The trace *Rhopalia clavigera* isp. n. reflects the development of its maker *Eugomontia sacculata* Kornmann, 1960

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Abstract. Complex boring patterns often reflect the complexity of life cycle of the euendoliths that produce them. They are illustrated here by different stages in the development of the euendolithic ulotrichacean chlorophyte *Eugomontia sacculata* reconstructed on the basis of its complex trace in the shells of *Mya arenaria* in brackish waters of the Baltic Sea at Gdansk, Poland. The trace consists of different types of boring morphologies as distinctive from one another as many traces specific to separate organisms. Because they occur associated, they may be misinterpreted as separate members of an ichnocoenosis. We propose to describe them as parts of a complex trace instead, because they are based on the genetic program of a single organism, but expressed in different proportions at different stages of its development. A new ichnospecies, *Rhopalia clavigera* isp. n., is described to characterize these traces.

Keywords. Complex traces, development, *Eugomontia*, ichnofossils, microborings, *Rhopalia clavigera*, salinity

Introduction

Most microbial euendoliths are known from modern marine environments with very few described and reported from freshwater or brackish settings. In contrast, many fossil microborings, which have modern counterparts similar to the borings of marine euendoliths, were described from paleoenvironments interpreted as brackish (Pomerol and Feugueur 1986; Radtke 1991). In the study of paleoenvironments there are few sedimentary clues to estimate past salinities, although the salinity is generally considered an important parameter responsible for selective separation of marine and freshwater taxa of plants and animals. Boring traces preserve well in the fossil record and show relatively high morphological specificity which, in addition to their small size, makes them good potential environmental indicators (Vogel et al. 2000; Glaub et al. 2007). The effect of salinity on endolith distribution has been studied using experimentally exposed substrates in the waters of the Skagerrak where

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salinities fluctuated with the change of currents between normal marine waters of the North Sea and brackish waters of the Baltic Sea; these substrates have all recruited assemblages of marine euendoliths (Wisshak et al. 2005; Wisshak 2006).

The objective of this study was to explore the extension of marine euendoliths into the brackish ranges of stable, consistently low salinities below 10 ppt of NaCl in the Baltic Sea at Gdansk, Poland. Our study in a low salinity and low diversity environment had an additional benefit by providing numerous euendolithic populations of a single taxon at different stages of its development.

We report here the prevalence of complex borings produced by the chlorophyte *Eugomontia sacculata* Kornmann, 1960 in naturally exposed shells of *Mya arenaria* Linnaeus, 1758. The organism exhibited conspicuous dominance producing coherent internal biofilms (sensu Golubic and Schneider 2003) comprised of networks of intertwined filaments. The organism produced a number of colonies at different stages of development. Its complex boring system is described as a new ichnofossil. *Eugomontia sacculata* was found euendolithically in carbonate substrates with a wide distribution, mostly reported from northern latitudes (e.g., Wilkinson and Burrows 1970; Wilkinson 1974; Akpan and Farrow 1984; Akpan 1986; Burrows 1991; Tittley et al. 2005) but also from the Mediterranean (Gallardo et al. 1993) and the Red Sea (Gektidis et al. 2007). Nielsen (1987) described a second species *Eugomontia stelligera* from cultures isolated from shells in New Zealand, which has not been observed in natural settings.

Materials and methods

A collection of dead shells of the bivalve *Mya arenaria*, which have been exposed to euendolith colonization in shallow brackish waters on the coast of the Baltic Sea at Gdansk, was examined for the presence and distribution of microborings and resident microbial euendoliths. Shells were studied for the presence of discoloration by phototrophic euendoliths using dissecting microscope. Forty shells and shell fragments from two different collection sites were separated for further analysis. The areas affected by endoliths in each sample were fragmented and sub-sampled. A ca. 10 mm^2 shell fragment from the same area was analyzed using different methods: (a) The surface of a shell fragment was analyzed using scanning electron microscope (SEM). (b) Another fragment was dissolved in 3% HCl exposing a coherent biofilm of euendoliths, which was observed under dissecting microscope, cut in half and mounted on microscope slides, each half with the other side up, so that both sides of the endolithic biofilm could be examined. (c) A fragment was treated with acetone and impregnated with slow polymerizing Araldite resin (Fluka, Bregenz, Austria), then excised and decalcified with dilute HCl (Golubic et al. 1983). The resin casts were observed by SEM. The boring replicas were measured using in-scale photomicrographs and Sigma-Scan Image software (SigmaScan, San Raphael, CA). The measurements of euendolith colonies at different stages of development were carried out and compared with the resin casts of their borings with 25-50 measurements for each of the following parameters: Minimum and maximum width of filaments observed by light microscopy at 400 x magnification and of cylindrical tunnels measured from SEM images; width and length (= depth of penetration) of largest sporangial swellings and casts of their boreholes, respectively, were measured in each of the colonies. Fully developed swellings extend perpendicular to the substrate surface. The results were expressed as mean ± standard deviation (number of measurements) and graphed as cross diagrams with arms of one standard deviation and the mean at the intersection. The distribution of measurements was tested for normalcy, and the distance of two standard deviations from the mean included most of the individual data.

Results

Shells of the bivalve *Mya arenaria* collected in shallow waters of the Baltic coast were consistently dominated by the euendolithic ulotrichacean chlorophyte *Eugomontia sacculata*, accompanied by the cyanobacteria *Hyella* Bornet and Flahault, 1888 and *Cyanosaccus* Lukas and Golubic, 1981 as minor components. *Eugomontia* Kornmann, 1960 was resident in most shells and formed complex boring systems at different stages of development. The accompanying cyanobacteria occurred in minor patches mostly separate from the colonies of *Eugomontia*. The identification was made by correlating the morphology of the borings with that of the resident euendoliths extracted from the same substrate fragment. Developmental sequences were reconstructed from resin casts by comparing a large number of boring systems arranged by size.

Eugomontia formed two different basic types of borings which prevail at different times of its development (Fig. 1). The endolithic portions of the thallus normally originate at point locations where the organism penetrates the surface of the shell from where it spreads by growing filaments directly beneath the surface of the substrate. Filaments radiate in all direction, forming a shallow circular colony. The resin replicas reveal a dense system of ramified tunnels with the highest density in the parts proximal to the point of entry, gradually decreasing toward the periphery (Fig. 1A). The second stage consists of the development of endolithic sacs with reproductive function (sporangia). The sacs start as simple spindle-shaped widening of the tunnels, but soon become asymmetric and then elongate perpendicular to the filaments, oriented toward the interior of the substrate. Less common are slight terminal swellings of filaments on short lateral branches. At this stage, the tunnels without widening are limited to the colony margin (Fig. 1B) where the expansion of the colony slowly continues. The development of sacs, possibly triggered by an environmental stimulus, is initiated in the central (oldest) region of the colony, proximal to the point of entry, from where it rapidly spreads toward the periphery, so that ultimately the entire colony including the margins are characterized by sac formation (Fig. 1C). The proportion of the colony covered by sacs varies from system to system, although the largest sacs and their highest density are found in the proximal regions of the colony.

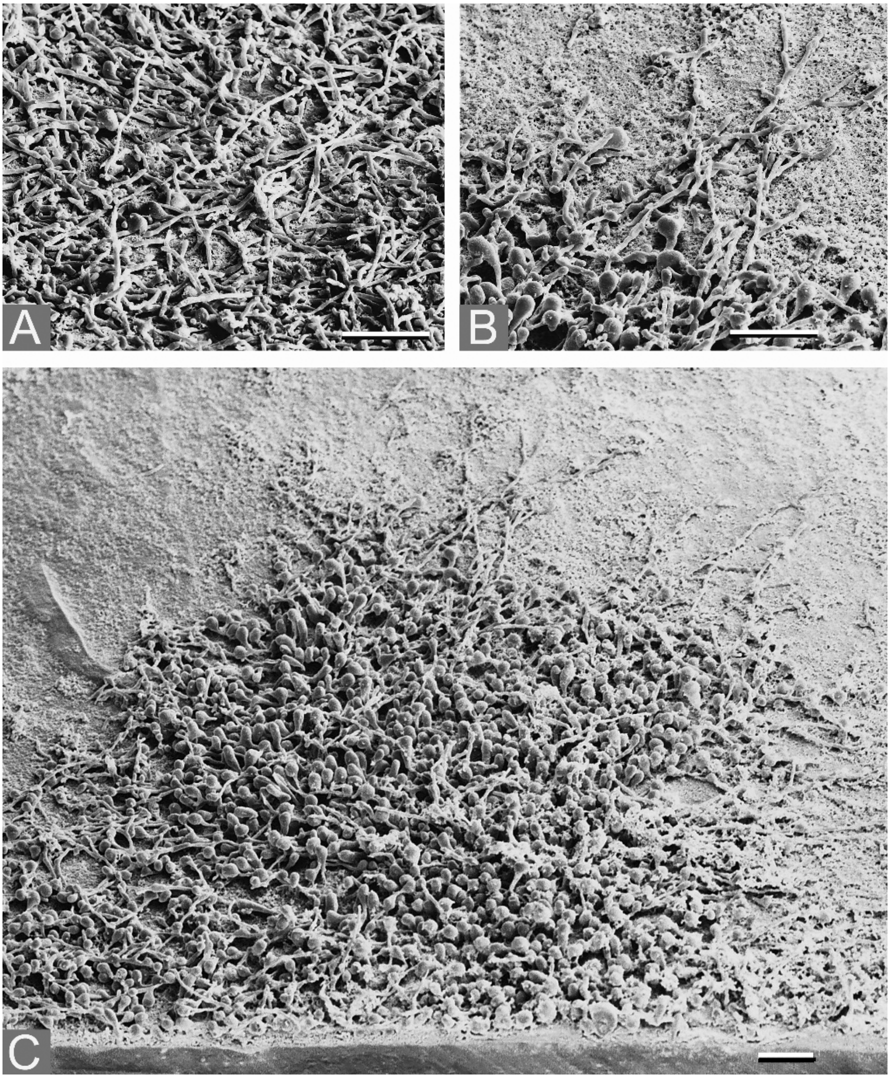


Fig. 1 Complex boring system of *Rhopalia clavigera* isp. n., produced by *Eugomontia sacculata*. **A** Early development of the boring is dominated by branched cylindrical tunnels produced by septate filaments radiating from a center outward. **B** Development of sporangial swelling advances to the margins of the system, leaving only exploratory filaments on the edges of the colony. **C** A mature colony with club-shaped enlargements extending perpendicular to the filaments and substrate surface. All scale bars: 100 µm

The tunnels are cylindrical 3 to 6 µm in diameter, with the mean ± standard deviation of 4.5 ± 0.8 µm (25 measurements), whereas the fully developed sacs are clearly elongated toward the interior of the substrate, 21.2 ± 2.9 µm wide and 42.1 ± 5.4 µm (25 measurements) long (Fig. 2). Displayed are maximum and minimum diameters for each tunnel, whereas the sacs were measured and displayed as length vs. width.

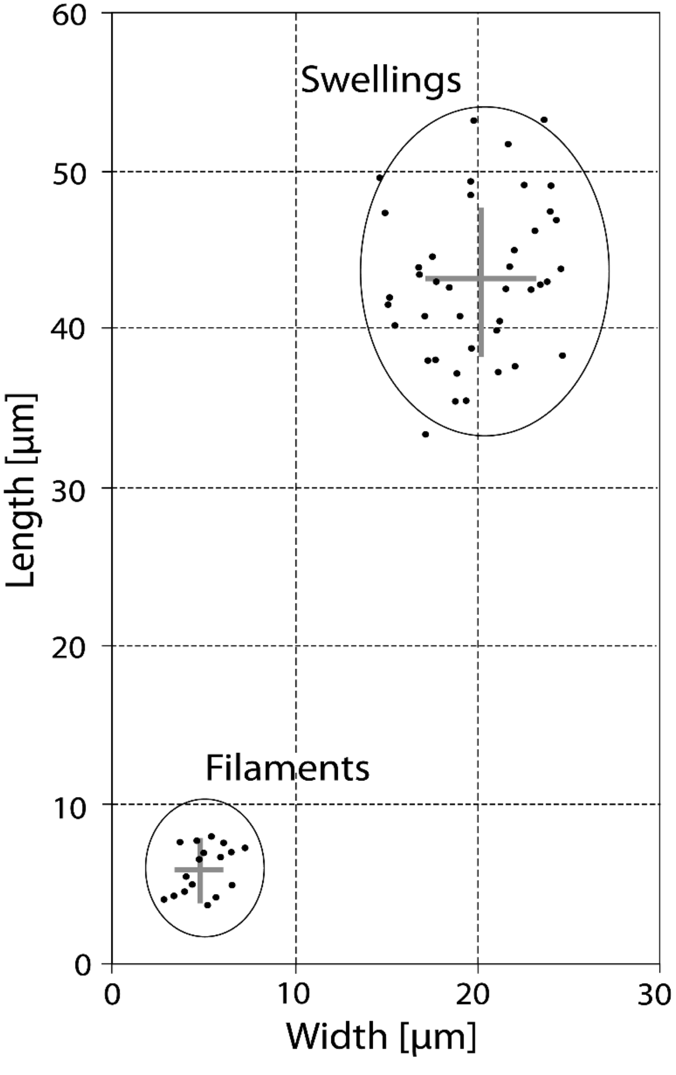


Fig. 2 Cross-plots for dimensions of two different modules of the complex boring *Rhopalia clavigera* isp. n. The means and standard deviation for the maximum vs. minimum diameters of the branched tunnels (lower left) and for the length vs. width of the swellings (upper right). Note that the field covering 2 standard deviations from the mean (oval) includes 95% of the sample

The relationship between the euendolith *Eugomontia sacculata*, its differentiation in filaments and sporangia and the morphology of its boring system is summarized in Figure 3. Filaments extracted by dissolution of the substrate (Fig. 3A) correspond in detail with the resin casts of their borings, including pointed tips (Fig 3B). Sporangial swellings are modifications of filaments, which remain attached to each other (Fig. 3C). Both are faithfully replicated in the casts (Fig. 3D). The sequence

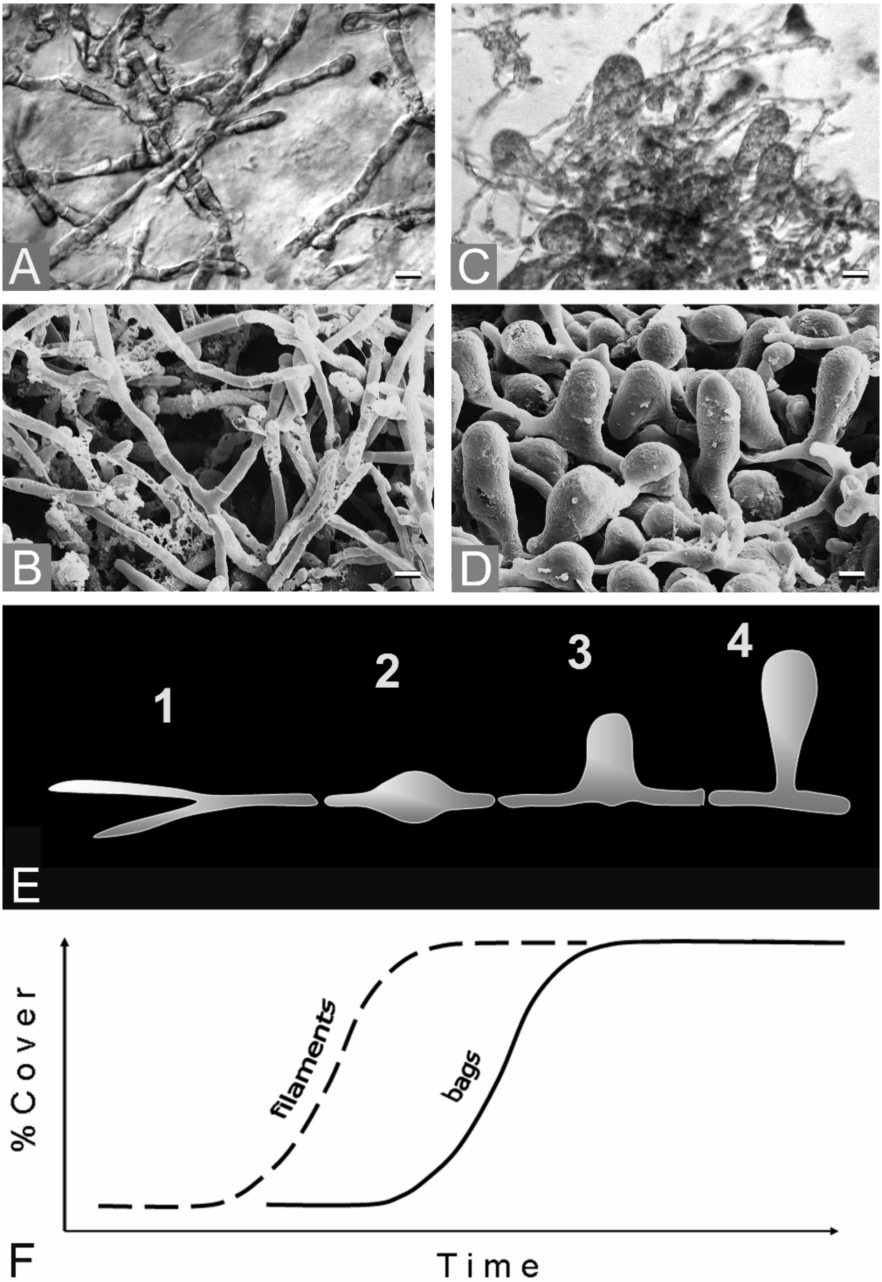


Fig. 3 The euendolith *Eugomontia sacculata* and its boring *Rhopalia clavigera* isp. n. **A** Branched septate filaments. **B** Resin cast of filamental tunnels. **C** Cluster of sporangial swellings connected to filaments. **D** Resin cast of a cluster of fully developed sacs containing sporangial swellings. **E** Reconstruction of differentiation (from 1 to 4) and colony expansion (from 4 to 1). **F** Temporal model in the development and expansion of the two modules. All scale bars: 10 µm

of developmental stages is presented schematically in Figure 3E, starting with branched tunnels, which undergo lateral swellings that develop into upright bags. In this diagram the growth of the boring system proceeds from right to left, while the differentiation in form and function proceeds from left to right. The estimated timing of the changes in boring patterns and their relative rates are presented diagrammatically (Fig. 3F).

In conclusion, the borings of *Eugomontia sacculata* reflect the changes in the course of the development of the organism. As a result, the shape of the boring includes very different elements ranging from filaments to sporangial sacs. The sacs expand toward the interior of the substrate, resulting in an upright posture of the resin replica. As the sporangial swellings mature, the sacs expand toward the substrate surface, producing a tube (see Kornmann 1960) and form a perforation in the shell where the spores are released.

Systematic ichnology

Ichnogenus *Rhopalia* Radtke, 1991

Original diagnosis: Club-shaped to spherical swellings connected with a system of tunnels (after Radtke 1991, translated from German).

Rhopalia clavigera **isp. n.**

Fig. 4B

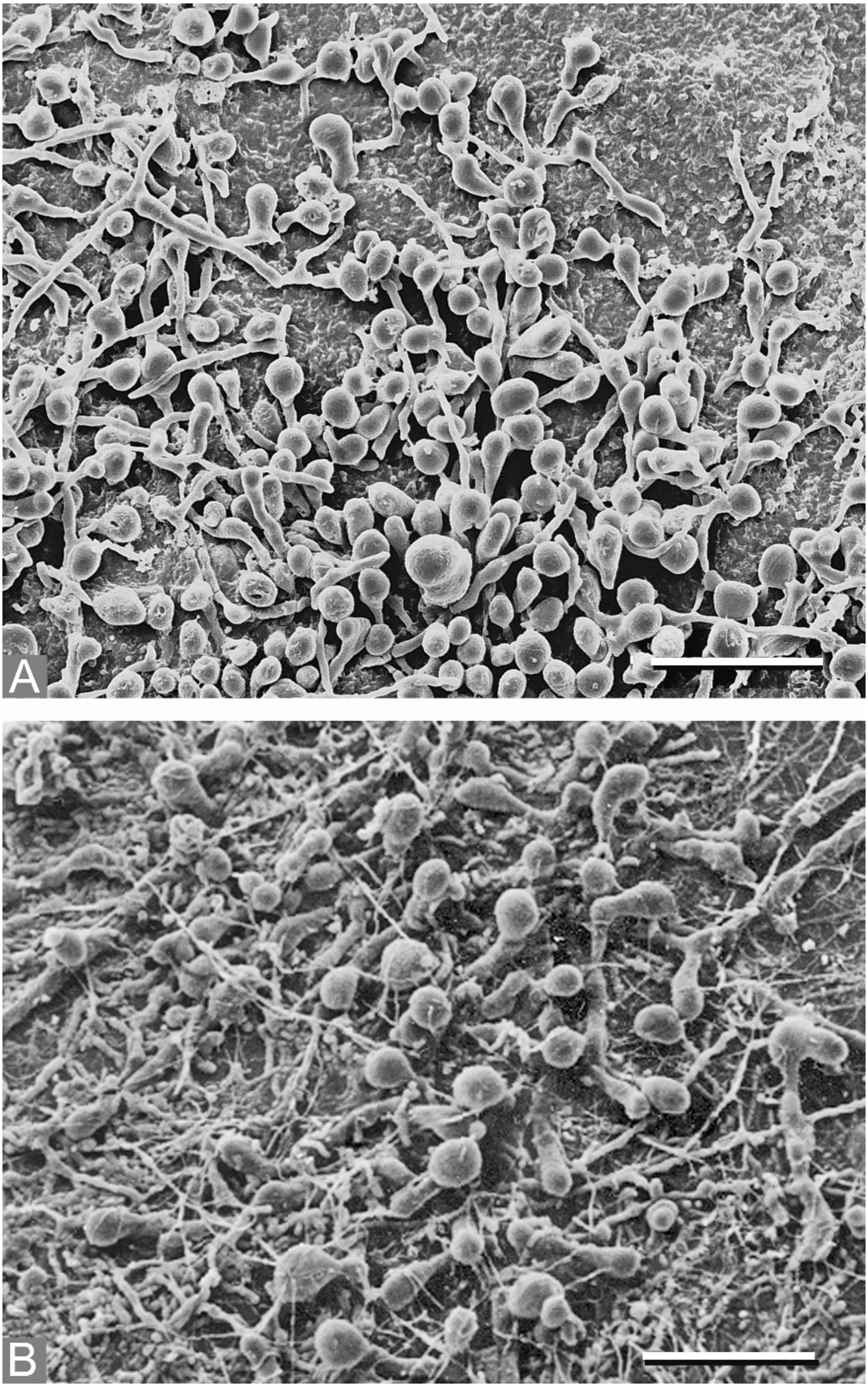
1990 *Eugomontia sacculata* – Günther, 237, plate 54, fig. 6
1991 *Rhopalia catenata* – Radtke, 77, sample Bo7/41, plate 9, fig. 3; [partim]

Etymology: *claviger* (Latin) = club-carrying

Type material, locality and horizon: The holotype as shown in Figure 4B is a resin cast of borings in a shell fragment of *Callista* Poli, 1791 from the Paris Basin at Venteuil, France (Middle Lutetian, Middle Eocene). Collection of the Institute of Geology-Paleontology, University of Frankfurt a. M., Germany, inventory number Bo 7/26 (see also Radtke 1991: location marked in fig. 6).

Diagnosis: Borings comprised of two basic morphotypes and the transitions between them. The system spreads by branching tunnels, which radiate underneath the substrate surface from a single point of entry. The system deepens starting in the central portions by developing elongate lateral swellings perpendicular to the radiating tunnels and to the surface of the substrate.

Description: The boring starts from a single point of entry and expands radial forming a shallow network system which is circular in outline and expanding. The initial growth produces cylindrical tunnels, later expanding into deeper penetrating sacs, which empty to the substrate surface. The boring consists of two principal


A
B

modules connected with transitional forms. **Module 1 – tunnels**: Tunnels cylindrical in cross section of relatively constant diameter of 4.5 ± 0.8 μm (25 measurements) branching at various angles, formed by an intertwined network of septate filaments. This module predominates in the early stages of growth and is responsible for lateral expansion of the system. The mature systems retain this early module at the periphery of the colony as exploratory filaments (Figs. 1A-B, 2 lower left, 3C). **Module 2 – sacs**: Sacs are series of elongated, club-shaped lateral expansions from the tunnels toward the interior of the substrate and perpendicular to the tunnels and the substrate surface. They contain sporangial swellings of the endolith. Sacs originate from lateral expansions of each cell in the filament, bounded by narrow interconnections at the positions of filament cross walls. Sac formation starts from the colony center and expands toward the periphery (Figs. 1C, 2 upper right, 3B).

Remarks and differential diagnosis: *Rhopalia clavigera* isp. n. is a complex system of microborings that tightly outlines the filaments and reproductive sacs of the ulotrichacean chlorophyte *Eugomontia sacculata* Kornmann, 1960 and reflects the changes in the development of the latter, including the timing and rates characteristic of this development. The borings are characterized by several features that serve as differential diagnosis toward other traces of the same ichnogenus: Frequent conical tips of the filaments, fairly constant diameters along the cylindrical tunnels, narrow variability range of tunnel diameters and narrow interconnections between swellings (mostly <5 μm). These properties clearly distinguish *Rhopalia clavigera* from *Rhopalia catenata* Radtke, 1991. Lack of spiny attachments to the surface and elongated, inward oriented rather than isodiametric swellings comprise the distinction from *Rhopalia spinosa* Radtke and Golubic, 2005.

Discussion

Development and differentiation in form and function

Microborings frequently conform to the shape of the euendoliths that produce them and reflect their specific boring behavior. However, the shape of the microborer as well as its behavior may change in the course of the development of the organism. As a consequence, borehole morphology may undergo considerable variation or a complete change that requires qualitative and quantitative assessments. We suggest that a biometric evaluation of spatial and temporal borehole variability would improve the definition of ichnotaxa. Comparison between resident euendoliths and their borings helps to distinguish between properties specific to different biotaxa in an assemblage, from those that characterize parts of the same biotaxon or stages in the development of the same biotaxon.

In the case of the microboring *Rhopalia clavigera* and its producer *Eugomontia sacculata*, each of the borehole morphotypes illustrated in Fig. 3E (numbered 1

Fig. 4 Comparison of modern and ancient *Rhopalia clavigera* isp. n. **A** Club-shaped swellings distributed up to the margin in a late stage of a modern *Rhopalia clavigera* in a *Mya arenaria* shell. **B** Holotype of *Rhopalia clavigera* isp. n. Middle Eocene, Paris Basin. Scale bars: 100 μm through 4) is sufficiently distinct to be described as a separate ichnofossil. Their co-occurrence may then be misinterpreted as an ichnocoenosis, particularly when the material available for comparison is limited as it is often the case with fossils. A confusion concerning the euendolith identity is another problem and is a part of the history of the study of *Eugomontia sacculata*, which is still not completely resolved.

The organism was initially described under the name *Gomontia polyrhiza* (Lagerheim) Bornet and Flahault, 1888, which included an earlier described taxon *Codiolum polyrhizum* Lagerheim, 1885 under the assumption that both constituted parts of the same organism (Bornet and Flahault 1888, 1889). The work on cultures by Kylin (1935) and later by Kornmann (1959, 1960) showed that the two endolithic morphs are phases in the life cycles of two different organisms, which required formal renaming of the taxon to *Eugomontia sacculata* Kornmann, 1960. The name *Gomontia polyrhiza* has since been used for Lagerheim's organism, because 'Codiolum' turned out to be a developmental stage in the life cycle of several ulotrichacean algae. Recent studies using 18S rRNA gene sequencing discovered that genera *Monostroma* Thuret, 1857, *Collinsiella* Setchell and Gardner, 1903, *Gomontia* and *Eugomontia*, which all have euendolithic phases, form a phylogenetically tight cluster, so that they might be considered the same genus (O'Kelly et al. 2004). Exept for the stage of dissemination by zoospores and gametes, *Eugomontia sacculata* appears to be the only species in this group that is euendolithic throughout its entire life cycle, including sporophytic and gametophytic generations.

Timing of cell differentiation and boring behavior

Boring activity is initiated from single points of entry by rapid radial growth of septate endolithic filaments which produce cylindrical tunnels. High density of borings is maintained by filament branching. As the colonies spread horizontally, they may interfere with each other, causing a deeper penetration into the substrate in older (proximal) parts of the colony. In the second phase of the development, the peripheral expansion of the colony slows down, while the cells along the filament increase in diameter between the septa and grow sac-like outgrowths, initially symmetrical and later oriented toward the interior of the substrate. The differentiation into sacs starts in the oldest parts of the colony, close to the point of the entry into the substrate, and the maturation progresses outward so as to catch up with the peripheral growth (Fig. 1C). As a consequence of this timing, young colonies may be predominantly comprised of cylindrical tunnels whereas older colonies are entirely made of sacs up to the periphery (Fig. 4A). The life cycle of *Eugomontia sacculata* includes an isomorphic alternation of haploid and diploid generations, both producing sporangial swellings, although possibly with different timing of the onset and rates of progression (Kornmann 1960).

Similarity and convergent evolution

The ability to penetrate carbonate substrate and to continue to live inside it evolved in a number of different microorganisms, including members of Cyanobacteria, Chlorophyta and Rhodophyta among phototrophs and several endoliths of fungal affinity (reviewed by Wisshak 2006). Because of the selective pressure associated with the endolithic mode of life, which is common to all euendoliths, similar morphological features among unrelated organisms may be explained by convergent evolution. These include the adaptations facilitating substrate colonization, nutrient supply, exchange of metabolic products and reproduction. Occupation of new substrate by euendoliths requires only a small free surface area, because the endoliths continue to grow underneath the substrate surface, thus avoiding competition by the epilithic community. Accordingly, the early stages are often inconspicuous, limited to a small, spore-sized perforation on the substrate surface. Once inside, the phototrophic euendoliths stay close to the substrate surface and have to cope with the shading by epiliths. Maintenance of repeated contacts with the surface is required for nutrient supply and release of metabolic products, and separate perforations are made for the release of reproductive cells. Accordingly, many unrelated euendoliths radiate from the initial points of entry, produce shallow borings, and maintain repeated contacts with the substrate surface and the surrounding water. Because of similarities due to adaptation to common conditions, it is recommended that differential diagnoses be included in descriptions of ichnotaxa.

Studying complex traces

Euendolithic organisms form a spatial network or an internal biofilm (Golubic and Schneider 2003) which is inaccessible to direct observation because of the opacity of the carbonate substrate. This spatial network, however, collapses following dissolution of the substrate, which makes an assessment of the biological identity of the organisms difficult. Casting of borings by polymerizing resins followed by SEM observations enables the perception of borings in their three-dimensional arrangement, which does not include the resident microorganisms. A parallel study applying complementary methods to subsamples has produced optimal results in a combined study of both the traces and their makers.

Traces exhibiting different degrees of complexity are produced by both prokaryotic and eukaryotic euendoliths. Among phototrophic prokaryotes, relatively simple boring systems of *Fascichnus* (Radtke, 1991) produced by species of *Hyella* may vary in size over a wide range, possibly reflecting taxonomic diversification (Radtke and Golubic 2005). Yet, one of these species, *Hyella vacans* Gektidis and Golubic, 1996 shows a progressive change from binary fission of cells during the initial boring phase to multiple fission of the reproductive phase, at an accelerated rate in which the reproduction ‘catches up’ with the apical growth (Gektidis and Golubic 1996). The process is similar to that illustrated here for the eukaryotic *Eugomontia*, but does not affect borehole morphology. Simple borings are also produced by filamentous cyanobacteria *Plectonema terebrans* Bornet and Flahault, 1889 and *Schizothrix perforans* (Ercegović) Geitler, 1927, both recently reclassified within the genus *Leptolyngbya* Anagnostidis and Komárek, 1988 (see Komárek and Anagnostidis 2005). They produce narrow tunnels similar to those made by hyphae of euendolithic fungi. More complex filamentous cyanobacteria show cell differentiation into carbon-fixing and nitrogen-fixing (heterocysts) cells. Among euendoliths, these are represented by the *Mastigocoleus testarum* Lagerheim, 1886 and its trace *Eurygonum nodosum* Schmidt, 1992 (see Glaub et al. 2007: fig. 21.2-5 and Günther 1990: plate 52 fig. 6 for illustrations). In the present contribution we have dealt with a higher degree of complexity that generally characterizes eukaryotic phototrophs, exhibiting changes in the course of their life cycle, particularly in cases of alternation of generations of anisomorphic haploid and diploid phases. The life cycle of endolithic rhodophytes (Conchocelis-stages) is even more complex (Conway and Cole 1977; Campbell 1980).

The study of microborings in modern settings has the advantage of the frequent encounter of microborers in residence, which enables not only a correlation of ichnotaxa with corresponding biotaxa, but also a study of euendolith differentiation in form and function during their development, which includes their boring behavior. Such analyses reveal predictable sequences and even timing of events leading to morphological complexity of traces. It is, therefore, preferable that the documented biological coherence be acknowledged by a formal description of a complex trace (see Miller 2007). Morphologically different elements of a complex trace can then be described as 'modules', which identify distinct but spatially or temporally connected morphological elements of a complex trace. Such a procedure was applied for the siphonal chlorophyte *Ostreobium quekettii* Bornet and Flahault, 1889 and its trace *Ichnoreticulina elegans* (Radtke, 1991) by Radtke and Golubic (2005). Similar ichnotaxonomic procedures identified as phases in development have been used in descriptions of other complex traces such as *Entobia* Bronn, 1837 produced by boring sponges, supported by identification of skeletal spicules of the resident euendolith (Bromley and D'Alessandro 1984, 1989). Fossil traces are often incomplete or fragmentary. Identifying more than one module of a trace adds to the degree of confidence in interpretation, an assessment which is generally recommended in the work on traces.

Euendoliths and salinity

The present study identified marine euendoliths that inhabit permanently brackish ranges with salinities of 10 ppt and less, although with a more pronounced dominance of few taxa. This observation is consistent with the general rule that extreme environments tend to be characterized by a reduced diversity, where few successful biotaxa are represented by a large number of individuals. We hypothesize, therefore, that microbial euendoliths evolved in the marine environment, where their diversity is highest, and experience low salinities and freshwater conditions as extreme. However, their tolerance to low salinities is considerable under fluctuating conditions (see Wisshak 2006) as well as in stable brackish conditions as shown in the present study. These findings suggest that further research is required to establish the lower salinity limits of marine euendolithic taxa and their traces.

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