Mar Biodiv (2018) 48:1855–1862
DOI 10.1007/s12526-017-0684-5

SENCKENBERG

CrossMark

ORIGINAL PAPER

Euendolithic *Conchocelis* stage (Bangiales, Rhodophyta) in the skeletons of live stylasterid reef corals

Aline Tribollet[1] · **Daniela Pica**[2] · **Stefania Puce**[2] · **Gudrun Radtke**[3] · **Susan E. Campbell**[4] · **Stjepko Golubic**[4]

Received: 18 October 2016 / Revised: 8 March 2017 / Accepted: 9 March 2017 / Published online: 22 March 2017
© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2017

Abstract Stylasterids are azooxanthellate lace corals, which may show an unusual colouration in coral reef ecosystems, ranging from red to purple on the light-exposed side of their colonies. In the present study, it was discovered that the calcareous skeletons of such corals are actually invaded and eroded by cryptic carbonate boring algae that represent *Conchocelis* phases in the life cycle of bangialean rhodophytes. For the first time, the shape, organisation and distribution of *Conchocelis* filaments within the skeletons of two different genera of lace corals are reported and documented by light and electron microscopy. Such description and characterisation of *Conchocelis* can help to distinguish between morphologically and taxonomically different endolithic microorganisms penetrating coral skeletons, including their recognition in fossil borings as indicators of depositional depth, i.e. of the extent of the photic zone and light conditions in ancient marine environments. The results are discussed in the light of a possible symbiotic or parasitic relationship between *Conchocelis* phases and their stylasterid host corals.

Communicated by B. W. Hoeksema

✉ Aline Tribollet
aline.tribollet@ird.fr

Stjepko Golubic
golubic@bu.edu

[1] IRD-Sorbonne Universités (Univ. Paris 6) UPMC-CNRS-MNHN, Laboratoire IPSL-LOCEAN, 4 Place Jussieu, 75005 Paris Cedex, France

[2] Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Ancona, Italy

[3] Hessisches Landesamt für Naturschutz, Umwelt und Geologie (HLNUG), Wiesbaden, Germany

[4] Biological Science Center, Boston University, Boston, MA, USA

Keywords Coral reefs · Coral skeleton · Cryptic development · Fossil record · Microborers

Introduction

The presence of microbial borings in fossil and modern animal skeletons has been noticed since the 19th century, attributed initially to fungi under the name *Mycelites ossifragus* Roux (1887). A wider spectrum of microorganisms that penetrate carbonate substrates became known after Bornet and Flahault (1888, 1889) described several new species of cyanobacteria, fungi and eukaryotic green algae in the shells of molluscs and, later on, when Ercegović (1932a, b) studied and described new cyanobacterial genera and species that penetrate coastal carbonate rocks across the intertidal and supratidal zones. The rock-penetrating habit was later found to occur as part of alternate generations in the development of various green and red algae and was studied in culture (Kornmann 1959, 1960, 1961, 1962; Kornmann and Sahling 1980).

Batters (1892) was the first to describe a carbonate-penetrating rhodophyte as a new genus and species, *Conchocelis rosea*, which is now referred to as the *Conchocelis* stage in the development of several red algae, especially Bangiales. It was Kathleen Drew (1949) who established that *Conchocelis* is, in fact, an endolithic phase in the development of *Porphyra umbilicalis*, the edible leafy red alga, which is an important part of diet in Japan (Nori). She noticed that *Porphyra*, which grows in England only between October and February, survives between March and September inside carbonate rocks and shells in the form of an alternating, euendolithic generation (Drew 1954, 1956). Thanks to her discoveries, the *Conchocelis* stages of a number of *Porphyra* species, including *P. arasaki*, *P. haitanensis*, *P. kunidae*, *P. pseudolinearis*, *P. seriata*, *P. tenera* and *P. yezoensis*, have been successfully grown in clam shells (Tseng and Borowitzka 2003). The development

and alternation of generations in *Porphyra* that included a *Conchocelis* stage were then studied in culture by Tseng and Chang (1955), Kornmann (1961), Kornmann and Sahling (1980) and Bao-Fu (1984). Under natural conditions (i.e. in situ), the *Conchocelis* stages were first reported in various carbonate substrates from cold marine ecosystems, where they occurred down to considerable depths (70 m), so they were proposed to be used for determination of the euphotic zone; in contrast, the leafy epilithic generation of *Porphyra* was found mostly in the intertidal zone (Clokie et al. 1979, 1981).

Microboring organisms or microbial euendoliths (Golubic et al. 1981) evolved among cyanobacteria, green and red algae, fungi and lichens. They colonise all types of carbonate substrates in marine and freshwater ecosystems from polar to tropical environments and are major agents in marine bioerosion in coral reef ecosystems (reviewed by Tribollet et al. 2011). Green algae among phototrophic euendoliths, which are known to penetrate both dead carbonate substrates as well as live and growing scleractinian corals, are well established in modern (Odum and Odum 1955; Lukas 1973; Le Campion-Alsumard et al. 1995) and ancient (Kołodziej et al. 2012) tropical settings. In contrast, the euendolithic rhodophytes have been less frequently observed in corals or any other carbonate substrates, thus receiving much less attention. Laborel and Le Campion-Alsumard (1979) were the first to report *Conchocelis* in abundance in live and growing scleractinian corals (*Dichocoenia* sp. and *Mycetophyllia* sp.) in the tropical Caribbean and Brazilian reefs. They observed that filaments of *Conchocelis* conferred a pinkish to purplish colour to the coral skeleton and apparently excluded other euendolithic microorganisms that usually inhabit the skeletons of live corals, such as the chlorophyte *Ostreobium quekettii* (Odum and Odum 1955; Lukas 1973; Le Campion-Alsumard et al. 1995).

More recently, stylasterid hydroids (also known as lace corals) on Indonesian coral reefs were found to exhibit an unusual pinkish to purplish colouration, which was attributed to boring cyanobacteria in their skeletons (Puce et al. 2009), similar to those observed in cold water azooxanthellate corals (Försterra and Häussermann 2008; Tribollet et al. 2011, fig. 10). The light-dependent distribution of the red pigmentation within the lace coral colonies indicated the phototrophic nature of these microbial euendoliths (Puce et al. 2009; Pica et al. 2016). A recent microscopic analysis of stylasterid colonies from the Indo-Pacific determined that the most abundant of these microboring organisms are, in fact, representing the eukaryotic *Conchocelis* stages of bangialean rhodophytes, rather than euendolithic cyanobacteria (Pica et al. 2016). The taxonomy of bangialean rhodophytes is currently under revision, supported by molecular analyses (Lindstrom et al. 2015).

In the present contribution, we analysed the microborings produced by euendolithic filaments of *Conchocelis* stages in the skeletons of selected species of live stylasterid corals from Indonesian reefs (see Pica et al. 2016), comparing the morphology of *Conchocelis* filaments with the outlines of their boreholes. The description and characterisation of the shapes, ramifications and boring patterns of *Conchocelis* may help to distinguish between morphologically and taxonomically different endolithic microorganisms penetrating coral skeletons, including their recognition in fossil borings as indicators of depositional depth, i.e. of the extent of the photic zone and light conditions in ancient marine environments (Clokie et al. 1979; Radtke 1993; Radtke et al. 1996; Vogel et al. 2000). It may also stimulate studies of specific bioerosion rates as reviewed by Tribollet (2008) and of a possible symbiotic or parasitic relationship between euendoliths and scleractinians (see Fine and Loya 2002), as well as stylasterid corals.

Materials and methods

From a large collection of stylasterid corals of Indonesia, microbial euendoliths were observed in 38 out of a total of 128 specimens (Pica et al. 2016). For the purpose of the present contribution, a selection of five specimens belonging to five different species of the genera *Stylaster* and *Distichopora* (see Table 1) were analysed for distribution, morphological differentiation and fine structure of microboring filaments inside their skeletons. The preceding study of euendolith

Table 1 Location and habitats of studied stylasterid corals from North Sulawesi (Indonesia)

Stylasterid species	Location	Coordinates	Depth	Habitat and light exposure
Distichopora cf. *vervoorti* ('violet')	Pulau Bangka	001°46′ 7.42″N 125°10′ 31.08″E	2 m	On vertical walls with direct light
Stylaster tenisonwoodsi ('orange')	Pulau Bangka	001°45′ 3.30″N 125° 7′ 59.72″E	5 m	Underneath large *Porites* colonies without direct light
Stylaster cf. *eximius* ('pink')	Siladen, Bunaken Marine National Park	001°37′ 34.81″N 124°48′ 10.97″E	20 m	On vertical walls with direct light
Stylaster sp. ('white')	Siladen, Bunaken Marine National Park	001°37′ 34.81″N 124°48′ 10.97″E	25 m	Inside small caves on vertical walls with no direct light
Distichopora sp. ('white')	Siladen, Bunaken Marine National Park	001°37′ 34.81″N 124°48′ 10.97″E	35 m	Inside small caves on vertical walls with no direct light

abundance in the stylasterid skeletons of the same collection reported by Pica et al. (2016) showed that all specimens of the above corals harboured the same type of euendolithic filaments.

The samples were collected on coral reefs at North Sulawesi, Indonesia at depths from 2 to 35 m (see Pica et al. 2016; Table 1). They were preserved dry or in 70% ethanol. Small fragments of coral branches (1–2 cm long) were first gradually dehydrated in ethanol and then embedded in the Struers SpeciFix epoxy resin (Golubic et al. 1970). After complete polymerisation at ambient temperature, thin sections were cut with a diamond saw to prepare petrographic thin sections about 30–40 μm thick (Tribollet et al. 2002). One subset of sections was partially decalcified (for few seconds in 3% HCl) and stained with Toluidine blue prior to observation under a light microscope (Nikon Eclipse LV100). The second subset of partially decalcified thin sections was gold-coated for observation under a scanning electron microscope (SEM; Zeiss EVO LS15 from the Alizés platform, IRD, Bondy, France).

The dimensions of filaments (diameter of tubules, and width and length of cellular units, swellings and connections between cells) were measured from pictures taken by light microscopy and SEM using Motic software (Motic China Group, Co., Ltd.). The results were expressed as mean ± standard deviation (SD). Taxonomic determinations were consulted with Guiry and Guiry (2017).

Results

Abundant multiply branched filaments composed of eukaryotic cells, pigmented red from the auxiliary light-harvesting pigment known as phycoerythrin (e.g. Glazer 1985), were observed penetrating the skeletons of *Stylaster tenisonwoodsi*, *Stylaster* cf. *eximius*, *Stylaster* sp., *Distichopora* sp. and *Distichopora* cf. *vervoorti*, concentrating on the light-exposed side of coral colonies (see fig. 4 in Pica et al. 2016). They provided a red to purple colour to coral colonies, which usually appear white or differently pigmented as orange or violet due to the naturally coloured skeleton and living tissues (Fox 1972). These microboring or euendolithic filaments were made visible in sections across the coral stem after the skeletal carbonate was dissolved by dilute HCl, stained with Toluidine blue solution (Fig. 1a, c–f). The boreholes produced by these filaments inside coral skeletons were analysed separately as resin-cast replicas using SEM (Figs. 1b and 2).

The microorganisms that formed the branched carbonate-penetrating filaments were recognised to be *Conchocelis* stages of bangialean rhodophytes, growing inside the coral coenosteum, without exiting into the pore space. They grew predominantly underneath and along the coenosteum interior surface. Short filament extensions were, however, observed connecting the filaments in the coenosteum interior with those outside.

The *Conchocelis* filaments in *S. tenisonwoodsi*, *S.* cf. *eximius*, *Stylaster* sp., *Distichopora* sp. and *Distichopora* cf. *vervoorti* contained membrane-bound organelles, such as chloroplasts, coloured red by the auxiliary light-harvesting pigment phycoerythrin. The filaments were composed of cells interconnected by pit connections located in the centre of cross-walls (see Li et al. 2006). The light photomicrographs (Fig. 1a) show an intricate meshwork of filaments forming branch clusters, which conform closely with the outline and orientation of the borings as replicated in polymerising resin and observed by SEM (Fig. 1b). Common types of *Conchocelis* filaments include series of cylindrical cells (5–10 μm in diameter) constricted at the cross-walls. The cells frequently widen upward, where they produce a cluster of branches at the apical side of the cell (Figs. 1c and 2f). The cylindrical filaments are usually replaced by series of spindle-shaped cells (9.5 ± 1.85 μm wide, 33.08 ± 7.9 μm long; $n = 35$), interconnected at their narrow ends (1.72 ± 0.18 μm wide; $n = 18$), sometimes extending for considerable distance within the skeletal carbonate (Fig. 1d, e). Spherical swellings (10–25 μm in diameter) occur solitary or in series (Fig. 1a, c). Terminal clusters of branches with club-shaped cell wall protrusions are morphological characters typical of *Conchocelis* (Figs. 1f and 2d).

The three-dimensional display of borings is shown by SEM images (Figs. 1b and 2). The borehole outlines maintain a close conformity with cell outlines, including details at the cell connections. Cylindrical boring traces of different shapes and branching patterns are shown in Fig. 2a–c and in more detail in Fig. 2d–g. Cylindrical tunnels with cross-wall constrictions are shown in all images of Fig. 2, which are especially clear in Fig. 2b, top and Fig. 2d–e. The traces of spindle-shaped cell units are shown in Fig. 2a, b. When viewed by SEM at higher magnification, they are seen as flat widenings (Fig. 2c, d, g), and so are the asymmetrical widenings with ramifications (Fig. 2a, b, f). Club-shaped terminal cell wall protrusions (Fig. 1f) are also well illustrated in three dimensions (Fig. 2d), as well as the clusters of branches concentrated on the apical poles of cell units (Fig. 2e, f). An important detail revealed by SEM at higher magnification is the exposed pit connections between cells (Fig. 2d, e, g).

The skeletons of the five stylasterid corals under study are all coloured red by *Conchocelis* filaments. The filaments of the siphonal chlorophyte *Ostreobium quekettii* and very fine tunnels probably belonging to fungi were recognised in *Distichopora* cf. *vervoorti*, although they were rare. The concentration of *Ostreobium* filaments was too low to confer a green colour to stylasterid skeletons as it is known for

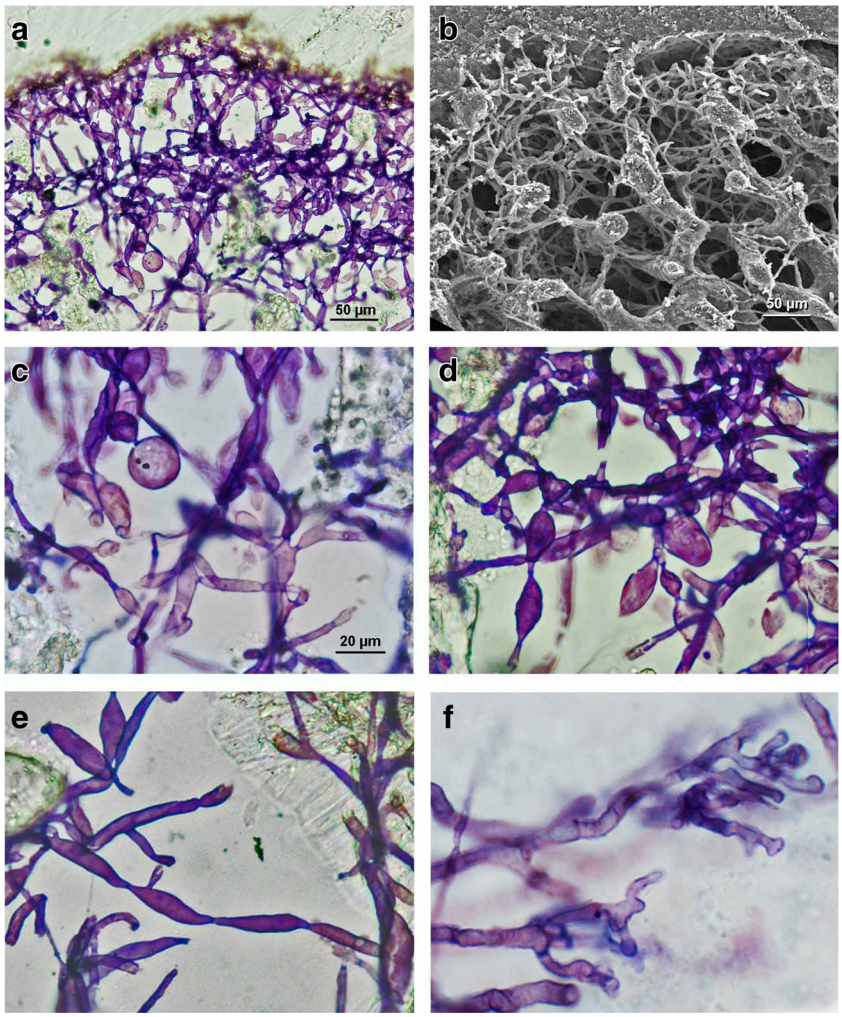

Fig. 1 Networks of euendolithic *Conchocelis* filaments inside the coenosteum of the lace coral *Stylaster* sp. View of a cross-section of the colony stem after removal of skeleton material. **a** Network of *Conchocelis* filaments stained with Toluidine blue. **b** Scanning electron microscope (SEM) image of the three-dimensional display of resin-cast microborings produced by the *Conchocelis* filaments shown in **a**, which constitutes the ichnofossil *Conchocelichnus* isp. **c** Detail of **a** with spherical and droplet-shaped swellings; clusters of filament branches in the background. **d** Network of cylindrical filaments and series of spindle-shaped cells. **e** Serial arrangement of spindle-shaped cells interconnected at the narrow ends. **f** Branching pattern of *Conchocelis* filaments showing club-shaped protrusions. The scale bar in **c** applies to **c**–**f**

scleractinian corals (e.g. Odum and Odum 1955; Lukas 1973; Le Campion-Alsumard et al. 1995).

Discussion

Puce et al. (2009) identified microboring organisms in the skeletons of *Stylaster* species as cyanobacteria. After the study of more stylasterid colonies, it was determined that the prevalent euendoliths in stylasterid corals are eukaryotic *Conchocelis* stages of bangialean red algae (Pica et al. 2016). The colonisation of stylasterid skeletons seems to be relatively widespread, as euendoliths were observed in at least two distinct genera of lace corals in the present study. The interrelationship between euendolithic microorganisms and their host corals opens several ecologically and taxonomically interesting questions. For example: (1) Is this relationship symbiotic, parasitic or commensal? (2) How does *Conchocelis* cope with the coral growth? (3) What is the longevity of the *Conchocelis* euendolithic residing in stylasterids? (4) What is the distribution of *Conchocelis* in space and time, and how does it relate to water clarity? (5) To which rhodophyte species do these developmental *Conchocelis* stages belong?

(1) Puce et al. (2009) suggested that phototrophic euendoliths in stylasterid corals may be symbiotic, if they exchange metabolites as it was proposed for the relation between the euendolithic chlorophyte *Ostreobium* and its scleractinian host corals by Schlichter et al. (1995) and Fine and Loya (2002), which may be especially beneficial in the event of coral bleaching (e.g. van Oppen and Lough 2009). Since stylasterid corals do not host zooxanthellae, such an arrangement may be beneficial throughout the life of the coral, despite some losses to its skeleton density due to dissolution by euendolithic microorganisms (see Tribollet 2008 for a review). How efficient are *Conchocelis* filaments in dissolving lace coral skeletons and what is the impact on their structural resilience remains to be determined. The filament abundance of *Conchocelis* certainly varies among different stylasterid

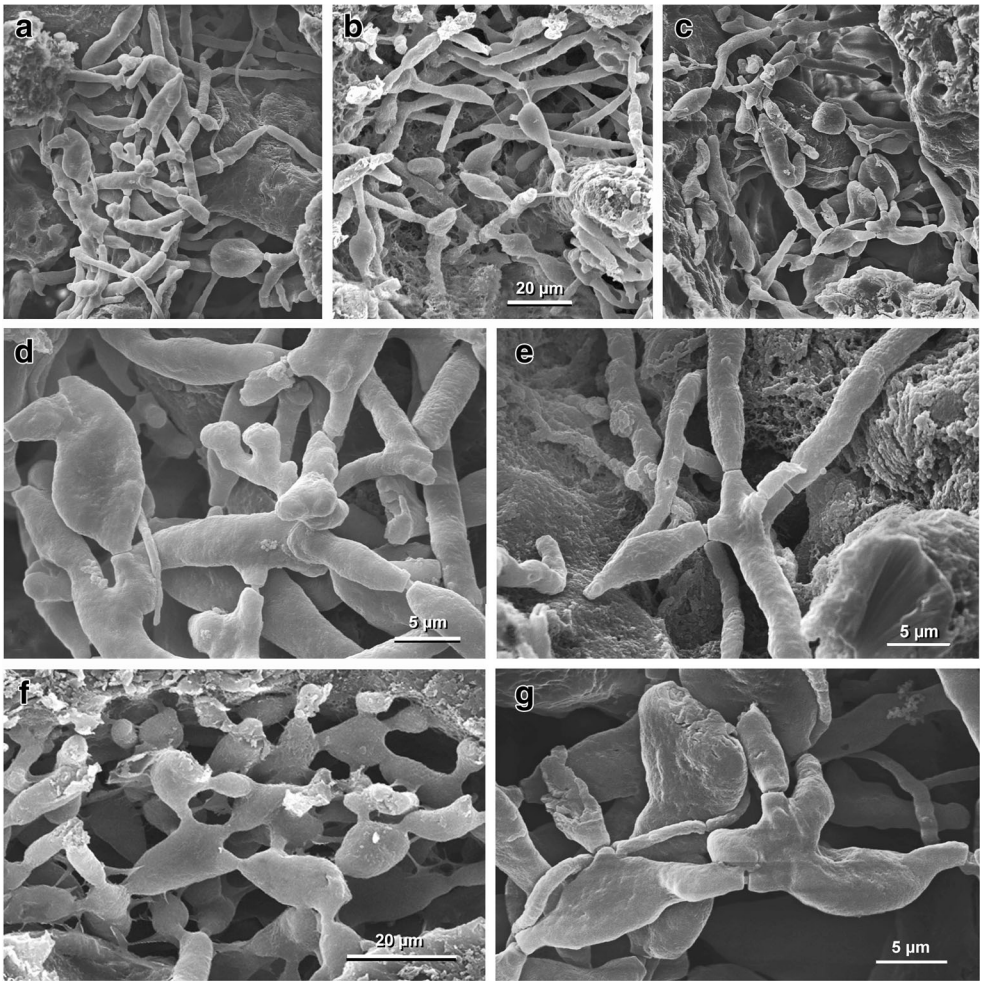

Fig. 2 *Conchocelichnus* isp. (Radtke et al. 2016), a complex trace fossil, presented as resin casts of borings that conform with the outlines of euendolithic *Conchocelis* filaments in shape and size (details from Fig. 1b) in the lace corals *Stylaster* sp. ('white') and *Stylaster tenisonwoodsi* ('orange'). **a** A dense cluster of microboring casts constructed from cylindrical cells constricted at the cross-walls, flat leaf-like cells with uni-directional branching. **b** Lose network of borings conforming to filaments with predominantly spindle-shaped cells exhibiting constrictions at the cross-walls between cells and swellings with branches positioned at one end. **c** An assemblage of interconnected differently shaped borings. **d** Detail of **a**, with filaments of different shapes and sizes, cell connections in series and lateral branches. Note the exposed pit connections between cells and irregular club-shaped cell wall protrusions (*centre*). **e** A cluster of branches with exposed pit connections, located at one of the ends of a cylindrical cell unit. **f** Series of cellular swellings exhibiting wider and narrower interconnections and branching localised at the upper end of the cellular swelling. **g** Detail of **c**. A group of cell units with flat widening. The scale bar in **b** apples to **a**–**c**

coral species but also among colonies of a same species (Pica et al. 2016). The potential benefit to the *Conchocelis* is to live under the protection of their hosts.

(2) The pink colouration in stylasterids has been observed to be particularly intensive in the lower parts of the colony, while gradually fading towards the tips, indicating a certain lag between the *Conchocelis* growth behind the accretion of the coral skeleton. This pattern may suggest that the *Conchocelis* filaments were present but "diluted" by the high rates of the lace coral growth (Pica et al. 2016), which would be similar to conditions observed in scleractinian corals (Godinot et al. 2012). According to such a hypothesis, the *Conchocelis* filaments would have colonised the stylasterid skeleton early, starting from its base while in contact with the substratum that may already have been colonised by microborers. An inversion of this condition has resulted in green banding produced by *Ostreobium* in massive scleractinian corals; as coral growth slowed down (see Fine and Loya 2002), it permitted intense ramification of the euendolith, which produced a green band (Lukas 1973; Le Campion-Alsumard et al. 1995). However, equivalent red bands in stylasterid corals were not observed. The stylasterids are known for relatively slow accretion rates of a few mm/year, especially in deep waters (Wisshak et al. 2009), while the penetration rates of *Conchocelis* filaments require further studies.

(3) The observations by Pica et al. (2016) on stylasterid corals also include abrupt terminations of the colour and of the presence of *Conchocelis*. This suggests that *Conchocelis* may have terminated its growth by the release of spores to start an epilithic phase. The leafy portion of bangialean rhodophytes is known to be seasonal, as determined by photoperiodic control of spore release (Dixon and Richardson 1969), although both foliose and euendolithic phases can be perpetuated independently, thus able to "short-circuit" the alternation of generations (Campbell and Cole 1984).

(4) The leafy, epilithic phase of bangialean rhodophytes is separated from the euendolithic growth of *Conchocelis* in space as well as in time. *Conchocelis* has been found in deep cold waters of the North Sea down to a depth of 78 m, while the leafy epilithic thallus was observed only in the intertidal zone (Clokie et al. 1981). The means of transportation of the propagules that connect the two phases remain an unresolved problem. The ability of *Conchocelis* as a rhodophyte to photosynthesise at low light levels (Vadas and Steneck 1988) accounts for its considerable depth distribution. Clokie et al. (1981) proposed, therefore, that *Conchocelis* may serve as a palaeobathymetric indicator for determining depositional depths in ancient oceans. Because the microborings of *Conchocelis* preserve well as fossils and can be recognised by their complex morphology, as shown in the present contribution, they may play an important role in determination of the ancient photic zone, together with traces of other phototrophic euendoliths among chlorophytes and cyanobacteria. In oligotrophic tropical and subtropical waters, the chlorophyte *Ostreobium* has been recorded at 200- and 300-m depths (LeCampion-Alsumard et al. 1982; Vogel et al. 2000). This euendolithic chlorophyte is known to have red-shifted pigments (chlorophylls), allowing life in poorly illuminated environments (Koehne et al. 1999; Magnusson et al. 2007). Tropical euendolithic cyanobacteria may also harbour specific chlorophyll pigments (chl d) to survive in low light regimes (Behrendt et al. 2011). Specialised pigments in *Conchocelis* require further study.

Euendolithic habit in the development of red algae has a long geological history. *Palaeoconchocelis starmachii* (Kazmierczak and Golubic 1979) penetrated crinoid ossicles during the upper Silurian over 425 million years ago and remained organically preserved inside its borehole, including pit connections between its cells (Campbell 1980). Fossil of the foliose phase of Bangialean rhodophyte *Bangiomorpha pubescens* is about 1000 million years old (Butterfield 2000, 2015). Other fossil findings refer exclusively to *Conchocelis* boring traces, recently described as ichnospecies *Conchocelichnus seilacheri* (Radtke et al. 2016). They were recorded along different Phanerozoic strata from the Silurian (Bundschuh 2000); Triassic (Schmidt 1992), Jurassic, Lower Cretaceous (Glaub 1994) and Lower Tertiary deposits (Radtke 1991).

(5) The species distinction in bangialean rhodophytes was traditionally based on the morphology of the foliose generation. The *Conchocelis* phase was identified indirectly while grown from carpospores of different *Porphyra* species identified by their leafy thalli. However, the molecular methods of gene sequencing have recently redefined the diversity of bangialean rhodophytes, so as to follow more closely the phylogenetic history (Lindstrom and Fredericq 2003; Wang et al. 2013; Lindstrom et al. 2015). Accordingly, the redefined genus *Porphyra* is presently restricted to five described species and a number of undescribed ones (see Müller et al. 2005; Lindstrom et al. 2015), while other species that used to be classified as *Porphyra* are now classified among seven other genera (Sutherland et al. 2011).

The *Conchocelis* observed in stylasterid corals from Indonesia most likely belong to a tropical bangialean taxon, such as *Porphyra marcosii* P.A. Cordero or *Pyropia vietnamensis* (Tak. Tanaka & Pham-Hoàng Ho) J.E. Sutherland & Monotilla (see Ruangchuay and Notoya 2003) or some other taxon found south of the Philippines (see Ame et al. 2010).

The discovery of *Conchocelis* stages of Bangiales in tropical hydrozoan lace corals expands our knowledge of the distribution of these rhodophytes in tropical reefs and stimulates further investigations of rhodophyte diversity and ecology, including those that colonise and penetrate the skeletons of live and growing corals.

Acknowledgements We thank Sandrine Caquineau for her assistance with the SEM on the platform Alysés at the Center IRD France-Nord (Bondy) and the Institut de Recherche pour le Développement for financial support. International collaborations were supported by the Alexander von Humboldt Foundation, Bonn, and Hanse Institute for Advanced Studies, Delmenhorst, Germany to S. Golubic. We also thank the Coral Eye Research Center for the logistic support in Indonesia. Specimens were imported by CITES permit code 04291/IV/SATS-LN/2011. We thank the editor Dr. Bert Hoeksema and the two anonymous reviewers for their positive and constructive comments and improvements of the manuscript.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

References

Ame EC, Ayson JP, Okuda K, Andres R (2010) *Porphyra* fisheries in the Northern Philippines: some environmental issues and the socio-economic impact on the Ilocano fisherfolk. Kuroshio Sci 4:53–58

Bao-Fu Z (1984) Studies on the morphology of conchocelis of *Porphyra katadai* var. *hemiphylla* and related species. Dev Hydrobiol 22:209–212

Batters EAL (1892) On *Conchocelis*, a new genus of perforating algae. Phycol Mem 1:25–29

Behrendt L, Larkum AWD, Norman A, Qvortrup K, Chen M, Ralph P, Sørensen SJ, Trampe E, Kühl M (2011) Endolithic chlorophyll d-containing phototrophs. ISME J 5:1072–1076

Bornet E, Flahault C (1888) Note sur deux nouveaux genres d'algues perforantes. J Bot 2:161–165

Bornet ME, Flahault C (1889) Sur quelques plantes vivant dans le test calcaire des mollusques. Bull Soc Bot Fr 36:147–176

Bundschuh M (2000) Silurische Mikrobohrspuren. Ihre Beschreibung und Verteilung in verschiedenen Faziesräumen (Schweden, Litauen, Großbritannien und USA). Dissertation, Johann Wolfgang Goethe University, pp. 1–129

Butterfield NJ (2000) *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. Paleobiology 26:386–404

Butterfield NJ (2015) Early evolution of the Eukaryota. Paleontology 58: 5–17

Campbell SE (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 SE, Cole K (1984) Developmental studies on cultured endolithic conchocelis (Rhodophyta). Hydrobiologia 116(117):201–208

Clokie JJP, Boney AD, Farrow GE (1979) The significance of Conchocelis as an indicator organism: data from the Firth of Clyde and N.W. Shelf. Br Phycol J 14:120–121

Clokie JJP, Scoffin TP, Boney AD (1981) Depth maxima of Conchocelis and *Phymatolithon rugulosum* on the N. W. Shelf and Rockall Plateau. Mar Ecol Prog Ser 4:131–133

Dixon PS, Richardson WN (1969) The life histories of *Bangia* and *Porphyra* and the photoperiodic control of spore production. Proc Int Seaweed Symp 6:133–139

Drew KM (1949) Conchocelis-phase in the life-history of *Porphyra umbilicalis* (L.) Kütz. Nature 164:748–749

Drew KM (1954) Studies in the Bangioideae III. The life-history of *Porphyra umbilicalis* (L.) Kütz. var. *lociniata* (Lightf.) J. Ag.: A. The Conchocelis-phase in culture. Ann Bot 18:183–184

Drew KM (1956) Reproduction in the Bangiophycidae. Bot Rev 22:553–611

Ercegović A (1932a) Ekološke i sociološke studije o litofitskim cijanoficejama sa jugoslavenske obale Jadrana. Rad Jugosl Akad Znan Umjet 244:129–220

Ercegović A (1932b) Études écologiques et sociologiques des Cyanophycées lithophytes de la côte Yougoslave de l'Adriatique. Bull Int Acad Yougosl Sci Beaux Arts 26:33–56

Fine M, Loya Y (2002) Endolithic algae: an alternative source of photoassimilates during coral bleaching. Proc R Soc Lond 269: 1205–1210

Försterra G, Häussermann V (2008) Unusual symbiotic relationships between microendolithic phototrophic organisms and azooxanthellate cold-water corals from Chilean fjords. Mar Ecol Prog Ser 370:121–125

Fox DL (1972) Pigmented calcareous skeletons of some corals. Comp Biochem Physiol B 43:919–927

Glaub I (1994) Mikrobohrspuren in ausgewählten Ablagerungsräumen des europäischen Jura und der Unterkreide. Cour Forschungsinst Senck 174:1–324

Glazer AN (1985) Light harvesting by phycobilisomes. Annu Rev Biophys Biophys Chem 14:47–77

Godinot C, Tribollet A, Grover R, Ferrier-Pagès C (2012) Bioerosion by euendoliths decreases in phosphate-enriched skeletons of living corals. Biogeosciences 9:2377–2384

Golubic S, Brent G, Lecampion T (1970) Scanning electron microscopy of endolithic algae and fungi using a multipurpose casting-embedding technique. Lethaia 3:203–209

Golubic S, Friedmann I, Schneider J (1981) The lithobiontic ecological niche, with special reference to microorganisms. J Sediment Petrol 51:475–478

Guiry MD, Guiry GM (2017) *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched in January 2016

Kazmierczak J, Golubic S (1979) *Paleoconchocelis starmachii* n. gen., n. sp., a Silurian endolithic rhodophyte (Bangiaceae). Acta Palaeontol Pol 24:405–408

Koehne B, Elli G, Jennings RC, Wilhelm C, Trissl H-W (1999) Spectroscopic and molecular characterization of a long wavelength absorbing antenna of *Ostreobium* sp. Biochim Biophys Acta 1412: 94–107

Kołodziej B, Golubic S, Bucur II, Radtke G, Tribollet A (2012) Early Cretaceous record of microboring organisms in skeletons of growing corals. Lethaia 45:34–45

Kornmann P (1959) Die heterogene Gattung *Gomontia* I. Der sporangiale Anteil, *Codiolum polyrhizum*. Helgoländer Wiss Meeresun 6:229–238

Kornmann P (1960) Die heterogene Gattung *Gomontia*. II. Der fadige Anteii, *Eaffomontia saccalata* nov. gen. nov. spec. Helgoländer Wiss Meeresun 7:59–71

Kornmann P (1961) Die Entwicklung von *Porphyra leucosticta* im Kulturversuch. Helgoländer Wiss Meeresun 8:167–175

Kornmann P (1962) Die Entwicklung von *Monostroma grevillei*. Helgoländer Wiss Meeresun 8:195–202

Kornmann P, Sahling PH (1980) Kalkbohrende Mikrothalli bei *Helminthocladia* und *Scinaia* (Nemaliales, Rhodophyta). Helgoländer Wiss Meeresun 34:31–40

Laborel J, Le Campion-Alsumard T (1979) Infestation massive du squelette de coraux vivants par des rhodophycées de type Conchocelis. CR Acad Sci Paris Ser D 288:1575–1577

LeCampion-Alsumard T, Campbell SE, Golubic S (1982) Endoliths and the depth of the photic zone: discussion. J Sediment Petrol 52:1333–1334

Le Campion-Alsumard T, Golubic S, Hutchings P (1995) Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia). Mar Ecol Prog Ser 117:149–157

Li S, Ming J, Delin D (2006) Formation of primary pit connection during conchocelis phase of *Porphyra yezoensis* (Bangiophyceae, Rhodophyta). Chin J Oceanol Limnol 24:291–294

Lindstrom SC, Fredericq S (2003) *rbcL* gene sequences reveal relationships among north-east Pacific species of *Porphyra* (Bangiales, Rhodophyta) and a new species, *P. aestivalis*. Phycol Res 51:211–224

Lindstrom SC, Hughey JR, Aguilar-Rosas LE (2015) Four new species of *Pyropia* (Bangiales, Rhodophyta) from the west coast of North America: the *Pyropia lanceolata* species complex updated. PhytoKeys 52:1–22

Lukas KJ (1973) Taxonomy and ecology of the endolithic microflora of reef corals, with a review of the literature on endolithic microphytes. Dissertation, University of Rhode Island

Magnusson SH, Fine M, Kühl M (2007) Light microclimate of endolithic phototrophs in the scleractinian corals *Montipora monasteriata* and *Porites cylindrica*. Mar Ecol Prog Ser 332:119–128

Müller KM, Cannone JJ, Sheath RG (2005) A molecular phylogenetic analysis of the Bangiales (Rhodophyta) and description of a new genus and species, *Pseudobangia kaycoleia*. Phycologia 44:146–155

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll, Marshall Islands. Ecol Monogr 25:291–320

Pica D, Tribollet A, Golubic S, Bo M, Di Camillo CG, Bavestrello G, Puce S (2016) Microboring organisms in living stylasterid corals (Cnidaria, Hydrozoa). Mar Biol Res 12:573–582

Puce S, Tazioli S, Bavestrello G (2009) First evidence of a specific association between a stylasterid coral (Cnidaria: Hydrozoa: Stylasteridae) and a boring cyanobacterium. Coral Reefs 28:177

Radtke G (1991) Die mikroendolithischen Spurenfossilien im Alt-Tertiär West-Europas und ihre palökologische Bedeutung. Cour Forschungsinst Senck 138:1–185

Radtke G (1993) The distribution of microborings in molluscan shells from recent reef environments at Lee Stocking Island, Bahamas. Facies 29:81–92

Radtke G, Le Campion-Alsumard T, Golubic S (1996) Microbial assemblages of the bioerosional "notch" along tropical limestone coasts. Algol Stud 83:469–482

Radtke G, Campbell SE, Golubic S (2016) *Conchocelichnus seilacheri* igen. et isp. nov., a complex microboring trace of Bangialean rhodophytes. Ichnos 23:228–236

Roux W (1887) Über eine im Knochen lebende Gruppe von Fadenpilzen (*Mycelites ossifragus*). Z Wiss Zool 45:227–254

Ruangchuay R, Notoya M (2003) Physiological responses of blade and conchocelis of *Porphyra vietnamensis* Tanaka et Pham-Hoang Ho (Bangiales, Rhodophyta) from Thailand in culture. Algae 18:21–28

Schlichter D, Zscharnack B, Krisch H (1995) Transfer of photoassimilates from endolithic algae to coral tissue. Naturwissenschaften 82:561–564

Schmidt H (1992) Mikrobohrspuren ausgewählter Faziesbereiche der tethyalen und germanischen Trias (Beschreibung, Vergleich und bathymetrische Interpretation). Frankf Geowiss Arb A 12:1–228

Sutherland DA, MacCready P, Banas NS, Smedstad LF (2011) A model study of the Salish Sea estuarine circulation. J Phys Oceanogr 41: 1125–1143

Tribollet A (2008) The boring microflora in modern coral reef ecosystems: a review of its roles. In: Wisshak M, Tapanila L (eds) Current developments in bioerosion. Springer, Berlin, pp 67–94

Tribollet A, Decherf G, Hutchings P, Peyrot-Clausade M (2002) Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers. Coral Reefs 21:424–432

Tribollet A, Radtke G, Golubic S (2011) Bioerosion. In: Reitner J, Thiel V (eds) Encyclopedia of geobiology. Springer, Berlin, pp 117–133

Tseng CK, Borowitzka M (2003) Algae culture. In: Lucas JS, Southgate PC (eds) Aquaculture: farming aquatic animals and plants. Blackwell, Oxford, pp 253–275

Tseng CK, Chang TJ (1955) Studies on the life history of *Porphyra tenera* Kjellm. Sci Sinica 4:375–398

Vadas RL, Steneck RS (1988) Zonation of deep water benthic algae in the Gulf of Maine. J Phycol 24:338–346

van Oppen MJH, Lough JM (eds) (2009) Coral bleaching. Springer, Berlin, pp 1–176

Vogel K, Gektidis M, Golubic S, Kiene WE, 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

Wang L, Mao Y, Kong F, Li G, Ma F, Zhang B, Sun P, Bi G, Zhang F, Xue H, Cao M (2013) Complete sequence and analysis of plastid genomes of two economically important red algae: *Pyropia haitanensis* and *Pyropia yezoensis*. PLoS One 8:e65902

Wisshak M, López-Correa M, Zibrowius H, Jakobsen J, Freiwald A (2009) Skeletal reorganisation affects geochemical signals, exemplified in the stylasterid hydrocoral *Errina dabneyi* (Azores Archipelago). Mar Ecol Prog Ser 397:197–208