Projects: Re 665/4 „Aktuopaläontologie überlebender, kretazischer Porifera-Gemeinschaften in lichtarmen Zonen des Großen Barriere-Riffs nahe Lizard Island, Australien", Project Leader: J. Reitner (Göttingen)
Re 665/8 „Steuernde Funktionen und Erhaltungspotentiale moderner und fossiler Porifera", Project Leader: J. Reitner (Göttingen)

Biocalcification Processes in Three Coralline Sponges from the Lizard Island Section (Great Barrier Reef, Australia): The Stromatoporoid *Astrosclera*, the Chaetetid *Spirastrella* (*Acanthochaetetes*) and the Sphinctozoid *Vaceletia* (Demospongiae)

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Area of Study: Lizard Island Section, Great Barrier Reef, Australia
Environment: Coral Reef, reef cave
Stratigraphy: Recent
Organisms: Coralline sponges
Depositional Setting: Reef cave
Constructive Processes: Biocalcification
Destructive Processes: Bioerosion
Preservation: —
Research Topic: Biocalcification processes

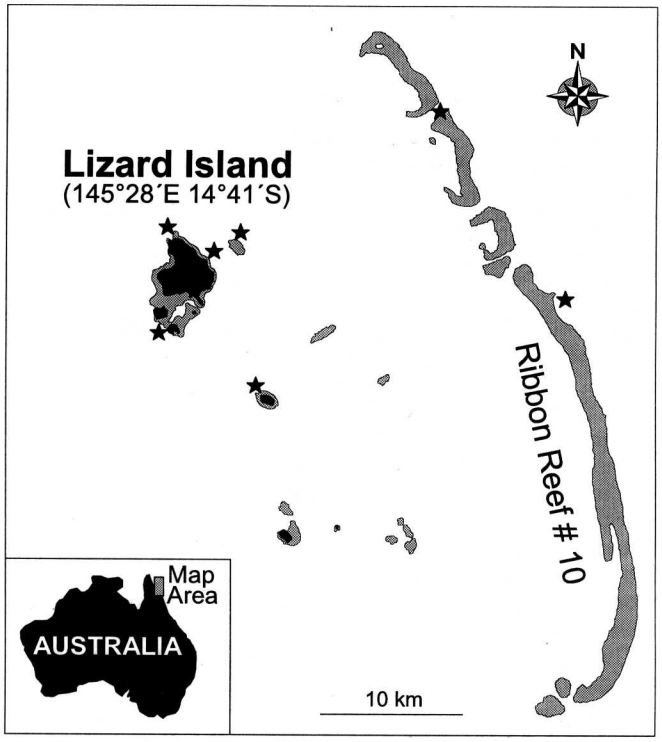

Fig. 1: Location of investigated reef caves at the Lizard Island Section of the Great Barrier Reef (Australia).

Abstract

The main biocalcification events in the phylogenetically distinct taxa *Astrosclera*, *S.* (*Acanthochaetetes*) and *Vaceletia* are described. Each taxon constructs its secondary calcareous skeleton in its own highly specialized way and provides therefore insight in the biocalcification processes of ancient reef constructors like stromatoporoids, chaetetids, and sphinctozoans.

1 Introduction

Calcified sponges were dominant reef building organisms since the beginning of the Phanerozoic. Replaced in their reef-building function by scleractinian corals in modern reefs, the living relatives of these calcified sponges ("coralline sponges") could be found in cryptic niches of almost all Recent coral reefs. They were the first metazoans producing a carbonate skeleton and their microstructural features have remained completely unchanged over the very long period of time. The biomineralization processes are extremely conservative and still present in extant calcified sponges. Within this group of organisms very little is known about the modalities of the formation of the basal skeleton so the present study will focus on this topic.

Biomineralization events have been investigated in three different taxa of coralline sponges from the Lizard Island Section of the Great Barrier Reef (Australia). The secondary calcareous skeleton of the agelasid stromatoporoid *Astrosclera* is made of aragonite spherulites (AYLING 1982, REITNER 1992, WÖRHEIDE et al. in press a, b). The hadromerid chaetetid *S.* (*Acanthochaetetes)* produces an high-Mg calcite skeleton beside the spicular skeleton (HARTMAN & GOREAU 1975, REITNER & ENGESER 1987, REITNER & GAUTRET 1996, WÖRHEIDE et al. in press b, BERGBAUER et al. 1996). The probably haplosclerid taxon *Vaceletia* exhibits no primary spicular skeleton and builds an aragonitic secondary basal skeleton (REITNER 1992).

The aim of the present study is to summarize the results of the studies on the different biomineralization events of these three taxa.

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2 Material and Methods

The investigated specimens of *Astrosclera*, *S. (Acanthochaetetes)*, and *Vaceletia* were all collected by SCUBA diving during several field trips from 1990 to 1996 in shallow water reef caves of the Lizard Island Section (Great Barrier Reef, Australia) (Fig. 1).

The procedures of specimen fixation, preservation, and the following methods of investigation were extensively described by REITNER (1993) and WÖRHEIDE et al. (in press a, b).

3 Results

3.1 *Astrosclera willeyana* LISTER 1900

The soft tissue of *Astrosclera willeyana* is organized in a dermal zone, a choanosomal part, and a prominent exhalant system (LISTER 1900). The soft tissue itself occupies only a few millimeters of the youngest portion of the basal skeleton. The inner choanosomal layer is characterized by a more or less dense mesohyle with numerous microbes (mostly *Vibrio*-types) and very small choanocyte chambers (5-20 µm). The microbes may represent 30-50 % of the biomass within this zone. The root-shaped exhalant canal system ends in so-called astrorhizae patterns often located on superficial mamelons. The basal skeleton is made of aragonitic spherulites.

The dermal layer and related mesohyle is free of microbes and enriched in motile cells. Most of them have an archaeocyte character. The mesohyle is formed by a dense network of EDTA insoluble fibers, in which the mobile cells are moving. Within the studied specimens up to 60 % of the mobile cells are spherulite forming (large vesicle cells=LVC).

The formation of the basal skeleton can be summarized as below (cf. WÖRHEIDE et al. in press a, b):

1) The size of the LVC ranges from 3-5 µm to about 20 µm, depending on the ontogenetic stage. The outer shape is round to egg shaped. They possess a large nucleus with a nucleolus, abundant mitochondria, and a lot of small vacuoles with reserve granules and/or phagocytised bacteria. The granules are extremely electron dense (osmophile) and therefore enriched in lipids.

2) During successive stages the LVC increase in size. Ontogenetical early stages are characterized by one large vacuole. It includes a minimum of 50 % of the total volume of the entire cell. At the last stage, the volume of the vacuole is more than three times larger than that of the remaining cell (WÖRHEIDE et al. in press b: Fig. 3).

3) The vacuole is primarily filled up with a three dimensional network of fibers and sheets, probably formed under control of the electron dense reserve bodies. Sheets and fibers are forming small containers (30-50 nm) in which the first seed crystals are formed. The entire vacuole is filled up with Ca^{2+}-binding glycoproteic mucus which exhibits a strong tetracycline and/or calcein induced fluorescence (cf. WÖRHEIDE et al. in press a: Pl. 1/2).

4) The seed crystals are euhedral and randomly orientated in early stages (2-3 µm). In the later stages of development (3-10 µm) the seed crystals get more orientated in direction of a c-axis of an aragonite crystal. All observed aragonite fiber crystals of the spherulites are compounds of 30-50 nm sized seed crystals (REITNER 1992). The aragonite fiber crystals are now more or less radially orientated and forming aster shaped spherulites with a large remaining space filled up with acidic organic mucus.

5) The aster spherulites are normally released at the 15 µm stage. At this stage the LVC is lysing, the membranes are broken and the aragonite asters are unattached in the mesohyle. In some sections an enrichment of small amoebocytes was observed which probably transport the asters to certain places.

6) The isolated asters grow together by epitaxial processes. The spherulite-fibers, not embedded in a cell anymore, grow in direction of the c-axis of the aragonite crystal. When the fibers get in contact with the fibers of other spherulites, they interfinger with them and stop to grow. The fibers not disrupted in growth grow until they interfinger with other spherulites. Due to this growth obsolescence, the spherulites get an asymmetrical shape in the older part of the basal skeleton. Mostly they show one elongated part and get an "egg-like" shape (cf. GAUTRET 1986: 83, Fig. 1d). After enzymatic proteolysis, which destroys the organic envelope, distinctive concentric growth lines are visible (cf. GAUTRET 1986: 106, Pl. III, Fig. 3+4). The fibers are about 0.5-1 µm in diameter and are composed of parallel arranged smaller fibers of about 50-70 nm in diameter (GAUTRET 1986).

7) The surface of the growing spherulites is covered by basopinacocytes. The space between the top of the fibers and the basopinacocytes is filled with acidic mucus, which exhibits a strong calcein induced yellow epifluorescence (cf. WÖRHEIDE et al. in press a: Pl. 1). This mucus functions as a buffer for Ca^{2+}-ions and controls therefore the speed and direction of the epitaxial growth of the aragonite fibers. The process of mucus formation and origin (secreting cell type) is not yet fully understood in detail.

The amino acid and monosaccharide composition were studied on an approximate 400 yrs old specimen from Ribbon Reef No. 10 (Lizard Island Section, Great Barrier Reef, Australia) (WÖRHEIDE et al. in press a). Amino acid and monosaccharide composition of the insoluble intracrystalline matrix are very stable in all portions of the skeleton. No strong diagenetic effect on the insoluble organic matrix (IOM) is visible due to the stable composition. The IOM is dominated by proteins and is represented by the intravacuole fibers and sheets forming the containers for the seed crystals. Collagen was not detected in the IOM.

The soluble organic matrix (SOM) is characterized by acidic glycoproteins, high amounts of proline, which is needed for the synthesis of glutamic acid, and high amounts of aminosugars. The glucids are the dominant fraction of the SOM. The character of the SOM is very typical for Ca^{2+}-binding mucus substances. A strong diagenetic effect is visible in the SOM, both in composition of amino acids and monosaccharides and in the quantity (cf. WÖRHEIDE et al. in press a).

3.2 *Spirastrella (Acanthochaetetes) wellsi* HARTMAN & GOREAU 1975

Only the 0.5-1 mm thick youngest part of the calicles of the chaetetid-type basal skeleton is occupied by the living soft tissue. Soft tissue and basal skeleton exhibit a vertical anatomy divided in five major zones. At the uppermost dermal area settles a thick crust layer of spiraster microscleres (Zone I) and tylostyle megascleres which are arranged in clear plumose bundles proving the close phylogenetic relationship to *Spirastrella*. Below the outer dermal area, the internal dermal area (Zone II) is formed by mesohyle tissue. It is enriched in mobile cells and devoid of choanocyte chambers. Large inhalant chambers (lacunae) and canals cross this zone, serving the choanosome with water filtered through the ostiae. The mesohyle is characterized by large cells (ca. 10 µm) containing numerous inclusions (LCG: large cells with granules) (REITNER 1992). These cells are mobile. LCG cells are not typical spherulous cells as known from *Vaceletia crypta*. Their shape varies often and

normally they exhibit a triangular and flat shape. Only in rare cases they show a spherulous shape.

The biocalcification process can be devided into three main locations and processes (cf. WÖRHEIDE et al. in press b):

1) LCG´s are enriched in the upper part of the tubes at the top of the walls. The LCG´s are responsible for the secretion of collagen fibrils (cf. REITNER & GAUTRET 1996: Pl. 50/1) and they probably derive from lophocytes. Collagen fibrils are forming strong bundles which cross through the basal pinacocyte layer, and anchor in the rigid skeleton (VACELET & GARRONE 1985, REITNER & GAUTRET 1996). The space between the basopinacoderm and the calcareous wall is filled up with acidic mucus substances, probably deriving from metabolic processes during the synthesis of the collagen fibrils. This mucus and the aquatic fluids are enriched in Ca^{2+}-ions, detected by a strong epifluorescence behavior in calcein and chloro-tetracycline stained specimens. The aquatic fluids exhibit an increased carbonate alkalinity. The source of the carbon is not related to the sponge metabolism but to the ambient seawater (REITNER 1992, 1993). The mucus is acting as the soluble organic matrix and is forming molecular monolayers in form of ß-sheet structures (cf. SIMKISS 1986) on the above described collagen fibrils. The collagen fibrils are acting as the insoluble organic matrix. The first nucleation of irregular Mg-calcite seed crystals takes place on the ß-sheet. The mature high Mg-calcite crystals formed by this process have a size of 0.5-1 µm and exhibit often an anhedral shape.

2) A second type of collagen fibrils is present. These fibrils are produced by lophocytes which are widely distributed in the intercellular mesohyle. *S. (Acanthochaetetes)* bears only few small sized microbes, located on these fibrils. At the top of the walls the fibrils become organized into a weak frame-building matrix. Remains of this matrix are entrapped inside skeletal structures after calcification. The main area of calcification is located in the very narrow space between the basopinacoderm and the mineralized surface of the basal skeleton. This space is filled up with acidic mucus substances. The basopinacocytes produce soft folded organic strings ("cooked spaghetti" sensu REITNER & GAUTRET 1996), which are templates for the acicular high Mg-calcite crystals. The mucus substances get organized on this templates in a molecular monolayer (ß-sheet, SOM, see above). Mineralization starts on the templates in form of very small seed crystals (50-100 nm). They grow together epitaxically (c-axis orientated) and during this process the folded templates become stretched. New formed high Mg-crystals exhibit therefore a strong "knobby" structure (cf. REITNER & GAUTRET 1996: Pl. 51/7). Due to further epitaxial crystal growth the irregular biocrystals become flat as known from the mature basal skeleton. The mature high Mg-calcite crystals have an elongated, acicular shape, an average length of 2-5 µm, and a diameter of 200-500 nm.

3) The third area where biomineralization happens are the horizontal tabulae which are dividing the calicle tubes of the chaetetid skeleton (zone IV). These are formed by the basopinacoderm also, first as a thin organic phragma or sheet. Below the choanosomal zone, LCG cells become sometimes enriched and cause the mineralization of the organic sheet. Continuously upward moving basopinacoderm is forming a space filled with Ca^{2+}-binding and mineralizing organic mucus as known from the upper portions. This mineralizing process happens only when LCG's are present (REITNER 1992).

The mineralization of the skeleton in all above described situations is only happening when the LCG´s are present and physiologically active.

The closed spaces between tabulae contain accumulations of modified archaeocytes with numerous storage granules (thesocyte-like cells) and few spiraster microscleres (zone V). These cells should play a role in regeneration processes (VACELET 1985, 1990) making the sponge able to start rising again when it has been drastically damaged.

The soluble matrix extracted from the superficial part of the skeleton contains high amounts of glycine, proline and hydroxyproline-rich compounds (collagenous affinity). Amino sugars are enriched in this zone. The presence of highly concentrated materials with collagenic or glucidic affinities results in the fact that relative amounts of acidic amino acids (Asp and Glu) appear less represented here than in the immediately underlying older part. However, absolute quantities of these two amino acids should be at least 3 to 5 times higher in the uppermost part of the skeleton (GAUTRET et al. in press). The transformation starting from the area immediately below the active mineralizing zone exhibits a regular tendency with decreasing acidic amino acids as the most obvious feature, whereas aromatic amino acids (Tyr and Phe), serine and amino sugars also decrease. The increasing constituents are basic and aliphatic amino acids (mainly glycine).

Insoluble matrices exhibit quite similar, collagenic amino acid compositions in all parts of the skeleton. Only the quantity of insoluble matrix changes in an important way, decreasing considerably from the surface to the base. This matrix completely differs from soluble compounds, with much less acidic amino acids, less serine and threonine and almost no amino sugars. It is strongly enriched in all aliphatics (Gly, Ala, Val, Leu), aromatics (Phe, Tyr), proline and hydroxyproline (for detailed data see REITNER & GAUTRET 1996).

3.3 *Vaceletia crypta* (VACELET 1977)

The primary organic skeleton of *Vaceletia* is non-spicular. It has a trabecular organization and is overlaid by a hemispherical top-layer ("dermal-layer"). The trabecles consist of irregular, organic filaments with a very thick central filament. This central filament has a supporting function and could be seen as an "organic spicule". A network of very thin fibers surrounds this central filament. The calcification of the secondary aragonitic skeleton starts between this organic fibers. This secondary skeleton consists of irregular aragonitic micrite. The central filament will not be calcified. The formation of the secondary skeleton is not a continuous process, it happens step by step in the following order (cf. REITNER 1992):

1) Formation of skeletal-pillars:

- Formation of a new, non calcified chamber with a hemispherical dermal top-layer and a trabecular organization and organic skeletal-pillars containing a thick central filament. These skeletal-pillars are filled with thin fibers.
- The whole space inside the pillar is filled up with acidic glycoproteic/proteoglycanic mucus.
- This space is filled up successively during the ontogenesis by aragonite crystals. The mineralization starts at the inside of the organic pillars. Further on the whole fibrous insoluble matrix of a newly formed pillar is substituted successively by aragonite crystals. The acidic mucus substances are reduced respectively.
- The thick central filament is not going to be mineralized. This central filament has only a primary initial supporting function, because the irregular fibers inside the pillars are not able to support the choanosome on their own.
- Newly formed chambers never show the complete structure and size of the ones later calcified. A chamber in statu nascendi is increasing slowly in size.

- The crystallization seems to start from the borders of the uncalcified skeletal elements. An initial, prismatic layer of aragonite crystals is observed. Larger crystals overlay this layer forming a loose network. The density of calcification is higher in the central part and the border of the pillars, in between the calcification is more slow.

2) Calcification of the inactive parts of the skeleton:
In the ontogenetic older parts of the skeleton a second calcification phenomenon is observed. The upward moving soft-tissue is able to form an organic phragma via the basopinacoderm. This phragma separates chambers which are filled up with acidic glycoproteic mucus ("soluble matrix", SOM). This SOM shows high concentrations of Asp (14.13 mol%) and Glu (11.42 mol%) in combination with high values of ARA (14 mol%), XYL (16.5 mol%), and GLC (22 mol%) (REITNER 1992). The SM is interspersed by polymerized mucus fibers which act as the insoluble organic matrix (IOM). The steps of mineralization are the same as with the pillars (REITNER 1992).

The described microstructures are often observed in similarly formed fossil sphinctozoans and the observed mineralization processes of the *Vaceletia*-type could be a model for all irregular, micritic-granular basal skeletons of stromatoporoidal and thalamidal organization. The investigation of the biocalcification processes of three newly discovered colonial *Vaceletia* types from the SW Pacific (REITNER & WÖRHEIDE 1995, WÖRHEIDE & REITNER 1996) are still in progress and could provide clues for the understanding of the biocalcification processes of colonial sphinctozoans, important reef building sponges in the Permo-Triassic.

4 Conclusions

The different *modi* of formation of the rigid calcareous basal skeleton in three different taxa of coralline sponges were described. Leading to a comparable endproduct, a rigid calcareous skeleton, each taxon forms the basal skeleton in its highly specialized way using different modifications of calcium carbonate (*Astrosclera* and *Vaceletia*=aragonite, *Acanthochaetetes*=high Mg-calcite).

In the cases of *Astrosclera* and *S. (Acanthochaetetes)* modified lophocytes initialize the mineralization. In *Astrosclera*, the LVC´s form a template of 3-dimensional fibers inside a large vacuole. The vacuole is filled with highly acidic mucus, rich in Asp and Glu. The fibers and the mucus act as the organic matrix for seed crystallization (WÖRHEIDE et al. in press a, b). This process could be described as "biologically controlled calcification". In *S. (Acanthochaetetes)*, the lophocytes secrete collagen fibers which also act as a template for the initial nucleation of the seed crystals. This process could be described as "biologically induced calcification".

At a later stage, modified basopinacocytes control the mineralization process. In *Astrosclera*, basopinacocytes cover the released and fused spherulites. The epitaxial growth of the spherulites is controlled by a highly acidic mucus between the crystal surface and the basopinacocytes. This mucus is highly soluble and exhibits a strong calcein induced epifluorescence. In *S. (Acanthochaetetes)*, the crystal growth is also controlled by acidic mucus substances, which fill up the space between the collagenous fibers and the basopinacocytes. The later stages in both cases could be described as "biologically induced calcification".

Vaceletia shows a different modus of calcareous skeleton formation. There, the calcification starts in a separated space inside organic pillars and is not under direct control of the sponge cells. Also in the later stage, when the chambers of the ontogenetic oldest parts of the skeleton are mineralized, the process happens not under direct control of the sponge. This process could be described as "matrix mediated calcification", induced by the sponge.

Very important in all cases is the presence of an organic matrix, forming a template for crystal nucleation (SIMKISS 1986, MANN et al. 1989). The presence of a soluble organic mucus, rich in Asp and Glu, is controlling the crystal growth in the earliest and latest stages of mineralization. The mineral preference, aragonite or Mg-Calcite, is controlled by the structure of the organic macromolecules, forming ß-sheets (SIMKISS 1986), and acting as the Ca^{2+} attractors. The distances of the carboxyl-groups of the macromoelcules control the crystallographic base plane of the initial calcite or aragonite crystal (MANN et al. 1989, REITNER 1993, WÖRHEIDE et al. in press b).

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