissecting microscope at CMRC and areas infested by endoliths were marked. The shells were then packed in formalin and transported to Frankfurt for further study. A technique employing cast-embedding, as described by GOLUBIC et al. (1970; 1983), was used to reveal borings and these casts were gold coated and photographed with a SEM. These SEM photographs (approximately 600) were used to determine the species of microboring and allow comparison of their morphology with casts of other endolithic organisms.

## 3 RESULTS

Traces of 22 different endolithic microborers were found to occur in the shell material from the five different sites. These microborings were comparable with traces made by

bacteria, cyanobacteria, green and red algae, fungi, and sponges. However, some traces were of unknown taxonomic affinity and did not relate to a particular species. For this reason, the studied traces and their resin casts are described here as ichnotaxa, following the recommendations of TAVERNIER et al. (1992). The majority of the ichnotaxonomy was based on traces found in fossils from the Early Tertiary of Western Europe (RADTKE, 1991). Further interpretation of the organisms that produced the traces was carried out using the following literature sources: EDWARDS & PERKINS (1974), SCHNEIDER (1976), PERKINS & TSENTAS (1976), ZEFF & PERKINS (1979), LE CAMPION-ALSUMARD (1979), BUDD & PERKINS (1980), CAMPBELL (1983), LE CAMPION-ALSUMARD & GOLUBIC (1985), HOFFMAN (1985) and GÜNTHER (1990). The distribution of the traces in the area of investigation is presented in Table 1.

### 3.1 Description of microborings

*Scolecia filosa* RADTKE (RADTKE, 1991: Pl. 8/3)
Plate 15/1

Consists of long, irregularly curved tunnels of relatively constant (2 μm) diameter. The tunnels commonly make loops within the substrate. This trace is comparable with traces made by the cyanobacterium *Plectonema terebrans* BORNET & FLAHAULT. LUKAS (1978) reports the distribution of *P. terebrans* in depths ranging from 0 to 370 m.

This trace was present at all 5 investigated sites. The greatest abundance occurred at site A (stromatolite reef, 4 to 5 m).

*Scolecia serrata* RADTKE (RADTKE, 1991: Pl. 8/4)

This microboring forms closely packed, often fused, tunnels (ø 0.5 to 1 μm) that expand horizontally immediately below the substrate surface. Accordingly the resin cast of this borings appears as a mat-like cover. The producer of this boring is unknown, however FREMY (1945) attributes this form to filamentous bacteria. This trace is found in the modern ocean, mainly in deep water (800 to 1600 m) indicating a heterotrophic nature of its maker.

*Scolecia serrata* occurred at all 5 investigated sites. It was most common at site A and B, but occurred in slightly greater abundance at site B (*Acropora palmata* reef, 2-3 m).

*Scolecia maeandria* RADTKE (RADTKE, 1991: Pl. 7/6; 8/1, 2)
Plate 15/2

This microboring forms branched, periodically constricted tunnels, 7.5 to 9 μm in diameter. The resin cast of the boring

| Traces / *Producer* | sites | | | | |
|---|---|---|---|---|---|
| | **A** n=20 | **B** n=16 | **C** n=16 | **D** n=30 | **F** n=18 |
| **Scolecia serrata** (bacterium) | + | + | - | - | - |
| **Scolecia maeandria** (?cyanobacterium) | - | + | | | |
| **Scolecia filosa** *Plectonema terebrans* (cyanobac.) | ++ | + | + | + | + |
| **Fasciculus parvus** *Hyella pyxis* (cyanobacterium) | - | ++ | - | - | + |
| **Fasciculus dactylus** *Hyella caespitosa* (cyanobacterium) | ++ | + | - | + | +++ |
| **Fasciculus frutex** *Hyella gigas* (cyanobacterium) | - | - | - | | |
| **Fasciculus grandis** *Ostreobium brabantium* (green alga) | | | - | - | + |
| **Fasciculus sp.** (cyanobac.) | | - | | | - |
| **Eurygonum nodosum** *Mastigocoleus testarum* (cyanobac.) | - | | + | - | - |
| **Reticulina elegans** *Ostreobium quekettii* (green alga) | + | - | +++ | + | ++ |
| **Cavernula pediculata** *Codiolum polyrhizum* (green alga) | | | ++ | | - |
| **Rhopalia catenata** *Eugomontia, Phaeophila* (green alga) | + | - | + | +++ | ++ |
| **Saccomorpha clava** *Dodgella priscus* (fungus) | - | + | | | |
| **Saccomorpha sphaerula** *Lithophythium gangliiforme* (fungus) | + | + | + | + | - |
| **Polyactina araneola** *Conchyliastrum enderi* (fungus) | - | ++ | | | - |
| **Orthogonum fusiferum** *Ostracoblabe implexa* (fungus) | - | | | - | - |
| **Orthogonum tubulare** (?) | | + | | | |
| **Entobia sp.** (sponge) | - | - | | + | - |
| **"Conchocelis"** *Phorphyra* (red alga) | | - | | + | |
| **"Sphaeroid form"** (?cyanobac.) | - | | + | | - |
| **"Pygmy form"** (?bacterium) | - | ++ | - | - | - |
| **"Echinoid form"** (?) | | - | - | + | - |

**Frecency:** - rare    + common    ++ abundant    +++ very abundant

Tab. 1. Distribution of microborings (*and their producers*) in molluscan shells from the different sites at Lee Stocking Island, Bahamas (n = number of the investigated samples). Site A: Stromatolite reef, 4 to 5 m. Site B: Windward *Acropora palmata* reef, 2 to 3 m. Site C: Windward shelf edge reef , 30 m. Site D: Leeward hard ground reef, 2 to 3 m. Site F: Windward reef, 10 to 12 m.

shows frequent interruptions. The borings spread parallel to the substrate surface. The maker of this trace is unknown. A similar cast was attributed to cyanobacteria by CAMPBELL (1983: Fig. 4b). The microboring was found frequently in site B. It only occurred in one sample from site A.

*Fasciculus parvus* Radtke (Radtke, 1991: Pl. 10/5, 6)

This boring pattern is characterized by small clusters of tunnels (ø 2 to 3 μm) usually parallel to the surface of the substrate. At site B, the tunnels were often perpendicular to the surface of the substrate and branched. The cast is correlated with the cyanobacterium *Hyella pyxis* Lukas & Hoffman (1984), which was described from subtropical marine environments at water depths between 5 and 22 m.

*F. parvus* occurred most abundantly at site B. It was less frequently found at site F (Windward reef, 12 m).

*Fasciculus dactylus* Radtke (Radtke, 1991: Pl. 10/1-4)
Plate 15/3

*F. dactylus* forms clusters of tunnels radiating deep into the substrate from a central point of entry. Single tunnels are rarely branched and fairly uniform in diameter (ø 7 to 10 μm). The casts show slight constrictions along the tunnels, possibly indicating positions of the cross walls between the cells of its maker. Sometimes this microboring spreads predominantly parallel to the substrate surface with smaller (ø 4.5 to 6 μm), laterally branched tunnels. This trace is comparable with borings of *Hyella caespitosa* Bornet & Flahault, a cyanobacterium that ranges from the lower intertidal zone to a depth of 100 m (Lukas, 1978; Le Campion-Alsumard & Golubic, 1985). Similar traces have also been found in the Early Tertiary Paris Basin (Radtke, in press: Pl. 1/2).

*F. dactylus* was particularly abundant at site F, followed by site A.

*Fasciculus frutex* Radtke (Radtke, 1991: Pl. 11/1-3)
Plate 15/5

This boring pattern is characterized by short and thick (ø 17 to 19 μm) filaments which are arranged in a radiating cluster. Repeated constrictions of the tunnels are common, sometimes accompanied by longitudinal constriction (Pl. 15/5). *F. frutex* has been originally compared with traces of *Hyella gigas* Lukas & Golubic (1983). However, there are certain similarities with *Hyella salutans* and *H. immanis* (Al-Thukair & Golubic, 1991a: Figs. 8, 9; 1991b: Fig. 2, 23).

The tunnels of this trace display a double-partition pattern (ø 16 to 22 μm).

This trace was very rare in the material studied. The trace occurred only once at sites A, B and C.

*Fasciculus grandis* Radtke (Radtke, 1991: Pl. 11/4, 5)
Plate 15/6

This trace is characterized by large, loose clusters of mostly dichotomously branched borings, penetrating deep into the substrate. The tips of the casts appear slightly swollen. The form is similar to traces of the green alga described by Weber-Van Bosse (1932) as *Ostreobium brabantium*. This is the largest algal boring known (Radtke, in press: Pl. 1/3). The organism occurs exclusively in tropical environments between 5 to 15 m water depth (Perkins & Tsentas, 1976).

The trace occurs commonly in site F, and rarely in C and D.

*Fasciculus* sp.
Plate 15/4

This trace has tunnel diameters of 9 to 16 μm. The microborings form dense, regularly radiating clusters with tunnels marked by dichotomous branching. This form is quite similar to *Hyella stella* Al-Thukair & Golubic (1991a: Fig. 11c) known from ooids of the Arabian Gulf. Green, Knoll & Swett (1988) described a fossil form of such morphology from Proterozoic silicified pisoliths from Greenland as the fossil *Eohyella dichotoma*. Günther (1990: Pl. 59/7) identified a dichotomously branched form spreading parallel to the substrate surface as *Abeliella* Mägdefrau (1937).

This form occurred rarely at sites B and F.

*Eurygonum nodosum* Schmidt (Schmidt, 1992: Pls. 7/6; 8/1)
Plate 16/1

The boring pattern is characterized by a shallow tunnel system with two types of branches. The long branches ('unlimited growth', ø 4 to 6 μm) are straight to lightly curved. Short lateral branches ('limited growth') of the same size with slight terminal swelling (ø 9 to 10 μm) originate from the long branches. The resin casts exhibit characteristic shoul-

Plate 15    Recent resin-cast microborings in molluscan shells: Lee Stocking Island/Bahamas

Fig. 1.    Typical loop structure of *Scolecia filosa* Radtke. In *Lima*, Lee Stocking Island/Bahamas, sample A7/3a, scale: 20 μm.

Fig. 2.    *Scolecia maeandria* Radtke showing frequent interruptions in the tunnel system. In *Tellina*, Lee Stocking Island/Bahamas, sample B3/3a, scale: 20 μm.

Fig 3.    *Fasciculus dactylus* Radtke showing single, rarely branched tunnels, comparable with borings of *Hyella caespitosa* Bornet & Flahault. In *Tellina*, Lee Stocking Island/Bahamas, sample B2/2a, scale: 20 μm.

Fig. 4.    *Fasciculus* sp. showing dense, regularly radiating clusters. Dichotomously branched tunnels are quite similar to *Hyella stella* Al-Thukair & Golubic. In *Tellina*, Lee Stocking Island/Bahamas, sample F3/4b, scale: 20 μm.

Fig. 5.    *Fasciculus frutex* Radtke showing double partition pattern. Similar to *Hyella immanis* Al-Thukair & Golubic. In *Tellina*, Lee Stocking Island/Bahamas, sample B2/2a, scale: 20 μm.

Fig. 6.    *Fasciculus grandis* Radtke showing large, loose clusters of dichotomously branched borings. Similar to traces of the green alga *Ostreobium brabantium* Weber-Van Bosse. In bivalve (indet.), Lee Stocking Island/Bahamas, sample F1/3a, scale: 20 μm.

Plate 15 85
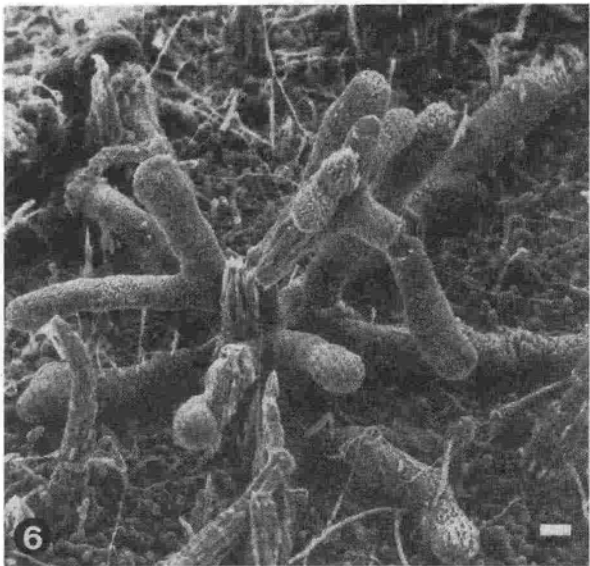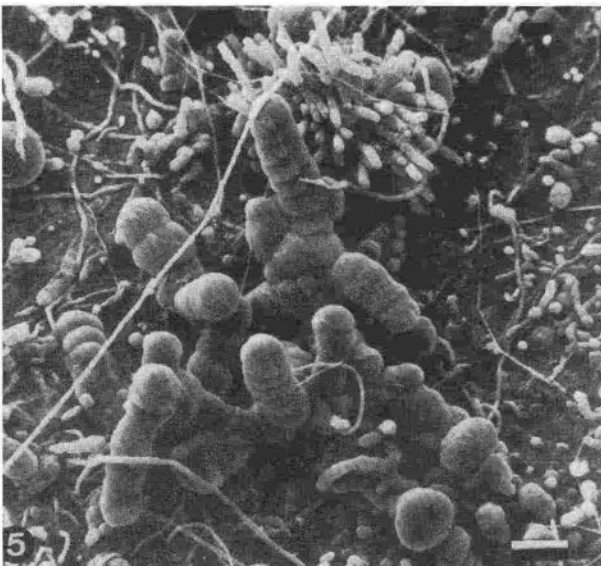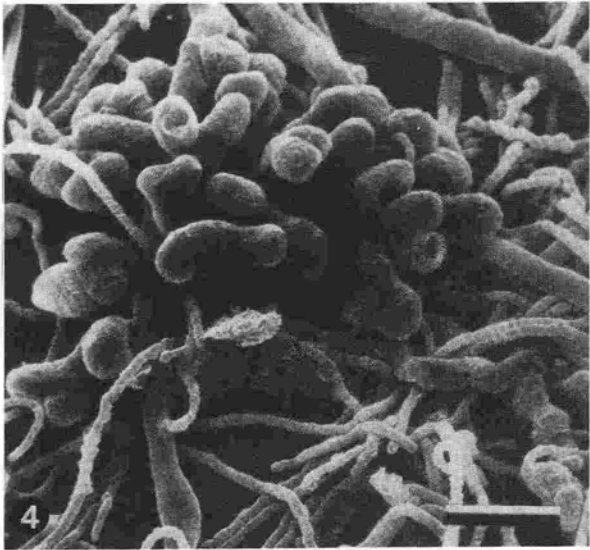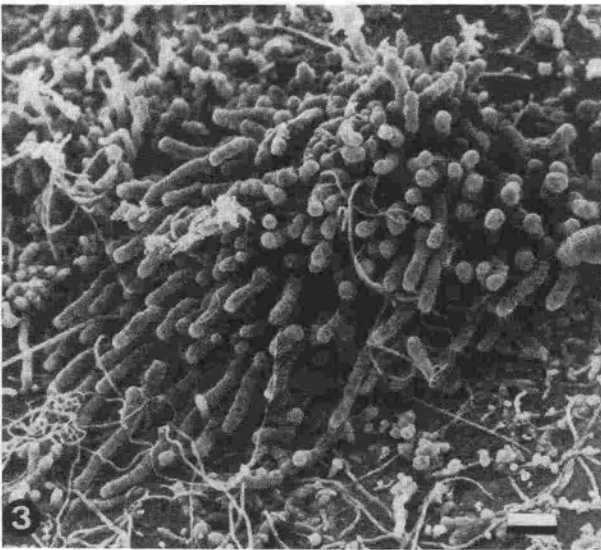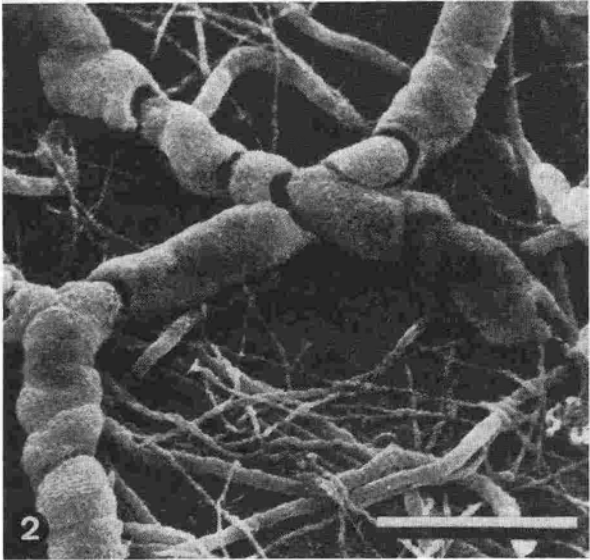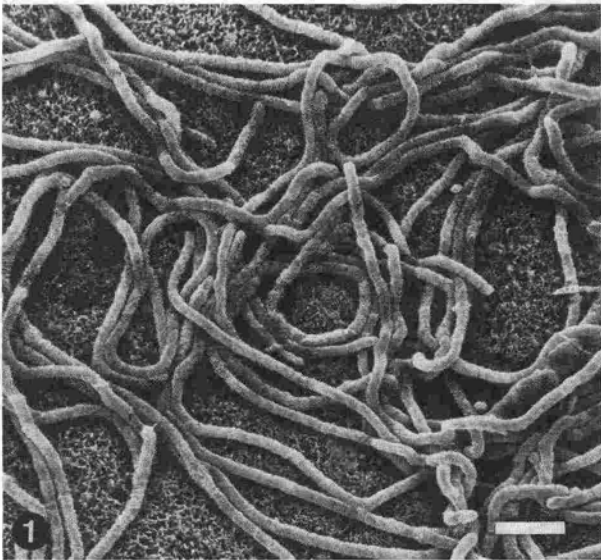
der-like attachments. The trace is comparable with that of *Mastigocoleus testarum* LAGERHEIM. PERKINS & TSENTAS (1976) described the organism from tropical marine environments in depths from 0 to 30 m, and GÜNTHER (1990) described them in depths from 0 to 45 m.

This trace is rare in the material studied. Slightly more were present at site C than at the other sites.

### *Reticulina elegans* RADTKE (RADTKE, 1991: Pl. 7/1-5)
Plate 16/3, 4

This trace is comprised of an intricate and variable network of tunnels, with occasional lobate swellings. The system consists of several branching orders. The principal branches are straight, dichotomous, and 4 to 5 µm in diameter. The higher orders of branching (up to 6 orders) decrease in diameter to an average of 2 µm and branch more densely. In the higher orders of branching the tunnels frequently run in a zig-zag pattern (Pl.16/3), often with lateral branches at the angles. Long straight intermediate order tunnels are common, with densely ramified side branches. Occasionally these lateral off-shoots bear flattened, lobate terminal swellings (10 and 23 µm; Pl. 16/4). These characteristic patterns are comparable with the boring traces of the siphonous green alga *Ostreobium quekettii* BORNET & FLAHAULT. LUKAS (1978) reported this organism to be prevalent at depths of 18 to 75 m, but can occur as deep as 200 m. Similar zig-zag branching patterns, without associated lobate enlargements, were found in Lower Tertiary shells where their abundant occurrence was used as an indicator of the lower photic zone (RADTKE, in press: Pl. 1/5).

In the studied material, the trace preferred the deeper bathymetric sites C (30 m) and F (12 m). It was rarely observed at the shallower sites A, D and B.

### *Cavernula pediculata* RADTKE (RADTKE, 1991: Pl. 12/5, 6)
Plate 16/2

This trace is a 30 to 70 µm deep, 25 to 45 µm wide spherical to bag-like depression connected to the substrate surface by short repeatedly ramified tubes. The connecting tubes look like rhizoids when resin-cast (Pl. 16/2, lower left). The microboring is comparable with traces of the green alga *Codiolum polyrhizum* (LAGERHEIM) KORNMANN. The species is described from water depth between 0 to 50 m (LE CAMPION-ALSUMARD, 1978; BUDD & PERKINS, 1980). RADTKE (1991) described a fossil trace of such morphology as an indicator of the upper photic zone.

In the studied material, the trace occurs abundantly at the deepest site C (30 m), and rarely at site F.

### *Rhopalia catenata* RADTKE (RADTKE, 1991: Pl. 9/1-6)
Plate 16/5, 6

The trace classified under this name consists of chain-like connected chambers distributed as a branched network immediately beneath the substrate surface. Two different types can be distinguished: a composite type with wider chambers and few spinose surface connections, and a slender type with many connections.

The periphery of the composite type colony is characterized by star-like radiating distal tunnels (∅ 4 to 6 µm). These may form small arches repeatedly connecting with the substrate surface. All tunnels show hair-like tubes (∅ 2 to 3 µm) to the surface of the substrate. Elongated chambers, connected to the substrate surface by a narrow tube, form in the older (proximal) portions of the tunnels. In the central portion of the colony, the chambers become wide and isodiametric, often angular in outline. The surface connecting tubes are below or to the side of these chambers. More than one connecting tube per chamber is sometimes observed. Branching is commonly opposite, forward inclined at angles between 90 and 60, always originating from a chamber. The chambers are 15 to 25 µm in diameter, interconnected by narrower necks (∅ 7 to 19 µm, Pl.16/5). Continuous transitions between the central and peripheral morphologies have been observed in cast specimens.

The slender type is less common. It consists of slender chambers, 6 to 12 µm wide, connected by even narrower necks (∅ 4 to 5 µm). The tunnels are connected to the substrate surface by numerous long and tapering connecting tubes (Pl. 16/6).

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Plate 16     Recent resin-cast microborings in molluscan shells: Lee Stocking Island/Bahamas

Fig. 1.     *Eurygonum nodosum* SCHMIDT. Shallow tunnel system characterized by shoulder-like attachments. In *Cardium*, Lee Stocking Island/Bahamas, sample C2/1b, scale: 20 µm.

Fig. 2.     *Cavernula pediculata* RADTKE. Bag-like depression with short branched tube connections to the substrate surface. In *Cardium*, Lee Stocking Island/Bahamas, sample C2/1a, scale: 20 µm.

Fig. 3.     *Reticulina elegans* RADTKE showing zig-zag pattern of higher orders of branching tunnels. Comparable with boring traces of the siphonous green alga *Ostreobium quekettii* BORNET & FLAHAULT. In bivalve (indet.), Lee Stocking Island/Bahamas, sample C4/2a, scale: 20 µm.

Fig. 4.     *Reticulina elegans* RADTKE. Intermediate order of branching tunnels characterized by lobate terminal swellings. In *Laevicardium*, Lee Stocking Island/Bahamas, sample D2/4a, scale: 20 µm.

Fig. 5.     Composite type of *Rhopalia catenata* RADTKE showing wide chambers and few spinose surface connections. Comparable with boring traces of *Phaeophila engleri* REINKE. In *Macoma constricta*, Lee Stocking Island/Bahamas, sample D6/3a, scale: 20 µm.

Fig. 6.     Slender chamber type tunnel system of *Rhopalia catenata* RADTKE showing numerous long and tapering connecting tubes to the substrate surface. Similar to traces of *Phaeophila dendroides* (CROUAN FR.) BATTERS. In *Tellina*, Lee Stocking Island/Bahamas, sample F3/3a, scale: 20 µm.

Plate 16                                                                                    87
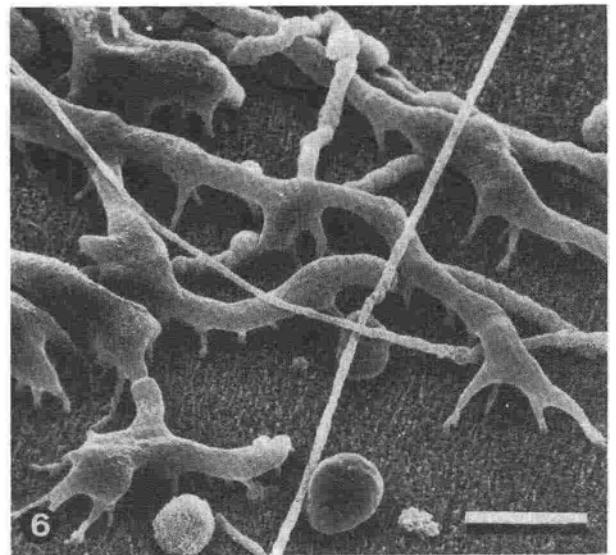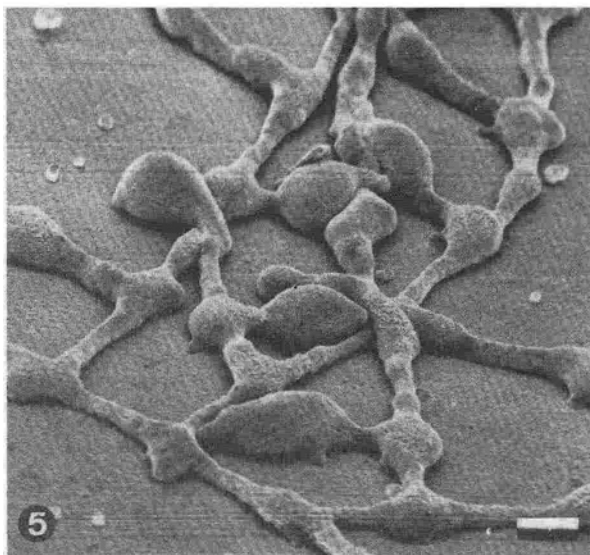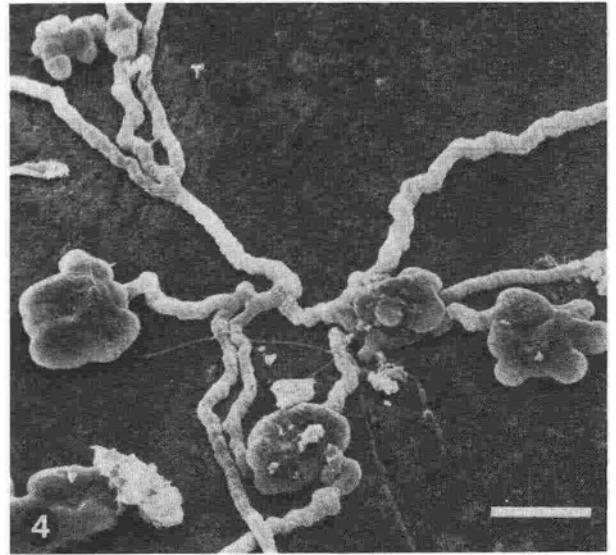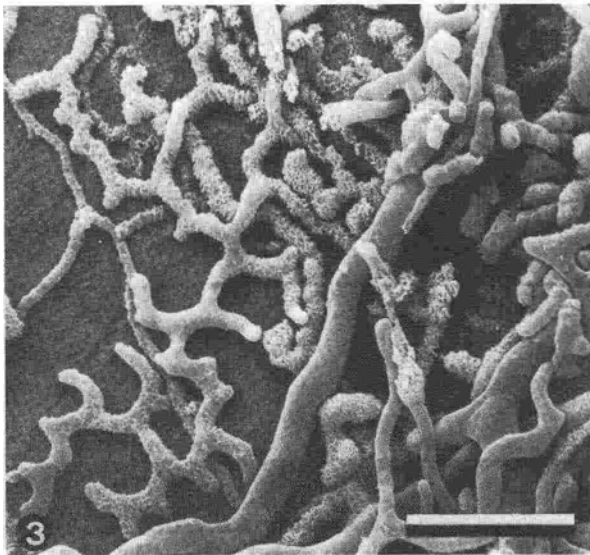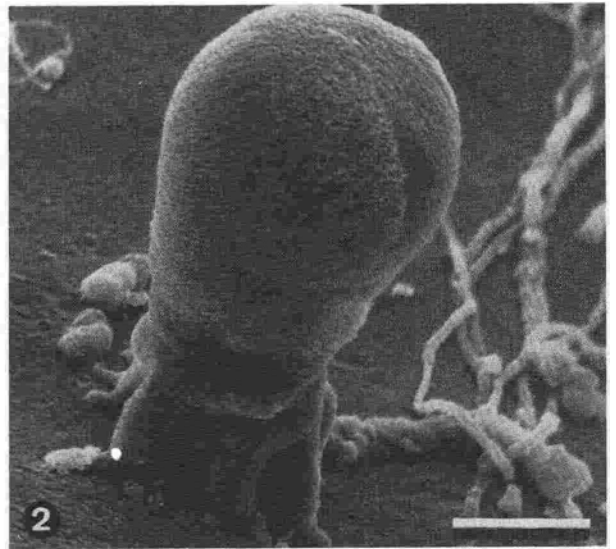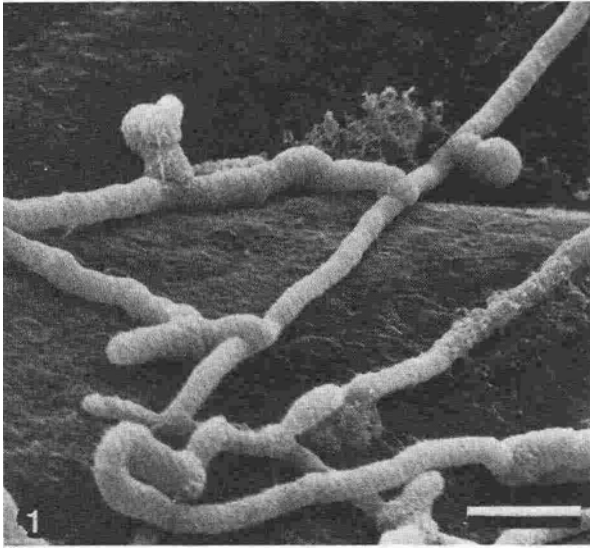
These traces can be produced by the green algae *Phaeophila engleri* REINKE (RADTKE, in press: Pl. 1/1), *P. dendroides* (CROUAN FR.) BATTERS or *Eugomontia sacculata* KORNMANN. The spinose connecting tubes beneath chambers have been observed by GOLUBIC & SCHNEIDER (1979) in *Phaeophila. Phaeophila* dominates in 10 to 45 m water depths (PERKINS & TSENTAS, 1976; BUDD & PERKINS, 1980).

Large composite colonies with chain-like central areas and large swellings are common at site D. Both, the slender and the large morphological types occur at site F, whereas at sites A and B only the slender type was found. It is possible that the different morphotypes of borings are produced by different developmental stages of *Phaeophila engleri.*

*Rhopalia catenata* occurs most abundantly at site D and to a lesser exent at site F.

### *Saccomorpha sphaerula* RADTKE (RADTKE, 1991: Pl. 14/1-3)
### Plate 17/1

This small trace has spherical chambers (ø 4 to 8 μm) interconnected with extremely fine, slightly curved or wavy, occasionally branched, tunnels (ø 0.5 μm). A similar trace has been described as a lower fungus *Lithopythium gangliiforme* BORNET & FLAHAULT. The trace occurs in shallow marine environments (GOLUBIC et al., 1975: Fig. 12.8 B; LE CAMPION-ALSUMARD, 1978). In the fossil record it is found in the Early Tertiary Paris Basin (RADTKE, in press: Pl. 1/4).

*S. sphaerula* occurs at all 5 studied sites.

### *Saccomorpha clava* RADTKE (RADTKE, 1991: Pl. 13/1-6)

The boring pattern of this trace consists of large (ø 10 to 20 μm) pyriform sacs connected to the surface by narrow (ø 4 to 6 μm) 'bottle-necks'. The sacs are interconnected with narrow (ø 2 μm) straight filaments. *S. clava* is comparable with traces of *Dodgella priscus* ZEBROWSKI. The organism has been documented from the deep sea in water depths down to 2350 m (ZEFF & PERKINS, 1979; BUDD & PERKINS, 1980; GOLUBIC et al., 1984). RADTKE (1991) reported it from the Oligocene of northern Germany and interpreted it to be a possible lower photic to dysphotic environmental indicator, when it is found exclusively together with *Orthogonum tubulare*. HÖHNK

(1969) found the organism in the intertidal zone of the North Sea.

In the investigated area the microboring was found mostly at site B.

### *Polyactina araneola* RADTKE (RADTKE, 1991: Pl. 12/1, 2)

The trace forms a deep, complex, star-shaped borehole. It is comprised of the following elements: an entry tunnel, a central chamber, radiating branches, and interconnected tunnels. A single entry tunnel widens gradually toward the interior of the substrate. The central chamber is variable in size (ø 10 to 30 m) and can be spherical, hemispherical to irregular. The radiating branches (ø 8 to 10 μm) are often constricted at their contact with the central chamber. They usually spread perpendicular to the entry tunnel, i.e. parallel to the substrate surface, sometimes bending gradually back toward it. The radiating branches (up to 100 μm long) are rounded or spindle-shaped, narrowing more or less abruptly into fine interconnecting tunnels (ca. 2 μm). *P. araneola* is comparable with traces of *Conchyliastrum enderi* ZEBROWSKI. This organism, attributed to fungi, was reported from water depths ranging from 0 to 530 m (HÖHNK, 1969; BUDD & PERKINS, 1980). In tropical oceans it was found only deeper than 18 m (BUDD & PERKINS, 1980). RADTKE (1991) interpreted *P. araneola* to be an indicator of the lower photic zone.

The trace occurs abundantly at site B, rarely at sites A and F.

### *Orthogonum fusiferum* RADTKE (RADTKE, 1991: Pl. 6/5, 6)
### Plate 17/2

This trace is characterized by sparsely branched fine tunnels (ø ca. 1.5 μm) with spindle-shaped swellings (ø ca. 5 μm). The ramifications are at angles close to 90 degrees, originating at or between swellings. *Orthogonum fusiferum* is comparable with traces of the lower fungus *Ostracoblabe implexa* BORNET & FLAHAULT, which has been described from water depths down to 200 m (LE CAMPION- ALSUMARD, 1978).

In the investigated material this trace only occurs rarely at sites A, D and F.

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Plate 17          Recent resin-cast microborings in molluscan shells: Lee Stocking Island/Bahamas

Fig. 1.      *Saccomorpha sphaerula* RADTKE. Spherical chambers interconnected by fine tunnels similar to a lower fungus *Lithopythium gangliiforme* BORNET & FLAHAULT. In *Cardium*, Lee Stocking Island/Bahamas, sample D5/1a, scale: 20 μm.

Fig. 2.      *Orthogonum fusiferum* RADTKE showing spindle-shaped swellings in a fine tunnel system. Comparable with traces of the lower fungus *Ostracoblabe implexa* BORNET & FLAHAULT. In *Macoma constricta*, Lee Stocking Island/Bahamas, sample D6/1a, scale: 20 μm.

Fig. 3.      'Sphaeroid form' showing solitary and crowded groups of spherical cavities. In *Cardium*, Lee Stocking Island/ Bahamas, sample C2/1a, scale: 20 μm.

Fig. 4.      'Pygmy form' showing very fine wavy, branched tunnel system. In *Lima*, Lee Stocking Island/Bahamas, sample B1/1b, scale: 5 μm.

Fig. 5.      Common type of 'echinoid form' showing entry tunnel ending in a flat palmate cavity and distal end fringed by hair-like extensions. In *Laevicardium*, Lee Stocking Island/Bahamas, sample D2/4a, scale: 20 μm.

Fig. 6.      Less common type of 'echinoid form' showing elongated distal cavity covered by fine spinous hairs. In *Laevicardium*, Lee Stocking Island/Bahamas, sample D2/2a, scale: 20 μm.

Plate 17 89

90
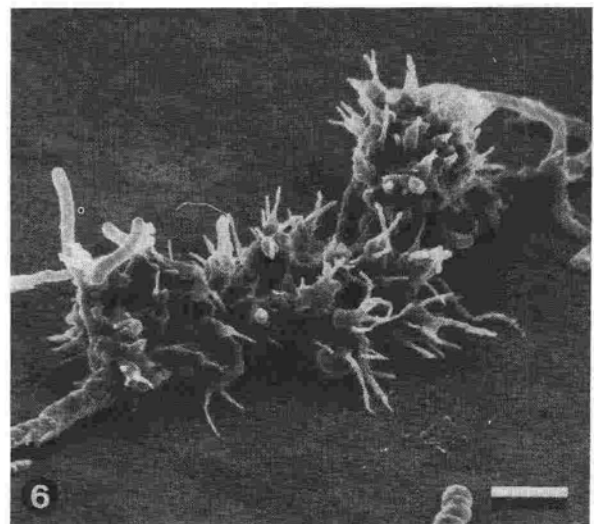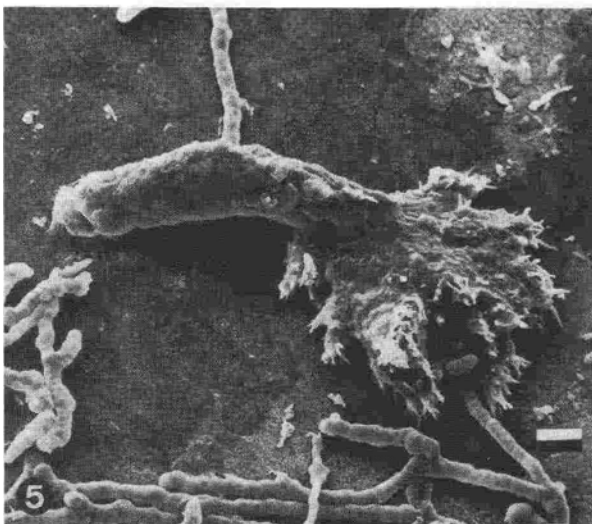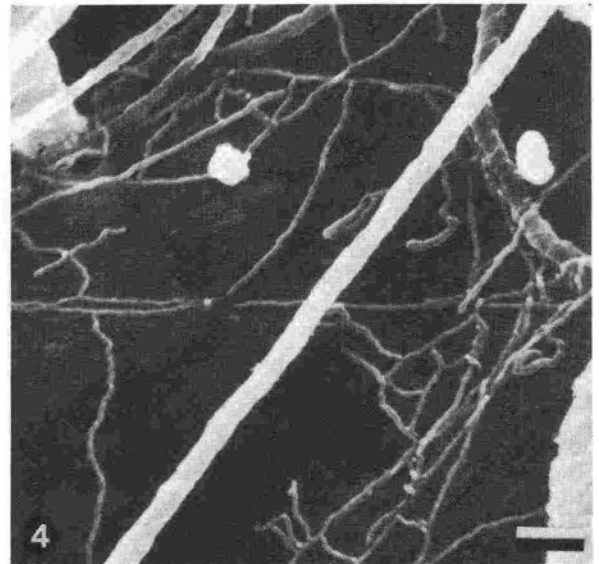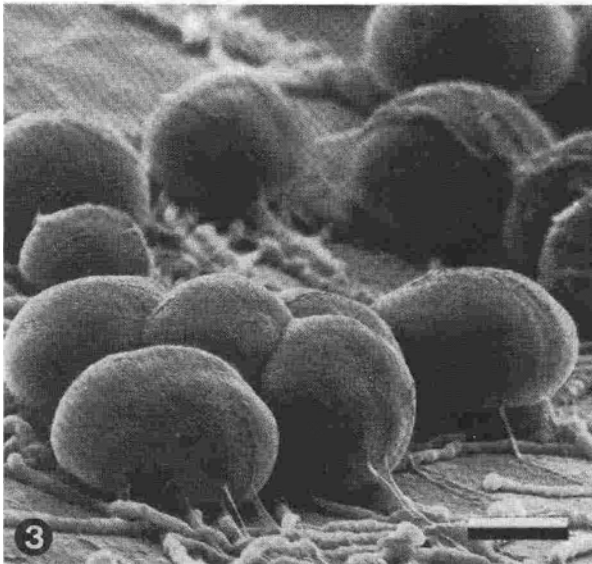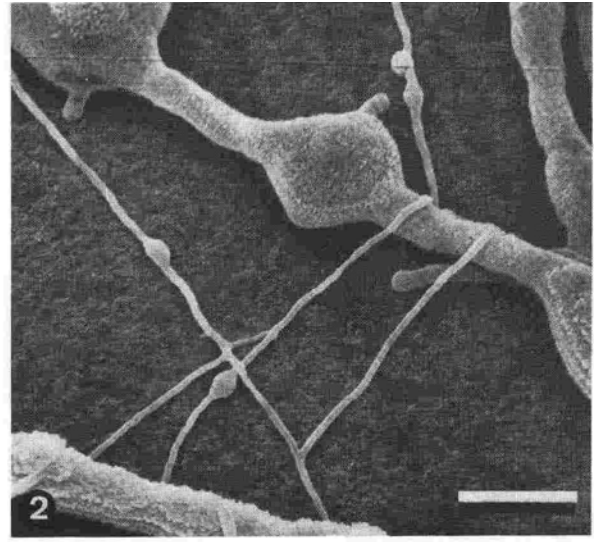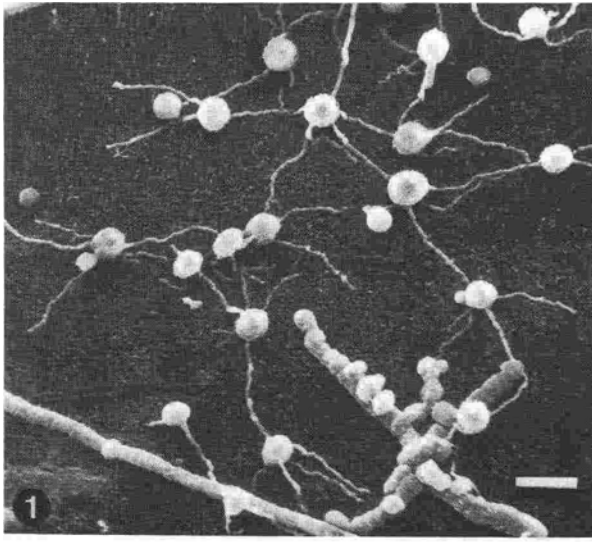
*Orthogonum tubulare* RADTKE (RADTKE, 1991: Pl. 5/3-6, Pl. 6/1, 2)

A shallow branched tunnel system forming characteristic rectangular networks parallel to the substrate surface. Tunnels are 15 to 20 µm in diameter. In the Oligocene of northern Germany, this trace occurs together with *Saccomorpha clava*, and this association, in the absence of other microborings, was proposed to be a lower photic to dysphotic indicator (RADTKE, in press: Pl. 1/6). Modern occurrences, usually described in the literature as 'tubular-form' (EDWARD & PERKINS, 1974; ZEFF & PERKINS, 1979; BUDD & PERKINS, 1980) are found in water depths between 119 to 2350 m.

Numerous specimens of this trace were found only at site B.

### *Entobia* sp. (BROMLEY & D'ALESSANDRO, 1984)

Small clionid sponge borings, shaped like a raspberry with chip scars ca. 20 µm in diameter, has been repeatedly observed in our material. Modern clionid sponges are reported to occur down to 100 m, and sometimes down to 4000 m depths.

In the investigated area, the trace appeared in low abundance at all sites except at site C.

### 'Conchocelis'

Conchocelis is the endolithic stage in the development of bangial Rhodophyceae. The trace corresponds to the bulbous swellings of the *Conchocelis* stage of *Porphyra nereocystis* (CAMPBELL, 1980). Casts of similar traces were illustrated by BUDD & PERKINS (1980: Fig. 6G) and AKPAN & FARROW (1984: Fig. 8). In the fossil record, RADTKE (1991: Pl. 11/6) reported similar traces occurring abundantly together with *Reticulina elegans* as an indicator of the lower photic zone.

This trace is common at site D, and rare at site B.

### 'Sphaeroid form'
### Plate 17/3

This form consists of solitary large (ø 15 to 45 µm) spherical, slightly compressed cavities, directly below the substrate surface. These speroids often occur crowded together. This morphology suggest a producer that is 'chasmolithic' as defined by GOLUBIC et al. (1975: Fig. 12.1). GÜNTHER (1990: Pl. 58/6) described similar traces as 'Uncertain Form 1', in depths from 4 to 47 m (more abundant from 25 to 47 m) in Cozumel, Mexico.

In the studied material this trace occurs more abundantly at site C.

### 'Pygmy form'
### Plate 17/4

Branching system of very fine wavy, branched tunnels (ø 0.4 to 0.5 µm) extending parallel to the substrate surface. Branching occurs regularly at angles of 60° to 90°. At the distal ends of these tunnels are kidney-shaped widenings, 0.6 µm wide and 3 to 4 µm long. The organism that makes these traces is unknown, but the very small size of the borings, suggests it is a bacterium.

This trace was observed at all sites. It was most common at site B.

### 'Echinoid form'
### Plate 17/5, 6

A composite trace consisting of a broad, entry tunnel (25 to 35 µm wide and 70 to 100 µm long) which broadens at the distal end into a flat palmate cavity (70 x 100 x 30 µm). The entry tunnel penetrates the substrate at a low angle and often continues to bend back towards the substrate surface. The edges of the palmate cavity extend into finger-like embayments fringed by fine hair-like extensions (ø 1 µm). The cast resembles a spiny or hairy paw (Pl. 17/5).

A second (less common) type has an elongated distal cavity. Its cast appears covered by fine spinous hairs over its entire surface (Pl. 17/6). The entry tunnel of this type is narrower (ca. 8 µm) and flatter. GÜNTHER (1990: Pl. 56/4, 5) illustrates a similar trace as 'Sponge Form 1' from Cozumel, Mexico, occurring most commonly in water depths between 15 to 25 m.

The 'echinoid form' occurs more commonly at site D.

## 3.2 Distribution of the microborings

The data suggest that the diversity of microborings in shells was similar for the 5 different collecting sites, both in terms of the number of ichnotaxa observed, and in terms of the dominance of particular ichnospecies. These results, although based on detailed observation of the samples, are only qualitative and are not proven by statistics. With larger sample sizes at the sites, the results may change. In addition, the samples are from molluscan material that have been exposed for unknown periods of time. Variations in the length of exposure between individual samples will influence the density of borings. However, the following results provide a broad assessment of microendolith distribution between the sites and a general interpretation of the data is possible.

The highest number of ichnospecies was observed at sites F and B with 17 different species, followed by site A with 16, and sites C and D with 14 ichnospecies. This same ranking occurs when the number of dominant individual microborings at each site are considered. Altogether, 22 distinct traces have been recorded in this study. Eight species occur in all sites: two (*Scolecia serrata*, 'pygmy form') are attributable to bacteria, three (*Scolecia filosa*, *Fasciculus parvus*, *F. dactylus*) to cyanobacteria, two (*Reticulina elegans*, *Rhopalia catenata*) to green algae, and one (*Saccomorpha sphaerula*) to fungi. Some ichnotaxa exhibited selective dominance at particular sites: *Polyactina araneola*, *Scolecia maeandria*, *Orthogonum tubulare* and *Saccomorpha clava* at site B; *Cavernula pediculata* and the 'sphaeroid form' at site C; *Fasciculus grandis* at site F, and 'Conchocelis' and the 'echinoid form' at site D. In decreasing order, the distribution of the traces were as follows: *Rhopalia catenata* (very abundant at site D, abundant at site F, and rare at site B); *Reticulina elegans* (very abundant at site C, abundant at site F, and rare at site B), *Fasciculus dactylus* (very abundant at site F). Site F showed the highest number of individual microborings.

## 3.3 Characterization of the sites by their endolithic traces (Tab. 1)

**Site A** (stromatolites, 4 to 5 m, strong tidal currents): *Scolecia filosa* and *Fasciculus dactylus* are most dominant at this site. Also common are *Scolecia serrata, Reticulina elegans, Rhopalia catenata* and *Saccomorpha sphaerula*, all other traces are rare. The strong tidal currents and periodic burial by shifting sand dunes at this site do not appear to inhibit the development of a rich microendolithic community.

**Site B** (windward *Acropora palmata* reef, 2 to 3 m): This site exhibited the highest diversity of microborings with *Scolecia serrata, Sc. maeandria, Fasciculus parvus, Saccomorpha clava, Polyactina araneola, Orthogonum tubulare* (which was exclusively found at this site and is usually found in deep water environments) and the 'pygmy form'. In contrast to the other sites, *Reticulina elegans* and *Rhopalia catenata* occur very rarely. *Eurygonum nodosum* is totally absent at this site.

The microboring community found at this site has been described in other studies (ZEFF & PERKINS, 1979; BUDD & PERKINS, 1980; RADTKE, 1991) to be associated with deep water environments in the tropics. The reason for the observed preference of this site by heterotrophic forms, that are usually recognized to dominate in deep water environments where phototrophs are excluded, is unclear.

**Site C** (windward shelf edge reef, 30 m) : This is the deepest investigated site. The microborings *Reticulina elegans, Cavernula pediculata* and 'sphaeroid form' dominate at this site. The latter occurs exclusively at site C. In adddition, *Eurygonum nodosum* occurs in greater abundance at this site than at the other sites. *Fasciculus dactylus* is rare. Conspicuous is the abundance of *Cavernula pediculata* at this site, whereas the appearance of the microboring in all other (shallower) sites is very rare or completely missing.

**Site D** (leeward hard ground reef, 2 to 3 m, strong tidal currents): *Rhopalia catenata* dominates at this site. The large clusters of this trace are interpreted to be the late stage of development of the producing organism. 'Conchocelis' was found in greatest abundance at this site. The 'echinoid form' and *Entobia* are very common compared to the other sites.

This site may have optimal conditions for the producer of the *Rhopalia catenata* trace (*Phaeophila*) because there promoted by fast settlement and occupation of substrate surface with optimal nutrient exchange. *Phaeophila* produces tubular hairs that protrude through the substrate surface into the water column and are thought to be an adaptation for nutrient supply. It occurs in its final stage of development.

**Site F** (windward reef, 10 to 12 m): The largest number of individual traces are recognized at this site. *Fasciculus dactylus, Rhopalia catenata* and *Reticulina elegans* are especially dominant. Compared to the other sites, *Fasciculus grandis* is particularly abundant.

## 4 DISCUSSION

The dominance of *Rhopalia catenata* at site D is in agreement with the known distribution of its producer *Phaeophila*

in shallow protected environments (PERKINS & TSENTAS, 1976; BUDD & PERKINS, 1980). Similarly, the dominance of *Reticulina elegans* at the deep site C corresponds to the optimal growth depth of *Ostreobium quekettii* (LUKAS, 1978). The dominance of the trace *Fasciculus dactylus* at the 10 to 12 m site F is unusual, because its producer, *Hyella caespitosa*, is normally widely distributed (LE CAMPION-ALSUMARD & GOLUBIC, 1985). The presence of large numbers of *Cavernula pediculata* at the 30 m site C and its absence at the shallower sites is conspicuous because LE CAMPION-ALSUMARD (1978) and BUDD & PERKINS (1980) found its producer, *Codiolum polyrhizum*, widely distributed in shallow water habitats.

The results are in accordance with the general known vertical distribution of boring microorganisms. The following dominant trace site associations were found: *Rhopalia catenata* at site D (2-3 m), *Reticulina elegans* at site C (30 m), and *Fasciculus dactylus* at site F (10-12 m). These associations are comparable with the depth distribution of the organisms that produce these traces (GOLUBIC et al., 1975: Fig. 12.2; PERKINS & TSENTAS 1976: Fig. 46; BUDD & PERKINS, 1980: Fig. 4; MAY et al., 1982: Fig. 62; GÜNTHER, 1990: Fig. 5) . No particular endolithic trace dominates at sites A (4-5 m) and B (2-3 m).

The results found in this investigation suggest that the distribution of microborers is inherently variable and that the microboring endolithic community may be sensitive to environmental conditions in shallow water carbonate environments. Further investigations of the distribution of microendoliths and their borings in natural substrates, in conjunction with experimental substrates that are presently under analysis, may provide a valuable tool for observing spatial and temporal changes in environmental condition in living and fossil reef habitats.

## ACKNOWLEDGEMENTS

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