Bioerosion of the scleractinian finger coral *Acropora humilis* from El-Ain El-Sukhna, Gulf of Suez- Red Sea

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Abstract

Bioerosion by boring organisms is one of the major destructive forces operating on reef. The aim of this study was to investigate the bioerosion by microflora of a scleractinian finger coral *Acropora humilis*, which collected from the reef edge of El Ain El Sukhna (Gulf of Suez-Red Sea) by using the Scanning Electron Microscope (SEM). The collected colonies of *A. humilis* were solid, very porous, and branching. These colonies have two colors; brown color with purple branch tips and yellow color with cream branch tips. Individual branches form fat fingers; 10 to 25 mm in diameter and less than 200 mm in length, tapering to large dome-shaped axial corallites. Small branchlets or incipient axial corallites usually occur at the base of main branches. Radial corallites are cup-shaped and have two sizes, the larger are usually in rows and have thick walls and only slightly increase in size down the sides of branches. Axial and radial corallites have a series of vertical rods arranged in concentric rings and horizontal radial and tangential bars. The radial bars form the sclerosepta along with the vertical rods. The tangential bars are synapticulae that connect adjacent sclerosepta to one another. Series of fasciculi form the characteristic scale-like appearance of *A. humilis* skeleton. The bioerosion was investigated at least in one branch of some colonies which were harbored by fungi, green algae and cyanobacteria; led to loss of tissues and erosion of rods, bars and fusiform crystals. *Acropora humilis* is subjected to bioerosion due to: its surface which covered by muco-polysaccharides, its high porosity and its branching form; whose facilitate colonization by boring organisms.

Key words: Scleractinian Coral, *Acropora humilis*, Skeleton, Crystals, Boring Microflora, Bioerosion, Scanning Electron Microscopy.

Introduction

Acropora Oken, 1815 is a genus of the scleractinian hermatypic coral in the family Acroporidae. It is one of the major reef corals responsible for building the immense calcium carbonate substructure that supports the thin living skin of a reef. The Latin name derives from the growth mode, where branches are formed by a central or axial polyp, which buds off numbers of a second kind, the radial polyps, from around its tip as it extends. New branches are formed by the development of new axial polyps along the branch, and as a result, all the polyps of a colony are closely interconnected and can grow in a coordinated manner (Veron, 1986). The polyps are supported within an open "synapticular" framework, allow for rapid growth with efficient use of calcium carbonate (Rosen, 1986; Nothdurft and Webb, 2007; Gladfelter, 2008) and provide habitat complexity for other reef biota (Munday, 2002). The polyp cavities are extended by the coenenchyme, a complex network of tubules containing extensions of the gastric cavity. Another form of skeleton, the epitheca, formed by calcite form of calcium carbonate, is present in very small quantities below the living tissues of the branch and acts as a sealant preventing infection and protecting the live polyps and coenenchyme from fluid loss (Barnes, 1972).

Skeletal growth and form in the acroporid corals has been studied at several different organizational scales, including the colony, the individual corallite, skeletal elements (rods and bars) that make up the corallite, sclerodermites that make up the skeletal elements, and individual calcium carbonate crystals (e.g. Gladfelter, 1977, 1982a, 1983; Chamberlain, 1978; Gladfelter and Gladfelter, 1979; Isa, 1986; Wallace, 1999; Veron, 2000; Clode and Marshall, 2003a, b). However, microboring organisms in acroporid corals have been considerably less studied because the higher porosity of this substrate makes its preparation more difficult (Kiene et al., 1995; Vogel et al., 2000; Chazottes et al., 2009).

Bioerosion and predation on scleractinian corals are indeed an important part of coral reefs dynamics. Scleractinian corals provide microhabitats and are used by a large

number of parasites and other associated organisms, which use the tissue and skeleton of the coral colonies as food or substrata (Frank et al., 1995; Floros et al., 2005; Rosenberg et al, 2007). Many taxa are involved and most of these coral associates stress the coral to some degree. Any natural or anthropogenic disturbances that lead to the loss of live coral tissue will ultimately increase the chances of bioeroder invasion. The bioerosion process can lead to important coral damage and even, depending on the intensity, can lead to mortality of coral colonies (Hubbard et al., 1990; Kleemann 2001). Rates of bioerosion may vary in space and time (Kiene and Hutchings, 1994; Chazottes et al., 1995; Conand et al., 1998; Pari et al., 1998). They are influenced by a number of biotic and abiotic factors (Risk et al., 1995) and more particularly by eutrophication, which has been shown to promote bioerosion intensity (Hallock, 1988; Pari, 1998; Holmes et al., 2000). The structure of the boring community is also related to the skeletal density (Highsmith, 1981) and the internal structure of the coral (Amor et al., 1991). The assemblages of euendolithic (boring) algae, fungi and cyanobacteria inhabiting the corallum of live corals are different from those that colonize dead and denuded coral skeletons (Delvoye 1992; Le Campion-Alsumard et al., 1995a, b).

The microboring organisms attack the substrates mainly by chemical dissolution forming a network of tunnels conforming to the shape of their bodies (Schneider, 1976; Vogel et al., 2000; Pantazidou et al., 2006). Fungi are capable of deep penetration into coral skeletons. The fungi hyphae produce narrow borings and penetrate the deepest recesses of coral skeletons, probably because of their ability to utilize the organic matrix of coral skeletons. Fungi have also been implicated in the etching of calcareous surfaces, the weakening and dissolution of calcareous sediments as well as the calcareous tube linings of various endoliths. Because of the difficulty of distinguishing between fungal and algal borings, estimates of dissolution rates due to boring fungi alone are not yet available (Glynn, 1997). In healthy growing reef corals, the relationship between the coral coelenterate, endolithic algae and fungi is in a state of

equilibrium, but can turn detrimental to coral health when reefs are exposed to environmental stress (Golubic et al., 2005).

Green (Chlorophyta) and red (Rhodophyta) algae have been implicated in the erosion of coral rock under various reef settings. Green and red algae occur on limestone surfaces, in cavities and within coral skeletons. Freshly fractured corals often reveal layers of green banding a few cm beneath the live coral surface. The green color is due to the presence of chlorophyll pigments, which intercept light passing through the coral's tissues and skeleton. This greenish layer is often referred to as the "*Ostreobium* band", named after a green alga that is commonly present in coral skeletons. However, the green band may also contain a variety of different kinds of algae. The importance of boring algae as bioeroders is controversial; some workers claim that they are among the most destructive agents of reef erosion whereas others maintain that they cause only minimal damage (Glynn, 1997).

Cyanobacteria still play an essential role in coral reef ecosystems by forming a major component of epiphytic, epilithic, and endolithic communities as well as of microbial mats. Cyanobacteria are grazed by reef organisms and also provide nitrogen to the coral reef ecosystems through nitrogen fixation. Furthermore, cyanobacteria are important in calcification and decalcification. All limestone surfaces have a layer of boring algae in which cyanobacteria often play a dominant role. Cyanobacteria use tactics beyond space occupation to inhibit coral recruitment. Cyanobacteria can also form pathogenic microbial consortia in association with other microbes on living coral tissues, causing coral tissue lysis and death, and considerable declines in coral reefs. Cyanobacteria produce metabolites that act as attractants for some species and deterrents for some grazers of the reef communities (Charpy et al., 2012).

In this study, we describe the microstructure of the polyps and skeleton of healthy and unhealthy scleractinian finger coral *A. humilis* and its associated microfloral communities by using scanning electron microscope.

Materials and Methods

Collection and maintenance

Colonies of finger coral (*Acropora humilis* Dana, 1846) were collected from the reef edge of El Ain El Sukhna (western coast of Gulf of Suez, Red Sea, Egypt) at a depth of 3-5 meters. The corals were transported in buckets of seawater to the laboratory, where they were maintained in sunlit, well-aerated, flow-through aquaria in natural seawater at 24–25 °C.

Branches preparation

Branches were separated from live colonies and fixed for microstructural investigations by immersing them immediately in $_4F_1G$, phosphate buffer solution (PH 7.2) at 4°C overnight. These branches were then post fixed in 2% OsO_4 in the same buffer at 4°C for 2 hours, then washed in the buffer and dehydrated at 4°C through a graded series of ethanol, and dried by means of the critical point method.

Skeleton preparation

Acropora humilis colonies were immersed in commercial bleach (12% NaOCl) at 60 °C for 30 min. The resultant colonies were rinsed well in running water and then several times in dH_2O to remove the overlying soft tissues. The skeletons were then dried at 60 °C for 24 h.

Morphological and microstructural investigations

Different samples of *A. humilis* were photographed by a digital camera. For microstructural investigations, the prepared branches and skeletons were mounted by using carbon paste on an Al-stub and coated with gold up to a thickness of 400Å in a sputter- coating unit (JFC-1100E). Investigations of the samples were performed in a JEOL JSM-5300 scanning electron microscope operated at 25 KV.

Results

Morphological investigations

The collected colonies of *Acropora humilis* were solid, very porous, and branching. These colonies have two colors; brown color with purple branch tips and yellow color with cream branch tips. The individual coral animal is called the polyp (axial and radial). The skeleton deposited by an individual polyp within a colony is the corallite which composed of calcium carbonate. Individual branches form fat fingers; 10 to 25 mm in diameter and less than 200 mm in length, tapering to large dome-shaped axial corallites. Small branchlets or incipient axial corallites usually occur at the base of main branches. Radial corallites are cup-shaped and have two sizes, the larger are usually in rows and have thick walls and only slightly increase in size down the sides of branches. Generally axial corallites are larger than radial corallites and all the corallites of a colony are closely interconnected (Fig. 1).

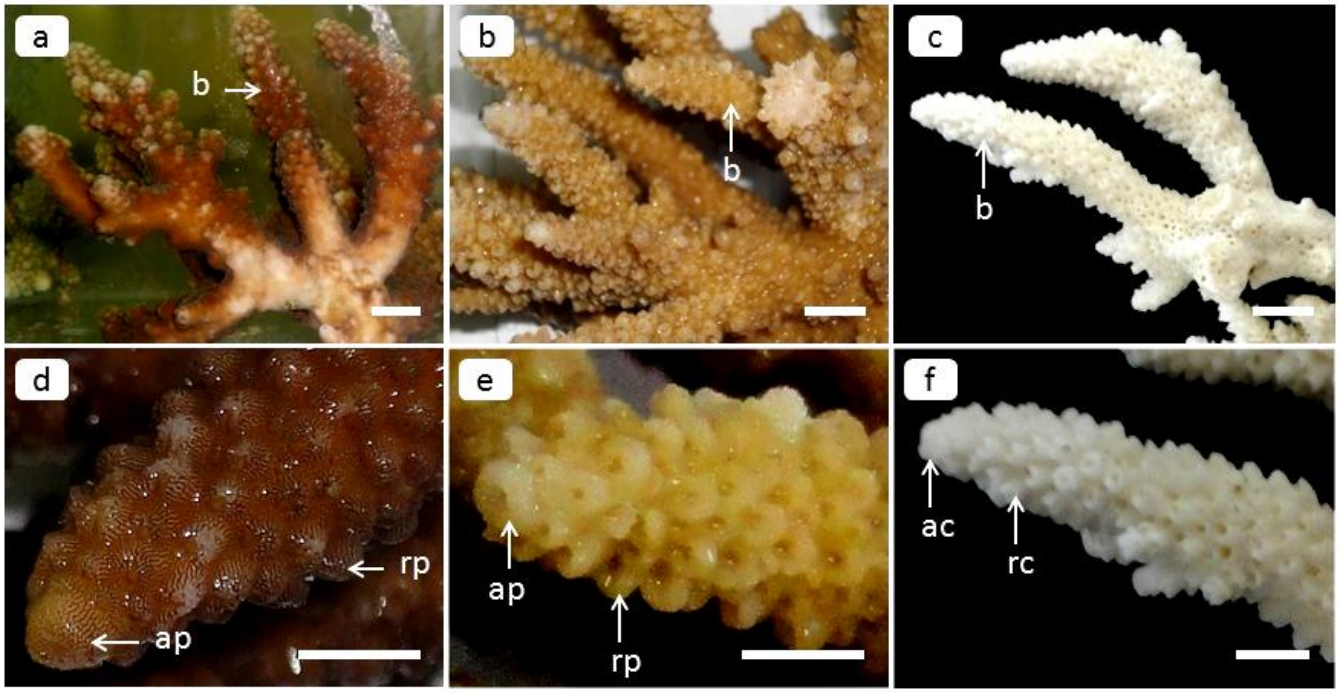

Figure 1: Photograph pictures of *Acropora humilis*: (a) Part of brown colony, (b) Part of yellow colony, (c) Skeleton of the colony, (d) Branch of brown colony, (e) Branch of yellow colony, (f) Skeleton of the branch. Abbr.: ac, axial corallite; ap, axial polyp; b, branch; rc, radial corallite; rp, radial polyp. Scale bar= 1 cm in a, b, c and 0.5 cm in d, e, f.

Microstructural investigations:

As shown in figure (2a, b), the individual branch of *Acropora humilis* is formed of an axial polyp and many radial polyps. The axial and radial corallites are the skeletons of the polyps (Fig. 2c, d). The corallite is defined by two regions, the calice and the theca. The upper oral surface of a corallite is the calice which opens to outside by a large opening known as calice opening or mouth opening. The calice opening is surrounded by a circle of sclerosepta. The theca is the wall of the corallite which consists of vertical rods arranged in concentric rings and horizontal radial and tangential bars. The radial bars form the sclerosepta along with the vertical units (the rods). The tangential bars are synapticulae that connect adjacent sclerosepta to one another (Fig. 2 e, f, g, h, i). Series of fasciculi form the characteristic scale-like appearance of *A. humilis* skeleton (Fig. 2j). Two types of crystals, fusiform (calcite) and blade or needle-shaped (aragonite) crystals have been observed at the growing edges of rods, bars and the sclerosepta of axial and radial corallites (Fig. 2k, l).

Microbial communities associated to *A. humilis* branches

Conidiophores with conidia of fungi were present inside the pore space of the skeleton of some polyps in which fusiform and blade-shaped crystals are distributed across the skeletal wall (Fig. 3a). The fungal hyphae were observed associated to the mucous which secreted by the polyps (Fig. 3b). Accumulation of cyanobacteria and green algae were observed at the surface of some corallites between the skeletal elements (rods and bars) (Fig. 3c, d, e, f). The bioerosion was investigated at least in one branch of some colonies which were harbored by fungi, cyanobacteria and green algae. The bioerosion led to loss of tissues, erosion of rods; bars and the sclerosepta (Fig. 3f, g, h), cracking of the calcite (calcium carbonate material) which forms the skeleton of the coral and mineralization by micro-granular calcite (Fig. 3i).

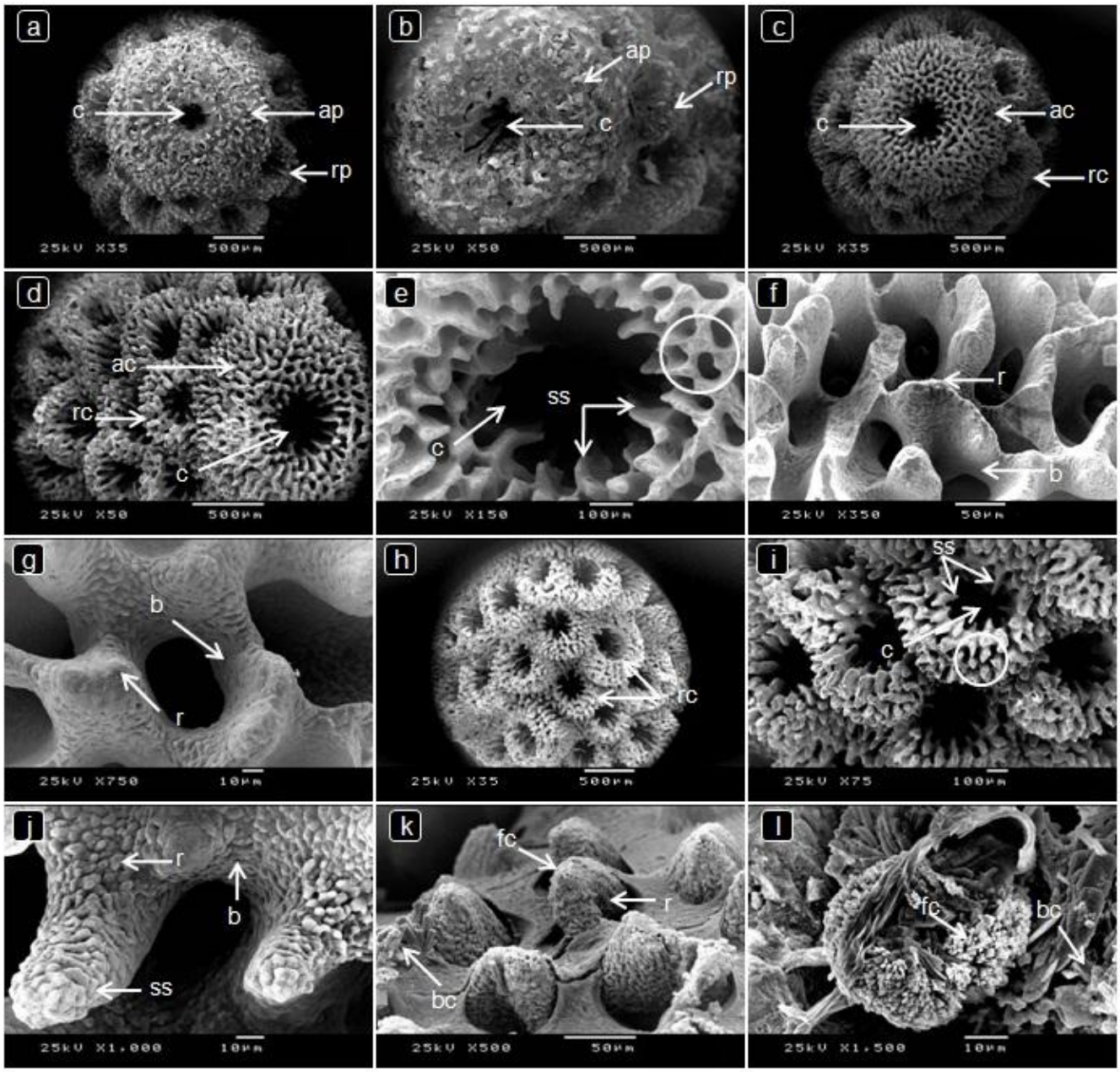

Figure2: Scanning electron micrographs of *A. humilis*: (a) Upper view of individual branch, (b) Lateral view of individual branch, (c) Upper view of the skeleton of the branch, (d) Lateral view of the skeleton of the branch, (e) Upper view of the axial corallite showing rods and bars (circle), (f, g) Rods and bars of the axial corallite, (h) Lateral view of the branch showing the radial corallites, (i) Radial corallites showing rods and bars (circle) (j) Rods, bars and sclerosepta of the radial corallites showing the series of fasciculi of scale-like appearance of the skeleton, (k) Fusiform and blade-shaped crystals at the growing edges of the rods, (l) High magnification of the fusiform and blade-shaped crystals. Abbr.: ac, axial corallite; ap, axial polyp; b, bar; bc, blade-shaped crystals; c, calice; fc, fusiform crystals; r, rod; rc, radial corallite; rp, radial polyp; ss, sclerosepta.

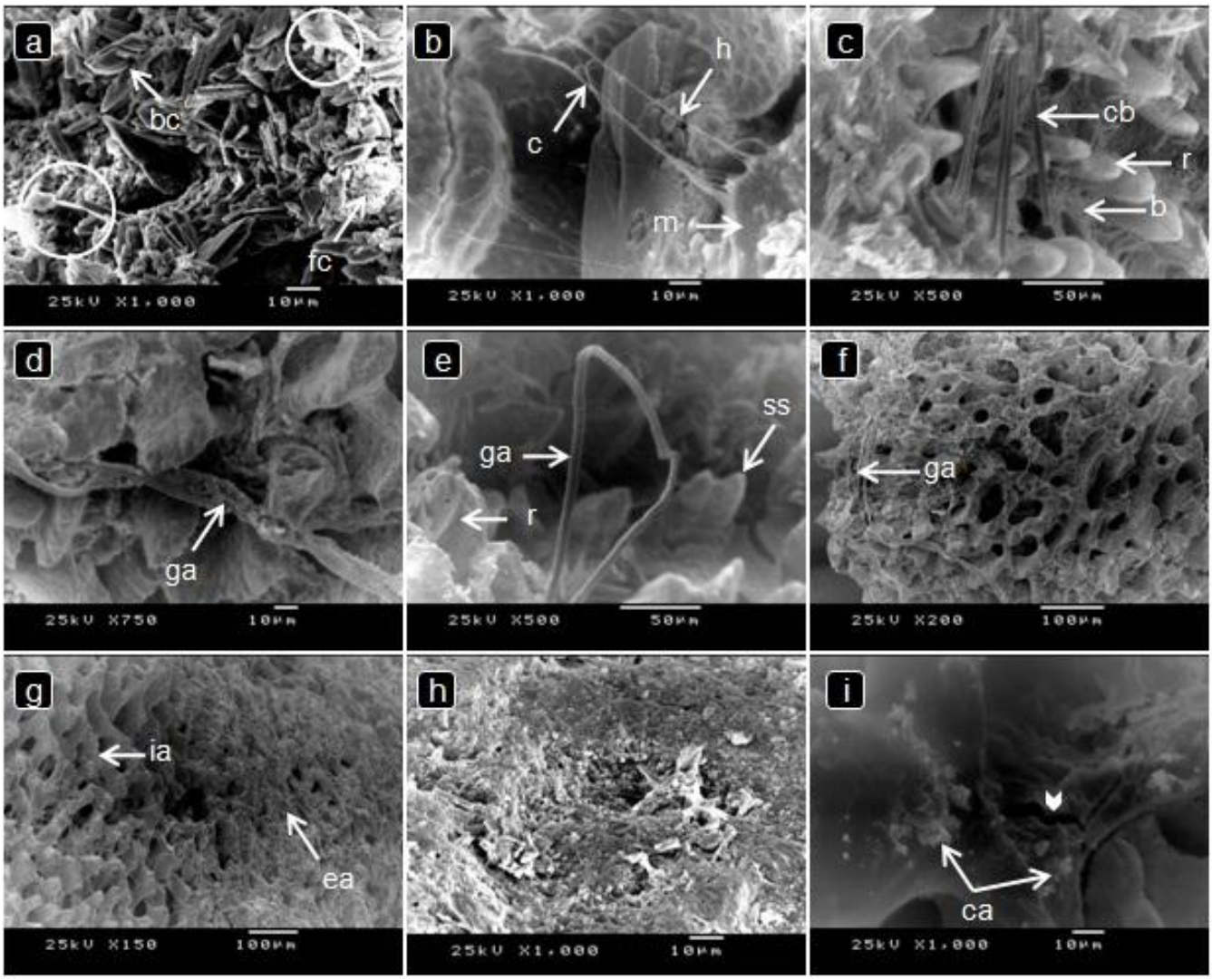

Figure3: Scanning electron micrographs of microbial communities associated with *A. humilis* branches: (a) Individual polyp infected by conidiophores with conidia (circle) of fungi, (b) Fungal hyphae associated with the mucous which secreted by the polyp, (c) Groups of cyanobacteria between the skeletal elements of the corallite, (d), (e) Green algae between the skeletal elements of the corallite, (f) Erosion of the skeletal elements of the corallite, (g) The surface of the corallite showing intact and eroded areas, (h) Fully eroded corallite, (i) Cracking of the skeleton (head arrow) and mineralization by micro-granular calcite. Abbr.: b, bar; bc, blade-shaped crystals; c, fungal conidia; ca, calcite; cb, cyanobacteria; ea, eroded area; fc, fusiform crystals; ga, green algae; h, fungal hyphae; ia, intact area; m, mucous; r, rod; ss, sclerosepta.

Discussion

The skeleton of *A. humilis* had fasciculate surface as reported for other corals (e.g. Sorauf, 1972; Jell, 1974; Gladfelter, 1982). Gladfelter (1982, 1983) reported that, clusters of blade-shaped crystals extended from fusiform crystals to ultimately form fascicule. Fusiform crystals have been suggested to be calcite, in contrast to the bulk of the skeleton, which is formed from aragonite as reported by Gladfelter (1983) and

Clode and Marshall (2003a). Fusiform crystals occur at sites on a skeleton where extension occurs. They have been observed on the distal margins of the axial corallites of four acroporid species, *A. cervicornis* (Gladfelter, 1982a, b; 1983); *A. hebes* (Isa, 1986); *A. formosa* (Clode and Marshall, 2003b) and *A. palmata* (Gladfelter, 2007). They also observed on the exert septa of *Galaxea fascicularis* (Hidaka 1991a, b; Clode and Marshall 2003a, b), and on the rods and bars extending in *A. palmata* colony via encrusting growth at its base (Gladfelter, 2007). Thus, fundamental mechanisms of calcification in scleractinian corals can be studied either using corallite growth or encrusting growth.

In this study, the bioerosion was detected in some branches of *Acropora humilis* colonies. *A. humilis* is subjected to bioerosion due to: its surface which covered by muco-polysaccharides, its high porosity and its branching form; whose facilitate colonization by boring microfloral organisms. Pascal and Vacelet (1981) revealed that the coral surface was covered by muco-polysaccharides, which provided a matrix for bacterial colonization leading to the formation of biofilm-forming microbial communities. Kim (1994) postulated that, mucus-covered coral surfaces are often colonized by bacteria and other microorganisms. However, a few studies suggested that corals might be associated with specific bacteria. Differences in the composition of the surface mucus produced by specific corals resulted in different populations of associated microbes (Rohwer et al., 2001; 2002). Furthermore, mucus-associated bacteria had specific carbon source utilization patterns that were consistently associated with certain coral species and varied among different species of coral as reported by Ritchie and Smith (1995).

The bioerosion by microflora led to loss of tissues and cracking of the skeleton of *A. humilis*, so the branches became mineralized by micro-granular calcite. Microfloral penetration into coral tissue has been described previously, resulting in the bleaching (loss of zooxanthellae) of the tissue as revealed by Banin et al. (2000). The physical

penetration of microflora into the coral tissue is aided by chemical dissolution that results in decaying coral tissue (Rutzler et al., 1983; Chacon, 2006).

Conidiophores with conidia of fungi were present in some polyps of *A. humilis* inside the pore space of the skeleton. Fungi have the ability to utilize the organic matrix of coral skeletons; therefore they produce narrow borings and penetrate the deepest recesses of coral skeletons. They are capable of deep penetration into coral skeletons by chemical dissolution as stated by Kendrick et al. (1982). Fungal hyphae were found to be common in corals and assumed the following ecological roles as recorded by Le Campion-Alsumard et al. (1995b): as euendoliths they penetrate coral skeleton; as cryptoendoliths they resided within pore spaces; and as endophytes they grew inside filaments of endolithic algae. The fungal hyphae permeated the skeletal carbonate and entered the pore spaces where the conidiophores developed. Such conidiophores were also found in the pores of *Porites lobata* as recorded by Priess et al. (2000). Kendrick et al. (1982) isolated a large number of fungi from corals, of which they could identify 12 genera, including *Aspergillus*. However, they could not determine which of their isolates were the dominant endoliths in the skeletons of growing corals. *Aspergillus* conidiophores of endolithic fungi were observed by Le Campion-Alsumard et al. (1995b) in situ in heavily infested skeletons of *Porites lobata*.

Green algae were observed at the surface of some corallites between the skeletal elements (rods and bars) of *A. humilis.* As the importance of boring algae as bioeroders is controversial; some workers claim that they are among the most destructive agents of reef erosion whereas others maintain that they cause only minimal damage. Fine and Loya (2002) revealed that endolithic algae in corals have been considered neutral or even beneficial to coral hosts, whereas fungi were considered parasitic and associated with coral diseases as stated by Alker (2001). The endolithic algae inhabit coral skeletons as a convenient shelter, sufficiently illuminated but protected by the polyps from the competing turf algae and small grazers, whereas the endolithic fungi are there primarily for food, attacking both the coral polyps and endolithic algae

(Golubic et al., 2005). Raghukumar and Raghukumar (1991) revealed that both of endolithic algae and fungal members grow from the skeleton interior upward and outward, keeping pace with the rate of coral growth and skeletal accretion. Glynn (1997) stated that it is so difficult to distinguish between fungal and algal borings, estimates of dissolution rates due to boring fungi alone are not yet available.

Cyanobacteria are one of the microflora that investigated on some corallites of *A. humilis* and may be one of the erosion causes. Hallock (2005) indicated that cyanobacteria are becoming increasingly prominent on declining reefs, as these microbes can tolerate strong solar radiation. The production of deterrent secondary metabolites by benthic cyanobacterial and similar microbial assemblages facilitates the formation of cyanobacterial blooms on coral reefs as recorded by Nagle and Paul (1998). DiSalvo (1969) indicated that these organisms may be important in the coral erosion under certain conditions. Risk and MacGeachy (1978) stated that bacteria can etch the surface of limestone crystals and dissolve the organic matrix of coral skeletons, causing internal bioerosion. Vogel (1993) said that several species of Cyanobacteria, formerly known as blue-green algae, are capable of eroding reef rock from the splash zone to depths of at least 75 meters. Species of *Hyella, Plectonema*, *Mastigocoleus*, and *Entophysalis*, for example, have been found on limestone surfaces, inside cavities, and penetrating reef rock.

Kuffner et al. (2006) demonstrated that algae and cyanobacteria use tactics beyond space occupation to inhibit coral recruitment. On reefs experiencing phase shifts or temporary algal blooms, the restocking of adult coral populations may be slowed due to recruitment inhibition by cyanobacteria, thereby perpetuating reduced coral cover and limiting coral community recovery. Titlyanov et al. (2007) revealed that cyanobacterial mats act as a poison for scleractinian corals and are able to kill live coral tissue.

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References

1. Alker A.P., Smith G.W., Kim K. (2001). Characterization of Aspergillus sydowii (Thom *et* Church), a fungal pathogen of Caribbean Sea fan corals. Hydrobiology, 460:105–111.
2. Amor A., Lopez Armengol M.F., Rodriguez A.M.I., Traversa L.P. (1991). Intertidal endolithic fauna and its relationship to the mineralogical, physical and chemical characteristics of the substrate. Mar. Biol., 111: 271–280.
3. Banin E., Ben-Haim Y., Israely T., Loya Y., Rosenberg E. (2000). Effect of the environment on the bacterial bleaching of corals. Water Air Soil Pollut., 123:337–352.
4. Barnes D.J. (1972). The structure and formation of growth-ridges in scleractinian coral skeletons. Proceedings of the Royal Society of London B, 182: 331–350.
5. Chacon E., Berrendero E., Pichel F.G. (2006). Biological signature of microboring cyanobacterial communities in marine carbonates from Cabo Rojo, Puerto Rico. Sedimentary Geology, 185: 215-228.
6. Chamberlain J.A. (1978). Mechanical properties of coral skeleton: compressive strength and its adaptive significance. Paleobiology, 4: 419– 435.
7. Charpy L., Casareto B.E., Langlade M.J., Suzuki Y. (2012). Cyanobacteria in Coral Reef Ecosystems: A Review. J. Mar. Biol., 1-9.
8. Chazotte V., Le Campion-Alsumard T., Peyrot-Clausade M. (1995). Bioerosion rates on coral reef: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). Palaeogeography, Palaeoclimatology, Palaeoecology, 113: 189-198.

9. Chazottes V., Cabioch G., Golubic S., Radtke G. (2009). Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia-Implications for pale depth reconstructions in Holocene corals. Palaeogeography, Palaeoclimatology, Palaeoecology, 280: 456–468.
10. Clode P.L., Marshall A.T. (2003a). Skeletal microstructure of *Galaxea fascicularis* exerts septa: a high-resolution SEM study. Biol. Bull., 204:146–154.
11. Clode P.L., Marshall A.T. (2003b). Variation in microstructure of the coral *Galaxea fascicularis*: effects of an aquarium environment and preparatory techniques. Biol. Bull., 204:138–145.
12. Conand C., Heeb M., Peyrot-Clausade M., Fontaine M.F. (1998). Evaluations of bioerosion by two types of the sea urchin *Echinometra mathaie* on several sites of a fringing reef in La Réunion (Indian Ocean) and comparison with other sites. In: Mooi, R., Telford, M. (Eds.), Echinoderms: San Francisco. A.A. Blakemore, Rotterdam, pp. 609–615.
13. Delvoye L. (1992). Endolithic algae in living stony corals: algal concentrations under influence of depth-dependent light conditions and coral tissue fluorescence in Aqancia agancites (L.) (Scleractmia, Anthozoa). Stud. nat. Hist. Caribbean Region, 71: 27-41.
14. Di Salvo L.H. (1969). Isolation of bacteria from the corallum of *Porites lobata* (Vaughn) and its possible significance. Amer. Zool., 9:735-740.
15. Fine M. and Loya Y. (2002). Endolithic algae: an alternative source of photoassimilates during coral bleaching. Proc. R. Soc. Lond. B. Biol. Sci. 269: 1205–1210.
16. Floros C.D., Samways M.G., Armstrong B. (2005). Polychaete (*Spirobranchus giganteus*) loading on South African corals. Aquat. Conserv, 15: 289-298.
17. Frank U., Brickner I., Rinkevich B., Loya Y., Bak R.P.M., Achituv Y., Ilan M. (1995). Allogeneic and xenogeneic interactions in reef building corals may induce tissue growth without calcification. Mar. Ecol. Progr. Ser., 124: 181-188.

18. Gladfelter E. (2008). Coral skeletons from calcium carbonate to intricate architecture. 11th International Coral Reef Symposium, Abstracts, p. 15.
19. Gladfelter E.H. (1977). Calcification and productivity in a dominant shallow water reef building coral, *Acropora palmata* (Lamarck). M.S. thesis. University of the Pacific, p 50.
20. Gladfelter E.H. (1982a). Skeletal development in *Acropora cervicornis*: I. Patterns of calcium carbonate accretion in the axial corallite. Coral Reefs, 1:45–51.
21. Gladfelter E.H. (1983). Skeletal development in *Acropora cervicornis* II. Diel patterns of calcium carbonate accretion. Coral Reefs, 2:91–100.
22. Gladfelter E.H. (2007). Skeletal development in *Acropora palmata* (Lamarck 1816): a scanning electron microscope (SEM) comparison demonstrating similar mechanisms of skeletal extension in axial versus encrusting growth. Coral Reefs, 26:883–892.
23. Gladfelter E.H., Gladfelter W.B. (1979). Growth and total carbonate production by *Acropora palmata* on a windward reef. In: Gladfelter EH, Gladfelter WB, Hubbard DK, Carpenter RC, Simpson GS (eds) Environmental studies of Buck Island Reef National Monument II. A report by West Indies Laboratory of Fairleigh Dickinson University to the US Department of the Interior, National Park Service, pp III-1–8.
24. Gladfelter W.B. (1982b). White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull. Mar. Sci., 32:639–643.
25. Glynn P.W. (1997). Bioerosion and Coral Reef Growth: A Dynamic Balance. Life and Death of Coral Reefs, Pp 69-98.
26. Golubic S., Radtke G., Le Campion-Alsumard T. (2005). Endolithic fungi in marine ecosystems. TRENDS in Microbiology, 13 (5): 229-235.
27. Hallock P. (1988). The role of nutrient availability in bioerosion: consequences to carbonate buildups. Palaeogeography, Palaeoclimatology, Palaeoecology, 63: 275-291.

28. Hallock P. (2005). Global change and modern coral reefs: new opportunities to understand shallow-water carbonate depositional processes, Sedimentary Geology, 175 (1–4): 19–33.
29. Hidaka M. (1991a). Deposition of fusiform crystals without apparent diurnal rhythm at the growing edge of septa of the coral *Galaxea fascicularis*. Coral Reefs, 10:41–45.
30. Hidaka M. (1991b). Fusiform and needle-shaped crystals found on the skeleton of a coral *Galaxea fascicularis*. In: Suga S, Nakahara H (eds) Mechanisms and phylogeny of mineralization in biological systems. Springer, Tokyo, pp 139–143.
31. Highsmith R.C. (1981). Coral bioerosion: damage relative to skeletal density. Amn. Nat., 117: 193–198.
32. Holmes K.E., Edinger E.N., Hariyadi, Limmon G.V., Risk M.J. (2000). Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. Mar. Pol. Bull., 40: 606–617.
33. Hubbard D.K., Miller A.I., Scaturo D. (1990). Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Islands): applications to the nature of reef systems in the fossil record. Journal of Sedimentary Petrology, 60: 335-360.
34. Isa Y. (1986). An electron microscope study on the mineralization of the skeleton of the staghorn coral *Acropora hebes*. Mar. Biol., 93:91–101.
35. Jell J. S. (1974). The microstructure of some scleractinian corals. Pp. 301–320 in Proceedings of the Second International Coral Reef Symposium, A. M. Cameron, ed. Great Barrier Reef Committee, Brisbane, Australia.
36. Kendrick B., Risk M., Michael ides J., Bergman K. (1982). Amphibious microborers: bioeroding fungi isolated from live corals. Bull. Mar. Sci., 32: 862–867.
37. Kiene W.E., Hutchings P.A. (1994). Bioerosion experiments at Lizard Island, Great Barrier Reef. Coral Reefs, 13: 91-98.

38. Kiene W.E., Radtke G., Gektidis M., Golubic S., Vogel K. (1995). Factors controlling the distribution of microbes in Bahamian reef environments. In: Schumacher, H., Kiene, W.E., Dullo, W.C. (Eds.), Factors controlling Holocene reef growth: an interdisciplinary approach: Facies, 32: 174–188.
39. Kim K. (1994). Antimicrobial activity in gorgonian corals (Coelenterata, Octocorallia). Coral Reefs, 13 (2): 75- 80.
40. Kleemann K. (2001). Marine Bioerosion, Universität Wien., 28p.
41. Kuffner I. B., Walters L. J., Becerro M. A., Paul V. J., Ritson-Williams, and Beach K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria," Marine Ecology Progress Series, 323: 107–117.
42. Le Campion-Alsumard T., Golubic S., Hutchings P. (1995a). Microbial endoliths in skeleton of live and dead corals: *Porites lobata* (Mooréa, French Polynesia). Mar. Ecol. Prog. Ser., 117: 149–157.
43. Le Campion-Alsumard T., Golubic S., Priess K. (1995b). Fungi in corals: symbiosis or disease? Interaction between polyps and fungi causes pearl-like skeleton biomineralization. Mar. Ecol. Prog. Ser., 117:137–147.
44. Munday P.L. (2002). Does habitat availability determine geographical-scale abundance of coral-dwelling fishes?. Coral Reefs, 21: 105–116.
45. Nagle D.G., Paul V. J. (1998). Chemical defense of a marine cyanobacterial bloom. J. Exp. Mar. Biol. Ecol., 225 (1): 29–38.
46. Nothdurft L.D., Webb G.E. (2007). Microstructure of common reef-building coral genera *Acropora*, *Pocillopora*, *Goniastrea* and *Porites*: constraints on spatial resolution in geochemical sampling. Facies, 53: 1–26.
47. Pantazidou A., Louvrou I., Economou-Amilli A. (2006). Endolithic shell-boring cyanobacteria and chlorophytes from the saline lagoon Achivadolimni on Milos Island, Greece. Eur. J. Phycol., 41(2): 189–200.

48. Pari N. (1998). Les éponges perforantes dans les milieux récifaux actuels et anciens: signification écologiques et paléoécologiques. Université d'Aix–Marseille I, Marseille
49. Pari N., Peyrot-Clausade M., Le Campion-Alsumard T., Hutchings P.A., Chazottes V., Golubic S., Le Campion, Fontaine, M. F. (1998). Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) after two years of exposure. Marine Ecology Progress Series, 166: 119-130.
50. Pascal H., Vacelet E. (1981). Bacterial utilization of mucus on the coral reef of Aqaba (Red Sea). Proc 4th Int. Coral. Reef. Symp., 1:669–677.
51. Priess K., Le Campion-Alsumard T., Golubic S., Gadel F., Thomassin B. (2000). Fungi in corals: black bands and density banding of *Porites lutea* and P. *lobata* skeleton. Mar. Biol., 136: 19–27.
52. Raghukumar C., Raghukumar S. (1991). Fungal invasion of massive corals. PSZN I: Mar. Ecol., 12:251–260.
53. Risk M. J., MacGeachy J. K. (1978). Aspects of bioerosion of modern Caribbean reefs. Rev. Biol. trop. 26 (1): 85-1 05.
54. Risk M.J., Sammarco P.W., Edinger E.N. (1995). Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. Coral Reefs, 14: 79-84.
55. Ritchie K.B., Smith G.W. (1995). Preferential carbon utilization by surface bacterial communities from water mass, normal, and white-band diseased *Acropora cervicornis*. Mol. Mar. Biol. Biotechnol., 4:345–354.
56. Rohwer F., Breitbart M., Jara J., Azam F., Knowlton, N. (2001). Diversity of bacteria associated with the Caribbean coral *Montastraea franksi.* Coral. Reefs, 20: 85-91.
57. Rohwer F., Seguritan V., Azam F., Knowlton N. (2002). Diversity and distribution of coral-associated bacteria. Mar. Ecol. Prog. Ser., 243:1–10.

58. Rosen B.R. (1986). Modular growth and form of corals: a matter of metamers?. Philosophical Transactions of the Royal Society of London B, 313: 115–142.
59. Rosenberg E., Koren O., Reshef L., Efrony R., Zilber-Rosenberg I. (2007). The role of microorganisms in coral health, disease and evolution. Nature Rev. Microbial., 5: 355–362.
60. Rutzler K., Santavy D.L., Antonius A. (1983). The black band disease of Atlantic reef corals. III. Distribution, Ecology and Development. PSZNI: Mar. Ecol., 4(4): 29-358.
61. Schneider J. (1976). Biological and inorganic factors in the destruction of limestone coasts. Contrib. Sediment., 6: 1–112.
62. Sorauf J. E. (1972). Skeletal microstructure and microarchitecture in Scleractinia (Coelenterata). Palaeontology, 15: 11–23.
63. Titlyanov E. A., Yakovleva I. M., and Titlyanova T. V. (2007). Interaction between benthic algae (Lyngbya bouillonii, Dictyota dichotoma) and scleractinian coral *Porites lutea* in direct contact. J. Exper. Mar. Biol. Ecol., 342: 282–291.
64. Veron J.E.N (1986). Corals of Australia and the Indo-Pacific. Angus & Robertson Publishers, UK.
65. Veron J.E.N. (2000). Corals of the world. Sea Challengers, Washington.
66. Vogel K. (1993). Bioeroders in fossil reefs. Facies 28:109-114.
67. Vogel K., Gektidis M., Golubic S., Kiene W.E., Radtke G. (2000). Experimental studies on microbia bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. Lethaia, 33: 190–204.
68. Wallace, C. (1999). Staghorn Corals of the World: A Revision of the Genus *Acropora*. Commonwealth Scientific and Industrial Research Organisation (CSIRO) Publishing, Collingwood Victoria, 438 p.