

Microborings from shallow marine habitats on both sides of the Panama Isthmus

By Gudrun RADTKE¹, Priska SCHÄFER², Heidi BLASCHEK² and Stjepko GOLUBIC³

(With 5 figures and 2 tables)

Manuscript submitted on August 7th 2010,
the revised manuscript on December 7th 2010

Abstract

Microborings in shells and shell fragments on Atlantic and Pacific coasts of Panama were analyzed and compared. Both coasts show considerable diversity of microboring morphotypes. The occupation by euendoliths within each sample is more uniform in shells of the Pacific than of the Caribbean coast, thus representing a lower overall diversity. The environmental characteristics of the water bodies along the two coasts of Panama are reviewed and discussed as possible causes of the differences observed. The finding is consistent with higher nutrient availability on the Pacific side of the Panama Isthmus associated with more extensive current exchange, including seasonal upwellings, than on the oligotrophic, warm water coast of the more enclosed Caribbean Sea. Three new morphotypes of microborings were found only on the Caribbean coast and one on the Pacific coast, possibly reflecting regional distinction of the euendolithic microflora. The implications of the observed in this modern setting for the fossil occurrences of microborings are discussed.

Keywords: Euendoliths, microborings, phototrophs, mollusks, Recent, tropics, shallow marine.

Zusammenfassung

Die Spuren mikrobieller Euendolithen in Molluskenschalen und Schalenfragmenten von der pazifischen und karibischen Küste beiderseits des Panama-Isthmus wurden untersucht und miteinander verglichen. Die Besiedlung durch Euendolithen innerhalb einer Schale ist an der pazifischen Seite einheitlicher als an der karibischen, was sich in einer geringeren Diversität ausdrückt. Die Umweltfaktoren, welche die Wassermassen der beiden Küsten Panamas kennzeichnen, wurden als mögliche Ursachen der beobachteten Unterschiede berücksichtigt. Auf der pazifischen

¹ Hessisches Landesamt für Umwelt und Geologie, Rheingastr. 186, 65203 Wiesbaden, Germany;
e-mail: gudrun.radtke@hlug.hessen.de

² Institut für Geowissenschaften, Universität Kiel, Ludewig-Meyn-Str. 10, 24118 Kiel, Germany;
e-mail: ps@gpi.uni-kiel.de

³ Biological Science Center, Boston University, 5 Cummington Str., Boston, MA 02215, U.S.A.;
e-mail: golubic@bu.edu

Seite korrelieren die Funde mit einer höheren Nährstoffzufuhr von kaltem Auftriebswasser (Upwelling) im Gegensatz zu den warmen Gewässern der oligotrophen karibischen Seite. Drei neue Morphotypen von Bohrspuren wurden auf der karibischen und eine auf der pazifischen Seite von Panama entdeckt, ein Anzeichen regionaler Unterschiede unter Euendolithen. Die Anwendung der rezenten Funde zur Deutung fossiler Mikrobohrspuren wurde diskutiert.

Schlüsselwörter: Euendolithen, Mikrobohrspuren, Phototrophe, Mollusken, Rezent, Tropen, Flachwasser.

Introduction

Microboring organisms or euendoliths penetrate limestone and other carbonate substrates and inhabit completely or partially the space they have excavated (GOLUBIC et al. 1981). They are occupants of a series of specialized ecological niches. Microborers are most common and most diversified in marine environments, but are also known from fresh water and air-exposed rocks (GOLUBIC & SCHNEIDER 2003). Phototrophic euendoliths predominate in shallow illuminated waters and show a depth-dependent distribution (RADTKE & GOLUBIC 2005) with a sharper expressed zonation in the intertidal and supratidal ranges (RADTKE et al. 1996). They are represented by coccoid and filamentous (including heterocystous) cyanobacteria, chlorophytes and developmental stages (Conchocelis) of rhodophytes. The heterotrophic euendoliths are not depth-dependent, and thus become exclusive occupants of carbonates in deep aphotic waters (GOLUBIC et al. 1984, 2005).

The microboring organisms produce traces with high preservation potential (instant fossils) and have a consistent presence in the fossil record throughout the Phanerozoic (GLAUB & VOGEL 2004; GLAUB et al. 2007). The earliest fossil occurrence of euendolithic cyanobacteria are known from the over 1,650 Ma old Dahongyu Formation, China (ZHANG & GOLUBIC 1987). The value of understanding distribution of modern euendoliths lies in the estimate of the depositional depth of ancient sediments where microborings remained preserved (GOLUBIC 1972; GOLUBIC et al. 1984). This paleoenvironmental indication value is of particular importance in subtidal ranges below the wave base, and in the assessment of geologically fast sea level changes (CHAZOTTES et al. 2009).

The study in modern marine environments offers the opportunity to record the environmental parameters that may be correlated with euendolith distribution, with the strategy of encompassing contrasting conditions and/or gradiental arrangements. The studies of euendoliths following their settlement and development on experimentally exposed carbonate substrates have been covering a wide latitudinal range from the northern marine settings of Skagerrak (WISSHAK et al. 2005) to tropical condition on the carbonate Platform of the Bahamas at Stocking Island (VOGEL et al. 2000) and Glovers Reef, Belize (CARREIRO-SILVA et al. 2009).

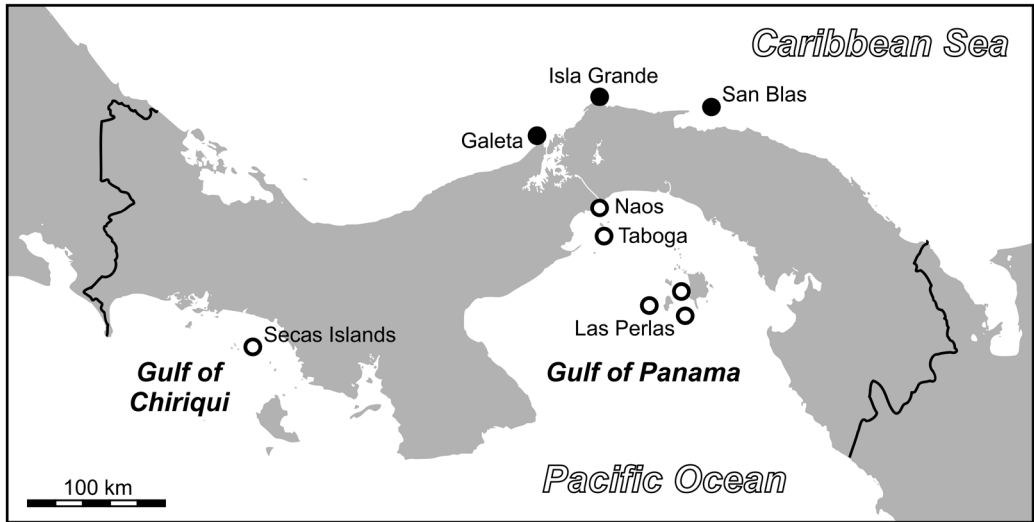


Fig. 1. Map of the Isthmus of Panama with sampling sites on the Caribbean coast (full circles) and Pacific coast (open circles) in the Gulf of Panama and the Gulf of Chiriqui.

The quantitative aspects of euendolith studies refer to the processes of bioerosion, concerned with rates of removal of carbonate by microbial euendoliths (TRIBOLLET et al. 2006a). Experiments with exposure of carbonate substrates to settlement of microborers have the potential to determine seasonality of settlement, substrate selection and the progression and removal rates of carbonate (TUDHOPE & RISK 1985; VOGEL et al. 2000; WISSHAK 2006). The activity of microborring organisms is followed by grazers, which remove layers of carbonate together with epi- and endoliths (SCHNEIDER 1976; GOLUBIC & SCHNEIDER 2003). These activities amount to considerable geomorphological forces in shaping of limestone coasts, including the formation of biokarst (SCHNEIDER & TORUNSKI 1983) and bioerosional notches (RADTKE et al. 1996). The joint action of microbial euendoliths and their grazers is significant in carbonate budgeting or coral reefs (CHAZOTTES et al. 1995; TRIBOLLET & GOLUBIC 2005). In the recent years, the question of microbioerosion in view of ocean acidification and sea water level rise has obtain additional significance (TRIBOLLET et al. 2006b). However, these processes are also subject to qualitative changes, which is the focus of the present contribution.

In the present contribution, we report on the distribution of euendolith assemblages and their traces on both sides of the Panama isthmus, by comparing an oligotrophic carbonate dominating and warm water coastal setting of the Caribbean Sea with the Pacific coastal setting flushed by nutrient enriched colder water from the upwelling currents along the Pacific coast of Panama.

Materials and Methods

Environmental setting

The coastal environments on the two sides of the Panama Isthmus reflect different geological histories: An active tectonic margin exists along the Panama Pacific coast and a passive margin along the Caribbean coast (COATES et al. 1992; COATES & OBANDO 1996). The formation of the lower Central American Isthmus extended from the mid Miocene to the late Pliocene over the once continuous seaway between North and South America thus forming a barrier between Pacific and Atlantic biota.

The climate and coastal hydrography of the Panama Isthmus is determined by the interaction of the trade winds with the Intertropical Convergence Zone (ITCZ) (D'CROZ & ROBERTSON 1997). The ITCZ lies in the South during December to May allowing the Trade Winds to blow across the isthmus generating strong seasonal upwelling in the Gulf of Panama. In contrast, the ITCZ moves northward during May to December and a large, low-pressure air mass settles over Panama interrupting the Trade Winds and bringing intense rainfalls. As a consequence, the coasts of Panama face distinctly different hydrographies and environments. The Caribbean coast is year-round under constant oligotrophic conditions characterized by high temperatures and salinities and low nutrient levels (Table 1). In contrast, the Gulf of Panama on the Pacific side is exposed to seasonal upwellings, accompanied by low water temperatures and high nutrient fluxes generating increased primary production. The two coasts are characterized by different faunal and floral elements (FORTUNATO & SCHÄFER 2009; REIJMER et al. 2011).

Table 1. Hydrographic parameters; compiled from D'CROZ & ROBERTSON 1997 (San Blas and Secchi data) and D'CROZ & O'DEA 2007 (Pacific).

Hydrographic parameters	Pacific				Caribbean	
	Gulf of Chiriqui		Gulf of Panama		San Blas	
	dry	wet	dry	wet	dry	wet
Temperature [°C]	28,0	27,5	18,0	27,7	27,9	28,7
Salinity [‰]	32,0	30,6	33,6	29,2	34,8	34,2
Nitrate	0,75	0,34	14,45	0,27	0,23	0,29
Phosphate	0,16	0,16	1,2	0,14	0,04	0,04
Chlorophyll-a [mg/m ³]	0,29	0,34	1,44	0,27	0,36	0,41
Euphotic zone [m]	54,9	37,1	13,8	40,4	–	–
Secchi disk [m]	–	–	9,3	9,3	16,6	16,4

The coastal topography along the Caribbean side of Panama is relatively low, with a narrow shelf rimmed by coral reefs (San Blas Archipelago, Isla Grande, Galeta), mangrove swamps and bays with small islands. The Pacific coast of Panama includes the Gulf of Panama in the East and the Gulf of Chiriqui (Secas Islands) in the West. The Gulf of Panama with a few islands (Naos Isla Taboga, Islas Perlas) is facing south, forming a gradually deepening shelf ramp with water depths rarely exceeding 75 m. The area of study and the sampling sites are shown in Fig. 1.

Table 2. Distribution of microborings on Panama coasts.

	Caribbean			Pacific							
	1+9	2+10	3+11	4+5	14	16	12b	12c	15	6	
	Sites San Blas	Isla Grande	Galeta	Naos	Taboga	Las Perlas	Las Perlas		Las Perlas	Chiriqui	
Waterdepth [m]	2	1	1	0,5	2–3	14,9	21		69,8	16–18	
Microborings											
Cyanobacteria	<i>Eurygonum nodosum</i>	x	x	xx			x		x		
	<i>Fascichnus parvus</i>	x							x		
	<i>Fascichnus dactylus</i>	xxx	xxx	xxx	xx	xx	xx		xxx	x	xxx
	<i>Fascichnus frutex</i>	xx		x			x		xx		
	<i>Abeliella bellafurca</i>	x		x			x		x		
	<i>Fascichnus grandis</i>		x	x							
	<i>Scolecia filosa</i>	xx	x	xxx	xx	xxx	xx	x	xx	xx	x
	<i>Planobola</i> isp.	xx	x	x	x		x		xx		x
Chlorophyta	<i>Rhopalia catenata</i>		x		x	x			x	x	
	<i>Rhopalia</i> "nodosa"	xx		x							
	<i>Rhopalia</i> "saltator"	xx									
	<i>Cavernula</i> "profunda"	x		x							
	<i>Ichonoreticulina elegans</i>					xx	x		x	xx	
Heterotrophs	<i>Orthogonum tubulare</i>	x			x		x	xx	x	x	
	<i>Orthogonum fusiferum</i>	xx	x		x	x	x		x	x	
	<i>Saccomorpha clava</i>	xx	x		x	x	x	xx	x	x	
	<i>Polyactina araneola</i>						x	x	x	xx	
	<i>Scolecia serrata</i>	xx					x		x		
	Pygmy form	x		x				x	x	x	
	"Spiderweb"	x		x	x	x	x	x	x		
	<i>Entobia</i> isp.	x		x			x	x	xx	x	
Foraminifera trace								x			
	x = present			xx = common			xxx = very common				

Collection

Surface sediment samples from the Gulf of Panama were collected during two cruises of the Research Vessel *Uracca* (STRI, Smithsonian Tropical Research Institute) in 2004 and 2005 using a Van Veen grab. Small shells and shell fragments (5 mm in diameter) were selected from the surface sediment samples. Shells and shell fragment of molluscs in shallow water were collected by snorkelling around islands Taboga, Las Perlas and from Naos beach near STRI Marine Biological Station. Samples from the Caribbean side were collected by snorkelling in inter-reef areas around San Blas Islands (1998) as well as from reef lagoons near Galeta Biological Station (STRI) and around Isla Grande (2005). The samples cover a water depth range from the intertidal down to 70 m (Table 2). All samples were dried and photo-documented. Microborings were analyzed in shells of gastropods and bivalves: Corbidae, Nuculanidae, *Plicatula*, *Taxodonta*, *Chama*. A total of 17 samples from the Caribbean side and 27 samples from the Pacific have been prepared as microboring casts and explored with Scanning Electron Microscopy (SEM). Light microscopy of dissolved shells was tested on 10 transparent shells, which showed microborings with cellular content.

Preparation

The shell fragments were embedded in araldite under vacuum condition, sectioned, polished and the remaining carbonate dissolved by dilute hydrochloric acid. The exposed casts were sputtered with gold-palladium, and the microborings were investigated and photographed using a SEM (Cam-Scan-CS-44). The preparation technique is described by GOLUBIC et al. (1970). Selected subsamples were dissolved in acid and analyzed by light microscopy.

Analysis

The microborings were identified in accordance with trace fossil classification practices (RADTKE 1991; RADTKE & GOLUBIC 2005; WISSHAK 2006; RADTKE et al. 2010), and morphometrically evaluated from digital images, using Sigma Scan (Sausalito, CA) program. Measurements were presented as mean \pm standard deviation of samples of 35 measurements. The rules of the ichnological terminology accept the names of ichnofossils only if encountered in ancient material. Microborings in modern settings do not have legal status. We use, therefore the descriptive names for characteristic new traces between quotation marks. The samples with newly discovered forms will be deposited in Senckenberg Museum, Frankfurt.

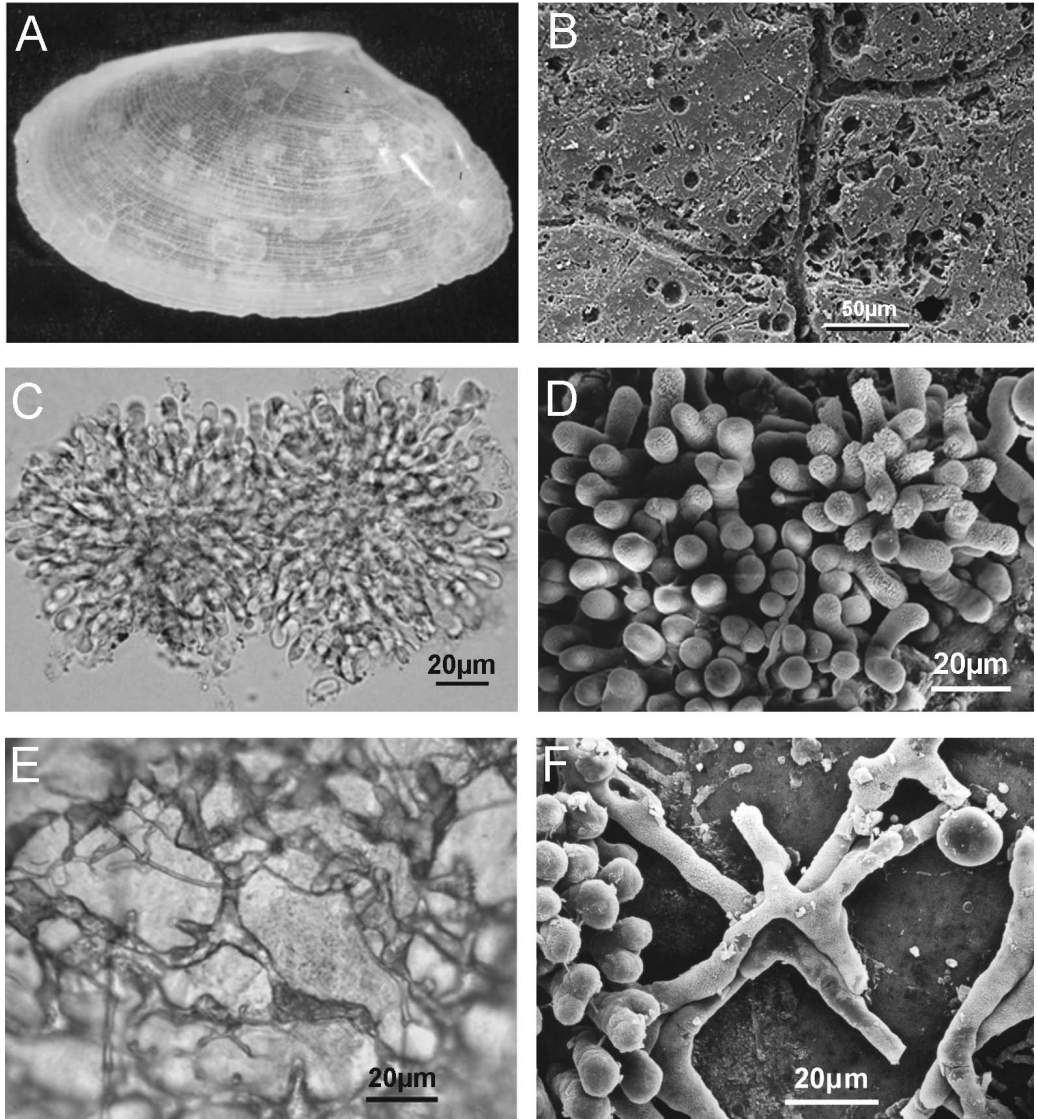


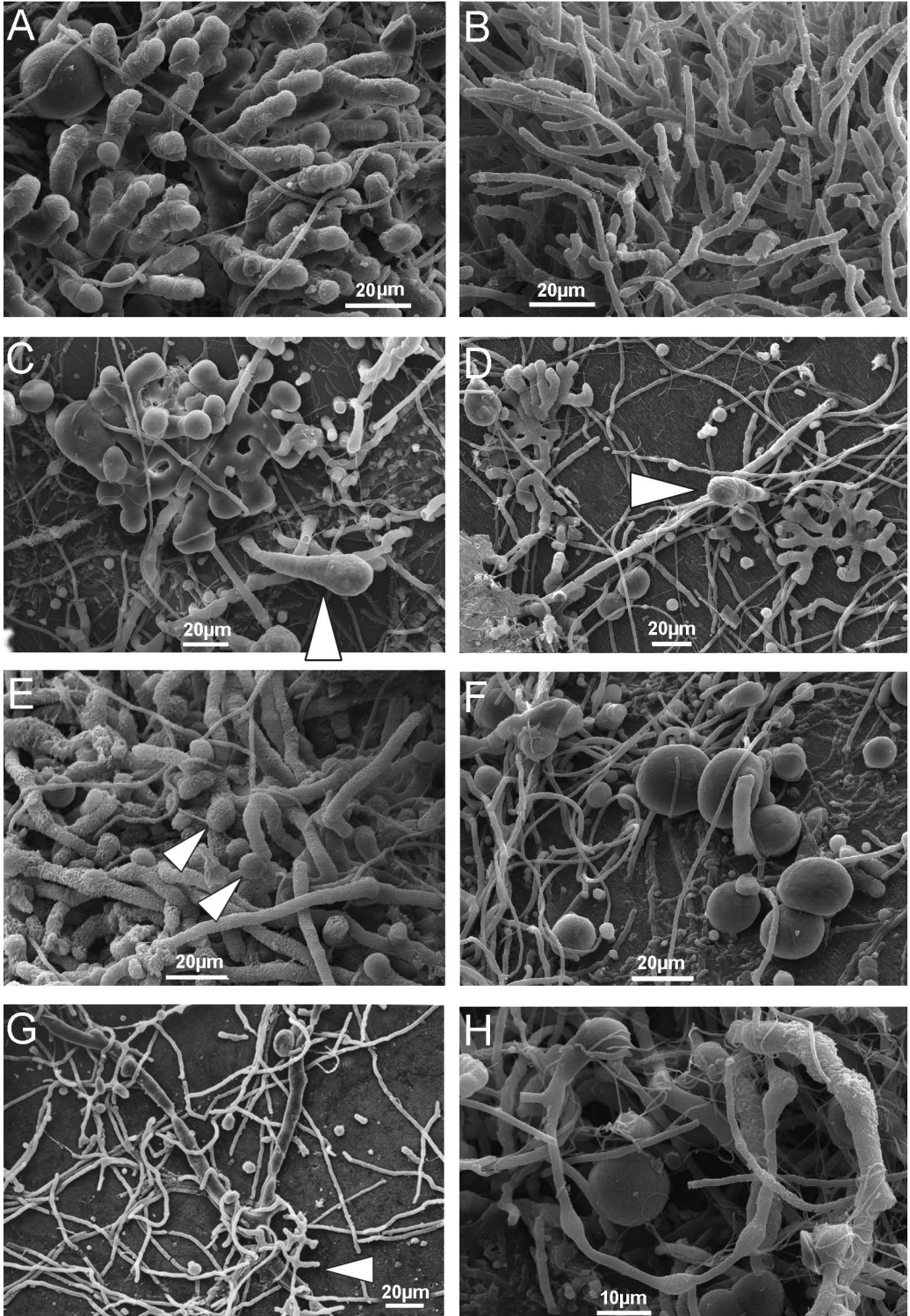
Fig. 2. Microbial euendoliths and their boring patterns in mollusc shells of Panama coasts. **A:** Microborings in translucent bivalve shell (ca. 1 cm wide) appear as opaque light-scattering fields. Individual borings are observable in dissecting microscopes. **B:** Scanning Electron Microscope (SEM) image of boreholes and shallow microboring tunnels, often with collapsed roofs. **C:** Light micrographs of two colonies of the coccoid microboring cyanobacterium *Hyella* sp., acid-extracted from a shell of *Galeta* on the Caribbean coast of Panama, 1 m depth. **D:** The trace *Fascichnus dactylus* produced by *Hyella* sp., Caribbean coast, Isla Grande, 1 m depth. **E:** Microboring green alga *Phaeophila engleri* in a transparent shell as seen by light microscopy, Caribbean coast at Isla Grande. **F:** Prostrate borings *Rhopalia catenata* produced by the chlorophyte *Phaeophila engleri* associated with *Fascichnus dactylus* (left), from Caribbean coast at Galeta.

Results

Traces of microborings in mollusk shells replicated in polymerizing resin were analyzed on both coasts of the Panama Isthmus, evaluated semiquantitatively and are summarized in Table 2. Traces *Fascichnus dactylus* (RADTKE, 1991) RADTKE & GOLUBIC, 2005 and *Scolecia filosa* RADTKE, 1991 were common on both coasts, but the frequency of occurrence of different *Fascichnus* traces was higher on the Caribbean side. The traces attributable to heterotrophic boring organisms were also present on both coasts with highest occurrence in deeper waters on the Pacific coast.

Thin translucent shells often revealed the presence of microborings at very low magnification (Fig. 2A). When viewed by scanning electron microscope (SEM) shell surfaces showed the entries of endoliths but also their distribution along the substrate surface. These borings extended immediately underneath the substrate surface and had often a collapsed roof (Fig. 2B). The most common inhabitants of the studied shells in shallow waters are the colonies of *Hyella* spp. (Fig. 2C) and their microboring traces *Fascichnus* spp. (Figs 2D; 3A, B). Other traces produced by cyanobacteria include, *Abeliella bellafurca* (Figs 3C–D), *Eurygonum nodosum* (Fig. 3E), *Planobola* isp. (Figs 3F, H) and *Scolecia filosa* (Fig. 3G). Chlorophytes are less common, represented by *Phaeophila engleri* REINKE, 1889 (Fig. 2E). Among the traces attributable to green algae, *Rhopalia catenata* RADTKE, 1991 (Fig. 2F) was present on both coasts, whereas the new types of traces with affinity to *Rhopalia*, informally named as *Rhopalia* “nodosa” and *R.* “saltator” have been observed exclusively on the Caribbean coast (Fig. 4). These traces are presumed to be produced by local chlorophyte taxa of the Caribbean Sea.

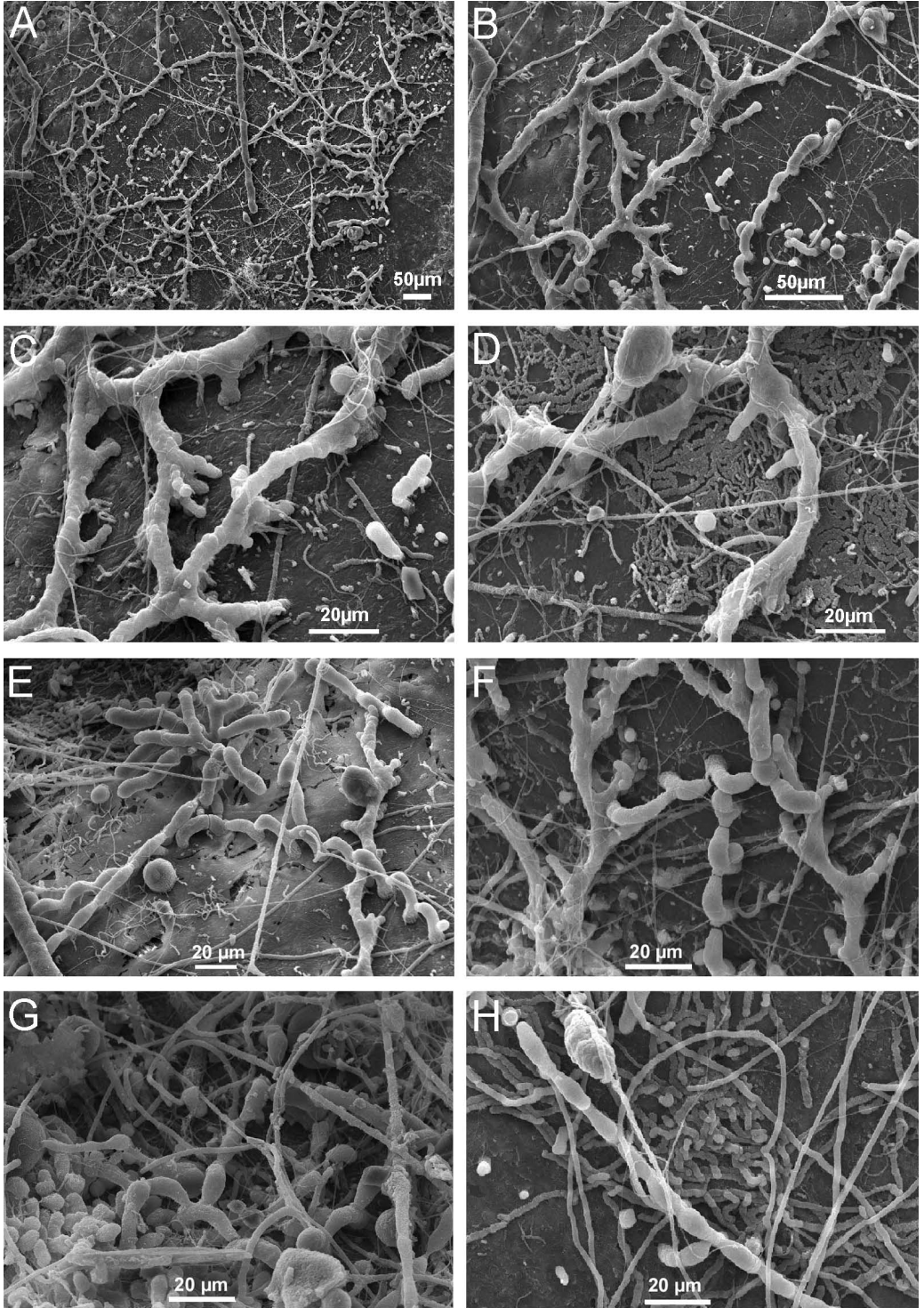
Fig. 3. Microboring traces from shallow waters (1–2 m deep) of the Caribbean coast. **A:** *Fascichnus dactylus* with bifurcated tunnels, fine tunnels across belong to *Scolecia filosa*, San Blas Islands. **B:** *Fascichnus parvus*. Note the narrow loose tunnels with lateral branching, San Blas Islands. **C:** Dichotomously branched tunnels of the trace *Abeliella bellafurca* accompanied by arched trace *Rhopalia* “saltator” and the elongated solitary club-shaped *Cavernula* “profunda” (arrow), San Blas Islands. **D:** Two rosette-shaped colonies of *Abeliella bellafurca*, the right one in company of the *Cavernula* “profunda” (arrow) and two borings of *Planobola* isp. Fine tunnels belong to *Scolecia filosa* and the very fine tunnels, less than 1 µm are classified as the Pygmy form (RADTKE 1993: 90, fig. 17/4), San Blas Islands. **E:** *Eurygonum nodosum* tunnels with typical lateral extensions (arrows), a trace of the cyanobacterium *Mastigocoleus testarum* characterized by lateral heterocysts, Galeta Islands. **F:** Spherical borings of *Planobola* isp. a trace of coccoid cyanobacteria, with fine tunnels of *Scolecia filosa*, San Blas Islands. **G:** *Scolecia botulifera* RADTKE, 1991 tunnels with periodic constrictions, a rare boring trace of the green algae *Ostreobium constrictum* with a fragment of *Ichnoreticulina elegans* (arrow), the trace of the related chlorophyte *Ostreobium quekettii*. Fine tunnels belong to *Scolecia filosa*, San Blas Islands. **H:** The boring *Orthogonum fusiferum* produced by the fungus *Ostracoblabe implexa* with typical spindle-shaped swellings and a few spherical boreholes of *Planobola* isp., San Blas Islands. ▶



Rhopalia “nodosa” (Figs 4A–D) is a newly discovered composite trace with distinct morphological features. When presented as resin cast, the trace forms parallel to substrate surface, a network of repeatedly branched filaments with irregular outline (Fig. 4A). Filaments approach each other, frequently appearing interconnected by anastomoses (Fig. 4B) rather than exhibiting avoidance like most euendolithic borings. The surfaces of the tunnels are beset by shallow node-like protrusions (Fig. 4C). The sections between branch points send numerous short connecting extensions to the substrate surface, which may alternate on either side of the main tunnel. The extensions touch the surface as single tubes, or may widen or divide into two to several points of contact (Figs 4C, D). The tunnels are cylindrical, $5.32 \pm 0.57 \mu\text{m}$ (mean \pm standard deviation) in diameter, exhibiting V-shape widening at the exit of each surface connecting extension, which could be perceived as swellings. The arrangement gives the filament an appearance of zigzag progression (Figs 4E, F).

Rhopalia “saltator” (Figs 4E–H) is a characteristic trace observed for the first time in the present contribution. The microboring organism (possibly a chlorophyte) produces a regular series of steep, short interconnected arches, attached to each other by a narrow neck and to the substrate surface by a wide circular contact (opening) at the opposite end (Figs 4E, F). This unusual pattern invokes an impression of a series of repetitive jumps. Oriented in the direction of boring activity, each arch produces two branches perpendicular to the substrate surface, of which one arm exits while the other forms the next arch. The boring direction is linear and straight with occasional additional branching that produces another linear series (Figs 4G, H). The average length of the arches is $19.5 \pm 2.9 \mu\text{m}$; their maximum width equals the diameter of the circular connection to the substrate and is $6.7 \pm 0.7 \mu\text{m}$ wide, whereas the necks interconnecting the arches are $4.57 \pm 0.56 \mu\text{m}$ in diameter.

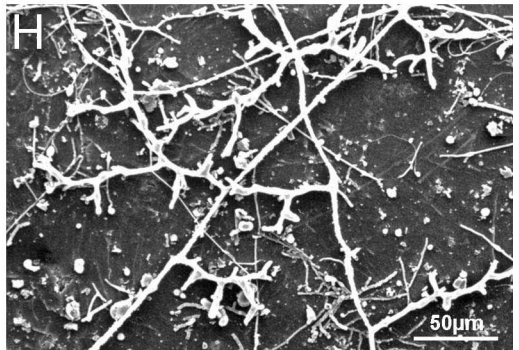
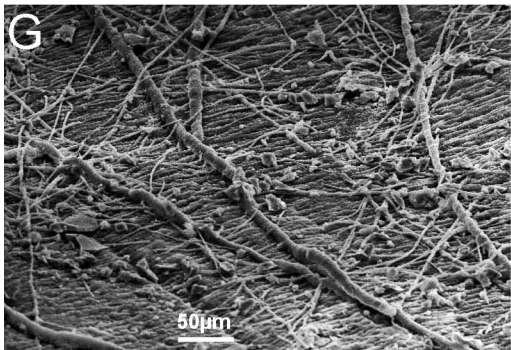
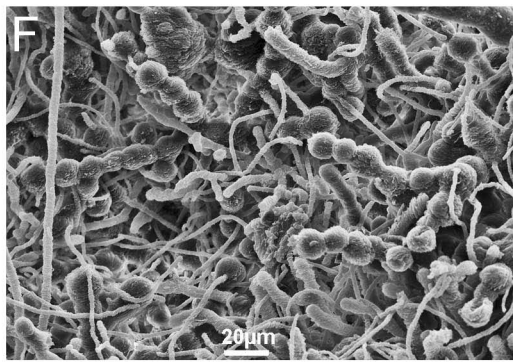
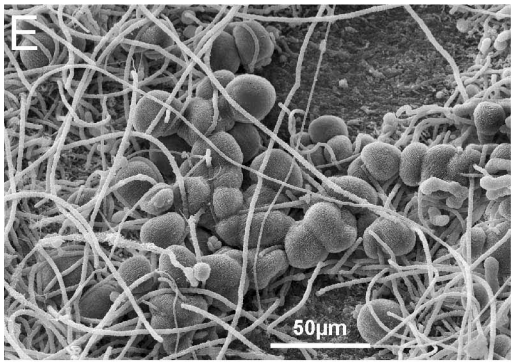
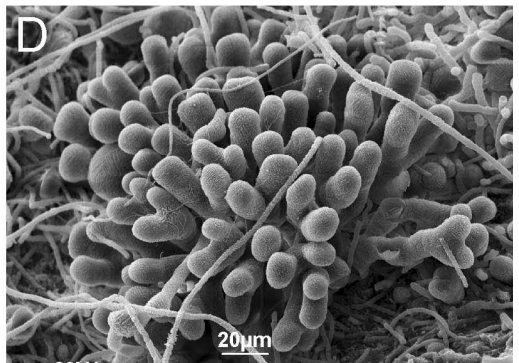
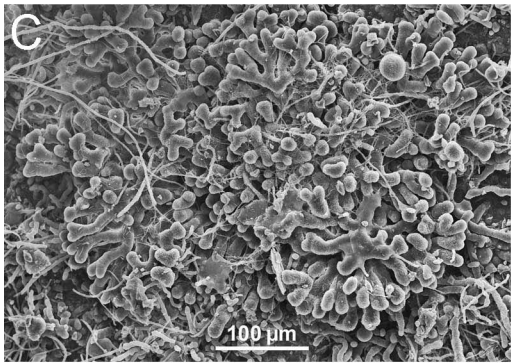
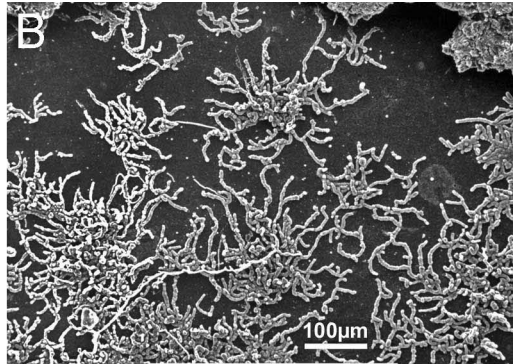
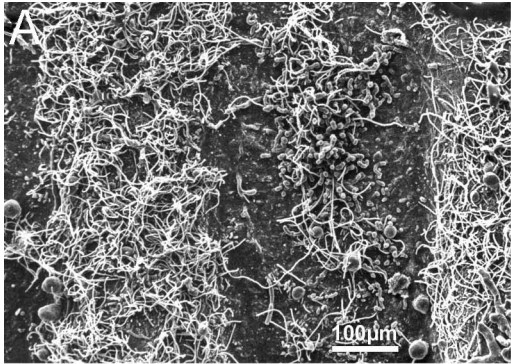
Fig. 4. Newly discovered modern traces of presumed euendolithic chlorophytes, *Rhopalia* “nodosa” (A–D) and *Rhopalia* “saltator” (E–H) from the Caribbean coast at San Blas Islands at 2 m depth. **A:** Overview of a field of borings with a number of tunnels of *Rhopalia* “nodosa”. The straight tunnel in the center is the trace *Orthogonum tubulare*. **B:** Detail of A (left) with tunnels of *Rhopalia* “nodosa”, with apparent anastomoses and with a tunnel of *Rhopalia* “saltator” (right). **C:** Detail of B. *Rhopalia* “nodosa” with characteristic nodes and connections with the substrate surface frequently widened or forked at the contact. **D:** Arched tunnel of *Rhopalia* “nodosa” with extended surface connections. The substrate surface is densely bored by meandering fine shallow tunnels of *Scolecia serrata*, spread parallel to the surface. **E:** *Rhopalia* “saltator”, characterized by straight series of repeated upright arches, with a tunnel of *Rhopalia* “nodosa” (right) and a background *Fascichnus dactylus* colony (center above). **F:** Crossing of tunnels of *Rhopalia* “saltator” (center) between two strings of *R.* “nodosa” (left and right). **G:** *Rhopalia* “saltator” with a right-angled branch, among a dense network of microborings. **H:** *Rhopalia* “saltator” with *Scolecia filosa* and *Fascichnus parvus*. ▶



Cavernula “profunda” (Figs 3C, D, arrows) comprises solitary club-shaped borings penetrating deep into shells up to 60 μm long, gradually increasing in diameter from about 5 μm at the base (entry into the substrate) to 15–18 μm at the top. The shape of the boring indicates a possibility of pleurocapsalean cyanobacteria as a maker of this trace.

The traces on the Pacific coast show a tendency for more uniform distribution of fewer, locally prevailing taxa, the dominance of which is often correlated with narrowly defined microenvironments, including such fine distinctions as the ribs of the bivalve host shells (Fig. 5A): the protruded ribs were colonized by *Fascichnus* and *Planobola* ispp., whereas the *Scolecia filosa* occupied the grooves of the shell. Uniform composition of traces is encountered in the samples from the Gulf of Chiriqui; these are dominated by *Fascichnus dactylus* (Fig. 5B). Radiating colonies of *Fascichnus* are also common in shells from the Gulf of Panama (Figs 5C, D). The next most common traces in the shells are *Planobola* ispp., which show a wide variability in diameters (up to 40 μm). This growth pattern indicates that these traces may have been produced by pleurocapsalean cyanobacteria, possibly including the pear-shaped microboring cyanobacterium *Cyanosaccus*. Fig. 5E illustrates a colony of such traces with a rare case where the boring appears to expand deeper into the shell. In addition to described traces, the shells of the Pacific coast of Panama (Las Perlas, sample 12c) contain a unique trace that has not been found anywhere else, designated here as *Fascichnus* “torulosus” (Fig. 5F). It consists of filamentous borings with distinct rhythmic constrictions that separate oval to globular units (15–18 μm wide) possibly marking the positions of cells. These borings occurred in shells of Las Perlas, Gulf of Panama. Branched tunnels of *Orthogonum tubulare* RADTKE, 1991 are less frequently encountered in the Pacific shells (Fig. 5G). *Ichnoreticulina elegans* (RADTKE, 1991) RADTKE & GOLUBIC, 2005 has been noticed in its typical form of growth (Fig. 5H); however it is probably more common but difficult to discern in densely bored substrates.

Fig. 5. Microboring traces in shells of the Pacific coast, mostly from the Gulf of Panama (B is from Gulf of Chiriqui). **A:** Differentiation of endolithic micro-niches in ribbed shells. Alternation of assemblages of *Scolecia filosa* in the depressions and *Fascichnus* dominated assemblages on exposed ribs with *Planobola* traces preferentially on the slopes between, Gulf of Panama at Naos, 0.5 m. **B:** Monospecific colonisation of a shell fragment by prostrate *Fascichnus dactylus*. Islas Secas, Gulf of Chiriqui, 18 m depth. **C:** *Abeliella* form of *Fascichnus dactylus*. Las Perlas (sample 12c), Gulf of Panama. **D:** *Fascichnus dactylus* colony, Las Perlas (sample 16), 15 m. **E:** Field of borings similar to *Planobola*, Las Perlas (sample 16), 15 m depth. **F:** An unknown microboring with branched torulose tunnels, comprised of oval segments separated by deep constrictions, Gulf of Panama, Las Perlas (sample 12c), 21 m depth. **G:** *Orthogonum tubulare* with thick straight tunnels with repeated shallow arches, Las Perlas (sample 12b), 21 m depth. **H:** *Ichnoreticulina elegans* a typical trace of the green alga *Ostreobium quekettii* with long fine straight tunnels and elaborate lateral branches, Taboga, 3 m depth. ►



Discussion

Shallow marine ichnocoenoses and the environment

Both Caribbean and Pacific coasts of Panama showed diversified assemblages of microborings, with an overall similar composition of euendolithic traces known from other moderate climate and tropical regions (PERKINS & TSENTAS 1976; RADTKE 1993; VOGEL et al. 2000). However, the two coasts of Panama showed also clear distinction regarding the presence of unique traces, observed only on the Caribbean or the Pacific coast. The Caribbean coast showed higher within-substrate diversity, while the between-substrate diversity was high on both coasts. This observation is consistent with the documented separation of micro-niches in shells with complex shell architecture (Fig. 5A). Each substrate on the Caribbean coast contained a varied and mixed assemblage of borings (e.g. Fig. 3) in contrast to shells on the Pacific coast, where the substrates tended to be dominated by single populations (Figs 5B, C).

Our survey of shells of the Caribbean coast encountered three new morphotypes of traces, with the affinities to the traces *Rhopalia* RADTKE, 1991 and *Cavernula* RADTKE, 1991. These traces, informally named here *Rhopalia* “nodosa”, *R.* “saltator” (Fig. 4) and *Cavernula* “profunda” (Figs 3C, D, arrows) exhibit distinctive repetitive patterns, which suggests that they are products of particular euendolithic microorganisms. Those affiliated with *Rhopalia* may have been formed by two chlorophytes that are different from *Phaeophila engleri*, the organism known to produce the trace *Rhopalia catenata* (RADTKE, 1991). Both *Rhopalia* traces occur quite commonly in the Caribbean shells, but were not found in shells on the Pacific side of the Panama Isthmus. The assessment of biogeographic distribution based on traces is limited, yet the two new ichnotaxa point to such possibility at least concerning euendolithic algae. *Cavernula* “profunda” differs from *Cavernula pediculata* RADTKE, 1991 by its single point of attachment to the substrate surface and its slender shape. *C. pediculata* is a trace attributed to euendolithic “Codiolum” stages of chlorophytes. The shape and gradual widening of the shaft of *C.* “profunda” suggests a different chlorophyte stage or, alternatively, cyanobacterial origin of this trace, specifically from pleurocapsalean cyanobacteria that reproduce by small propagules called baeocytes, such as *Cyanosaccus*. A slightly higher diversity of *Fascichnus* traces was recorded for the oligotrophic Caribbean side. The traces on the Pacific side were abundant but with more uniform prevalence of fewer ichnotaxa.

The number of traces attributed to heterotrophs is higher in shells in deeper waters on the Pacific side. This distinction correlates with fine grain sediment matrix where the shells were embedded and possibly further deprived of light. Lower oxidation rates of the organic matter embedded in these shells may have favored establishment of a community of heterotrophic euendoliths.

The difference observed in structure and composition of ichnocoenoses requires explanation. It correlates with considerable differences in physical and chemical properties

of the compared environments, but there are several possible parameters that may have affected the microboring community. The water temperature is more variable and on average much lower on the Pacific side, especially during the dry season when upwelling commonly occurs (Table 1). These conditions are more similar to those at higher latitudes, and may account for lower diversity. The nutrient flux and availability is also higher on the Pacific coast. The endolithic mode of life involves formation and maintenance of isolated and sheltered microenvironments with efficient local recycling of nutrients, which may contribute to the relative insensitivity (or a lag in response) of microboring organisms to external influences. The experiments with local fertilization of coral reefs had little effect on euendoliths (VOGEL et al. 2000), but these results were not conclusive, as the experiments carried out at a much smaller scale, using environmental enclosures in form of cages did record a positive response by phototrophic microbial endoliths to nitrate, as well as by heterotrophic euendoliths to organic nutrient input (CARREIRO-SILVA et al. 2009). A positive response of microbial euendoliths to petrochemically and organically polluted coasts (harbors) has been recorded earlier (CAMPBELL 1983).

Another plausible explanation for the observed differences in endolith colonization patterns refers to the availability of propagules due to difference in sedimentary conditions. The sediments covering much of the seafloor of the Pacific side of Panama are quartz-dominated terrigenous sands, whereas the seafloor of the Caribbean side is dominated by carbonates. Since microbial euendoliths inhabit carbonate particles down to sand size on the Caribbean side (see AL-THUKAIR & GOLUBIC 1991; RADTKE & GOLUBIC 2011), while they are limited to the relatively few available bioclasts scattered over the noncarbonate sands on the Pacific side, the recruitment of euendolith may differ as well.

Qualitative vs. quantitative aspects of bioerosion

The qualitative aspects of the study of microbial euendoliths and their traces deal with identity, distribution and environmental roles (niches) that different organisms and organism groups play in various stages of the bioerosion process. They include identification of the organisms involved in the process and their environmental dependencies, so as to determine their ecological responses and, by extension, the paleoecological indicator value of their traces. The study of euendoliths in modern environments is geared toward identifying the metabolic type of the organism that produces the boring, specifically to identify and evaluate the light-dependence of phototrophic microborers, and their vertical distribution along the gradient of diminishing light in the ocean. The traces of their fossil counterparts can then be used as paleobathymetric indicators, especially in depth beneath the effect of wave action where there are few sedimentary clues about the depositional depth (GOLUBIC et al. 1975). The quantitative aspects dealing with the rates of the microbioerosional processes and their environmental impacts have been the focus of experimental exposure of carbonate substrates to settlement and activity of euendoliths and the food chain they support (VOGEL et al. 1995; WISSHAK et al. 2005). The qualitative aspects, which are the focus of the present contribution may affect the rates and need therefore to be seriously considered.

Microborings as trace fossils

Microboring organisms produce “instant fossils”, which preserve well and are distributed throughout the fossil record (e.g. GLAUB et al. 2007). They are subject to ichnology, the study of other fossil traces of various biological activities in hard and soft substrates (BROMLEY 1996). The rules of naming trace fossils, which are a part of The International Code of Zoological Nomenclature (ICZN 1999); do not accept formal description of traces from modern settings reserving the formal names for fossil traces alone. Yet, most information about the production of a trace as a consequence of biological needs and behavioral response of its maker are available only in recent settings. We resorted, therefore, to informal names as guardians of information useful for interpretation of their fossil counterparts.

Similarly restrictive requirements have been practiced in the naming of microorganisms, which needed to be grown in axenic culture to deserve a name. This restriction has historically excluded many ecologically important but “unculturable” microorganisms (AMANN et al. 1995). With the recent advances in research introducing molecular tools in sequencing of the environmental DNA, the evidence of the existence of enormous, previously unsuspected diversity of organisms became evident, which includes representatives of entire phyla. For such incompletely documented new organisms and organismal groups, for which there is only a DNA signature available, the category “candidatus” has been created (RAPPE & GIOVANNONI 2003). In a corresponding fashion, we suggest that this concept of “nomenclatorial storage” of important information be adapted for traces, so we propose the candidate names for modern traces to be written with regular font and between quotation marks until a fossil trace of the same identity is found.

Power and limits in recognition of boring patterns

Microborings are traces of a peculiar behavior of microorganisms that penetrate carbonate substrates (GOLUBIC 1990). Unlike organisms that leave traces while burrowing in sandy sediments, the euendoliths produce firm traces that often conform rather precisely to the outer shape of the microborer. The boring behavior as well as the shape and size of the microboring organisms are often specific, reflecting the innate properties of the organisms involved.

The assemblage of borings in a carbonate substrate constitutes an ichnocoenosis (VOGEL et al. 1995). It is a cumulative record, which may involve several subsequent events of endolith penetration, thus containing elements of more than one biocoenosis. Coral skeletons, for example, are invaded during the lifetime of the host by a different microborer assemblage than those that colonized the skeleton after the death of the coral (LE CAMPION-ALSUMARD et al. 1995). Most mollusk shells are colonized after the death of the host animals. The residence time of microborers in the skeleton may also differ. Cyanobacteria are long-term residents, which release only reproduction cells (e.g. baeocytes) into the water column. Euendolithic chlorophytes and rhodophytes spend only some stages in

their life cycle inside the rock (KORNMANN 1960; CAMPBELL 1980). Septate chlorophytes are short term residents, as their borings are often found empty (VOGEL et al. 2000).

Comparative study of borings often permits reconstruction of the developmental cycle of the boring organism. Some microboring organisms have complex life-cycle and also produce complex traces, which need to be recognized and named as such (MILLER 2007). Examples include the borings of *Ostreobium quekettii* BORNET & FLAHAULT, 1889 and *Eugomontia sacculata* KORNMANN, 1960, which produce the composite traces *Ichnoreticulina elegans* and *Rhopalia clavigera*, respectively (RADTKE & GOLUBIC 2005; GOLUBIC & RADTKE 2008). The traces are comprised of long, straight periodically dichotomously branched tunnels, alternating with sections of tunnels with laterally inserted dense network of branches in rectangular arrangement, as well as sections in which the tubes widen to form differently shaped bags. Such traces could be mistakenly interpreted as belonging to several separate organisms. Complex traces in the current contribution are described as *Rhopalia* “nodosa” and *Rhopalia* “saltator”. The latter trace permitted a reconstruction of the direction of boring.

The existence of convergent adaptations and morphologies among different microboring organisms poses limitations in the interpretation of their traces. For example, the stalked euendolithic cyanobacteria of the genus *Solentia* and the most diverse shallow water pleurocapsalean genus *Hyella* produce quite similar borings classified as *Fascichnus* (see AL-THUKAIR & GOLUBIC 1991; RADTKE & GOLUBIC 2011). Different filamentous microboring organisms maintain repeated contacts with the substrate surface and grow parallel to it. The reproduction in many unrelated organisms takes place in sporangial swellings, and simple very thin tunnels are produced by phototrophic cyanobacterium *Plectonema terebrans* BORNET & FLAHAULT, 1889 (trace *Scolecia filosa* RADTKE, 1991) and also by the hyphae of organotrophic fungi. Fungal hyphae are different by their branching pattern, but often have long unbranched sections. The extremely fine submicron sized tunnels could be cast in resin and described as Pygmy form (RADTKE 1993) produced by unknown bacteria. Convergent morphology in traces of taxonomically and functionally different organisms limits their value as paleoenvironmental indicators.

Between microborers and the bored substrate exists an ecological interrelationship. Accordingly, morphological features of the trace may reflect the properties of the substrate as well as of the borer. The tunnels often carry etch marks on their inner surface that modify the outlines of their casts, possibly revealing the nature and extent of the dissolution process. Conversely, boring behavior can be modified by the properties of the substrate. Additional changes that affect fossil traces occur later as a part of taphonomy and diagenesis, which often occur soon after the death of the microborer (LE CAMPION-ALSUMARD et al. 1995). Precipitation of micrite inside boreholes has been proposed by BATHURST (1966) as a mechanism of formation of micritic envelopes around carbonate particles. This view has been recently revised by recognition that precipitation may occur contemporaneously with the boring activity and that endoliths may contributed to

consolidation of the substrate (e.g. the stromatolites in the Bahamas (MACINTYRE et al. 2000; REID & MACINTYRE 2000). Synchronous boring and precipitation mechanism has been proposed by GARCIA-PICHEL (2006) and subsequently observed in coral skeletons (NOTHDURFT et al. 2007).

Acknowledgments

The Government of Panama is thanked for fieldwork and collecting permits. The Smithsonian Tropical Research Institute (STRI) provided the scientific and logistic platform to conduct our fieldwork. We thank Ute SCHULDT (Kiel University) and Claudia FRANZ (Senckenberg Museum, Frankfurt) for SEM operation and processing of photomicrographs. Deutsche Forschungsgemeinschaft (DFG) is acknowledged for funding the research within the program “Impact of Gateways on Ocean Circulation, Climate, and Evolution” (FOR 451), project “Impact of gateway closure on carbonate ecosystems diversifications”. Alexander-von-Humboldt Foundation, Bonn and Hanse Institute for Advanced Studies, Delmenhorst, are thanked for the support of international collaborations. The critical review by Marina CARREIRO-SILVA (DOP) is gratefully acknowledged.

References

- AL-THUKAIR, A.A. & GOLUBIC, S. (1991): Five new *Hyella* species from the Arabian Gulf. – In: HICKEL, B., ANAGNOSTIDIS, K. & KOMÁREK, J. (eds): Cyanophyta/Cyanobacteria – Morphology, Taxonomy, Ecology. – Algological Studies, **64**: 167–197.
- AMANN, R.I., LUDWIG, W. & SCHLEIFER, K.-H. (1995): Phylogenetic identification and in situ detection of individual microbial cells without cultivation. – Microbiological Reviews, **59**: 143–169.
- BATHURST, R.G.C. (1966): Boring algae, micrite envelopes, and lithification of molluscan biosparites. – Geological Journal, **5**: 15–32.
- BORNET, M.E. & FLAHAULT, C. (1889): Sur quelques plantes vivant dans le test calcaire des mollusques. – Bulletin de la Société Botanique de France, **36**: 147–176.
- BROMLEY, R.G. (1996): Trace fossils: Biology, taphonomy and applications, 2nd edition. – 361 p., London (Chapman & Hall).
- CAMPBELL, S.E. (1980): *Palaeoconchocelis starmachii*, a carbonate boring microfossil from the Upper Silurian of Poland (425 million years old): implications for the evolution of the Bangiaceae (Rhodophyta). – Phycologia, **19**: 25–36.
- CAMPBELL, S.E. (1983): Petrochemical pollution: Endolith response. – Vies Journées d’ Études sur les Pollutions marines C.I.E.S.M., Cannes, Dec. 2–4, 1982: 183–189.
- CARREIRO-SILVA, M., McCLANAHAN, T.R. & KIENE, W.E. (2009): Effects of inorganic nutrients and organic matter on microbial euendolithic community composition and microbioerosion rates. – Marine Ecology Program Series, **392**: 1–15.

- CHAZOTTES, V., CABIOCH, G., GOLUBIC, S. & RADTKE, G. (2009): Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia – Implications for paleodepth reconstructions in Holocene corals. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280**: 456–468.
- , LE CAMPION-ALSUMARD, T. & PEYROT-CLAUSADE, M. (1995): Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **113**: 189–198.
- COATES, A.G., JACKSON, J.B.C., COLLINS, L.S., CRONIN, T.M., DOWSETT, H.J., BRYBELL, L., JUNG, P. & OBANDO, J.A. (1992): Closure of the Isthmus of Panama: the near-shore marine records of Costa Rica and western Panama. – *Geological Society of America, Bulletin*, **104**: 814–828.
- & OBANDO, J.A. (1996): The geologic evolution of the Central American Isthmus. – In: JACKSON, J.B.C., BUDD, A.F. & COATES, A.G. (eds): *Evolution and environment in tropical America*. – pp. 21–56, Univ. Chicago (Chicago Press).
- D’CROZ, L. & O’DEA, A. (2007): Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll II. – *Estuarine Coastal and Shelf Sciences*, **73**: 325–240.
- & ROBERTSON, D.R. (1997): Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. – *Proceedings 8th International Coral Reef Symposium*, **2**: 2053–2058.
- FORTUNATO, H. & SCHÄFER, P. (2009): Coralline algae as carbonate producers and habitat providers on the Eastern Pacific coast of Panama: preliminary assessment. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **253**: 145–161.
- GARCIA-PICHEL, F. (2006): Plausible mechanisms for the boring of carbonates by microbial phototrophs. – *Sedimentary Geology*, **185**: 205–213.
- GLAUB, I., GOLUBIC, S., GEKTIDIS, M., RADTKE, G. & VOGEL, K. (2007): Microborings and microbial endoliths: Geological implications. – In: MILLER, W. (ed.): *Trace Fossils: Concepts, Problems, Prospects*. – pp. 368–381, Amsterdam (Elsevier).
- & VOGEL, K. (2004): The stratigraphic record of microborings. – *Fossils & Strata*, **51**: 126–135.
- GOLUBIC, S. (1972): Scanning electron microscopy of Recent boring Cyanophyta and its possible paleontological application. – In: DESIKACHARY, T.V. (ed.): *Taxonomy and Biology of Blue-green Algae*. – pp. 167–170, University of Madras, India (Bangalore Press).
- (1990): Shell boring microorganisms. – In: BOUCOT, A. (ed.): *The Evolutionary Paleobiology of Behavior and Coevolution*. – pp. 347–352, Amsterdam (Elsevier).
- , BRENT, G. & LE CAMPION-ALSUMARD, T. (1970): Scanning electron microscopy of endolithic algae and fungi using a multipurpose casting-embedding technique. – *Lethaia*, **3**: 203–209.
- , CAMPBELL, S.E., DROBNE, K., CAMERON, B., BALSAM, W.L., CIMERMAN, F. & DUBOIS, L. (1984): Microbial endoliths: a benthic overprint in the sedimentary record, and a paleobathymetric cross-reference with foraminifera. – *Journal of Paleontology*, **58**: 351–361.
- , FRIEDMANN, I. & SCHNEIDER, J. (1981): The lithobiontic ecological niche, with special reference to microorganisms. – *Journal of Sedimentary Petrology*, **51**: 475–478.
- , PERKINS, R.D. & LUKAS, K.J. (1975): Boring microorganisms and microborings in carbonate substrates. – In: FREY, R.W. (ed.): *The Study of Trace Fossils*. – pp. 229–259, New York (Springer).

- & RADTKE, G. (2008): The trace *Rhopalia clavigera* isp. nov. reflects the development of its maker *Eugomontia sacculata*, KORNMANN 1960. – In: WISSHAK, M. & TAPANILA, L. (eds): Current Developments in Bioerosion. – pp. 95–108, Berlin (Springer).
- , RADTKE, G. & LE CAMPION-ALSUMARD, T. (2005): Endolithic fungi in marine ecosystems. – Trends in Microbiology, **13**: 229–235.
- & SCHNEIDER, J. (2003): Microbial endoliths as internal biofilms. – In: KRUMBEIN, W.E., DORNIEDEN, T. & VOLKMANN, M. (eds): Fossil and Recent Biofilms. – pp. 249–263, Dordrecht (Kluwer Academic Publishers).
- KORNMANN, P. (1960): Die heterogene Gattung *Gomontia*. II. Der fädige Anteil, *Eugomontia sacculata* nov. gen. nov. spec. – Helgoländer Wissenschaftliche Meeresuntersuchung, **7**: 59–71.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (ICZN) (1999): International Code of Zoological Nomenclature. – International Trust for Zoological Nomenclature, Natural History Museum, London, XXIX + 306 p.
- LE CAMPION-ALSUMARD, T., GOLUBIC, S. & HUTCHINGS, P. (1995): Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia). – Marine Ecology Progress Series, **117**: 149–157.
- MACINTYRE, I.G., PRUFERT-BEBOUT, L. & REID, R.P. (2000): The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. – Sedimentology, **47**: 915–921.
- MILLER, W. III (2007): Complex trace fossils. – In: MILLER, W. (ed.): Trace Fossils: Concepts, Problems, Prospects. – pp. 458–465, Amsterdam (Elsevier).
- NOTHDURFT, L.D., WEBB, G.E., BOSTROM, T. & RINTOUL, L. (2007): Calcite-filled borings in the most recently deposited skeleton in live-collected *Porites* (Scleractinia): Implications for trace element archives. – Geochimica et Cosmochimica Acta, **71**: 5423–5438.
- PERKINS, R.D. & TSENTAS, C.I. (1976): Microbial Infestation of Carbonate Substrates Planted on the St. Croix Shelf, West Indies. – Bulletin of the Geological Society of America, **87**: 1615–1628.
- RADTKE, G. (1991): Die mikroendolithischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung. – Courier Forschungsinstitut Senckenberg, **138**: 1–185.
- (1993): The distribution of microborings in molluscan shells from Recent reef environments at Lee Stocking Island, Bahamas. – Facies, **29**: 81–92.
- , GLAUB, I., VOGEL, K. & GOLUBIC, S. (2010): A new dichotomous microboring: *Abeliella bellafurca* isp. nov., distribution, variability and biological origin. – Ichnos, **17**: 25–33.
- & GOLUBIC, S. (2005): Microborings in mollusk shells, Bay of Safaga, Egypt: Morphometry and ichnology. – Facies, **51**: 125–141.
- & — (2011): Microbial euendolithic assemblages and microborings in intertidal and shallow marine habitats: insight in cyanobacterial speciation. – In: REITNER, J., QUERIC, N.-V. & ARP, G. (eds): Advances in Stromatolite Geobiology. – Lecture Notes in Earth Sciences, **131**: 213–244, Berlin (Springer).
- , LE CAMPION-ALSUMARD, T. & GOLUBIC, S. (1996): Microbial assemblages of the bioerosional “notch” along tropical limestone coasts. – Algological Studies, **83**: 469–482.

- RAPPE, M.S. & GIOVANNONI, S.J. (2003): The uncultured microbial majority. – *Annual Review of Microbiology*, **57**: 369–394.
- REID, R.P. & MACINTYRE, I.G. (2000): Microboring versus recrystallization: Further insight into the micritization process. – *Journal of Sedimentary Research*, **70**: 24–28.
- REIJMER, J.J.G., BAUCH, T. & SCHÄFER, P. (2011): Carbonate facies patterns in surface sediments of upwelling and non-upwelling shelf environments (Panama, East Pacific). – *Sedimentology*.
- REINKE, J. (1889): Algenflora der westlichen Ostsee deutschen Antheils. – Bericht der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel, **6**: 1–101.
- SCHNEIDER, J. (1976): Biological and inorganic factors in the destruction of limestone coasts. – *Contribution of Sedimentology*, **6**: 1–112.
- SCHNEIDER, J. & TORUNSKI, H. (1983): Biokarst on Limestone Coasts, Morphogenesis and Sediment Production. – *Marine Ecology*, **4**: 45–63.
- TRIBOLLET, A. & GOLUBIC, S. (2005): Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. – *Coral Reefs*, **24**: 422–434.
- , LANGDON, C., GOLUBIC, S. & ATKINSON, M. (2006a): Endolithic microflora are major primary producers in dead carbonate substrates of Hawaiian coral reefs. – *Journal of Phycology*, **42**: 292–303.
- , ATKINSON, M. & LANGDON, C. (2006b): Effects of elevated pCO₂ on epilithic and endolithic metabolism of reef carbonates. – *Global Change Biology*, **12**: 2200–2208.
- TUDHOPE, A.W. & RISK, M.J. (1985): Rate of dissolution of carbonate sediments of microboring organisms, Davies Reef, Australia. – *Journal of Sedimentary Petrology*, **55**: 440–447.
- VOGEL, K., BUNDSCHUH, M., GLAUB, I., HOFMANN, K., RADTKE, G. & SCHMIDT, H. (1995): Hard substrate ichnocoenoses and their relations to light intensity and marine bathymetry. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **195**: 49–61.
- , GEKTIDIS, M., GOLUBIC, S., KIENE, W.E. & RADTKE, G. (2000): Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. – *Lethaia*, **33**: 190–204.
- WISSHAK, M. (2006): High-Latitude Bioerosion, The Kosterfjord Experiment. – *Lecture Notes in Earth Sciences*, **109**: 202 p., Berlin (Springer).
- , GEKTIDIS, M., FREIWALD, A. & LUNDÄLV, T. (2005): Bioerosion along a bathymetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): An experimental study. – *Facies*, **51**: 93–117.
- ZHANG, Y. & GOLUBIC, S. (1987): Endolithic microfossils (cyanophyta) from early Proterozoic stromatolites, Hebei, China. – *Acta Micropaleontologica Sinica*, **4**: 1–12.