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A DESCRIPTION OF THE SKELETAL DEVELOPMENT PATTERN OF THE TEMPERATE CORAL CARYOPHYLLIA SMITHI BASED ON INTERNAL GROWTH LINES

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Scanning electron microscopy was used to study the microstructure and internal growth lines of the temperate ahermatypic coral Caryophyllia smithi (Cnidaria: Anthozoa). The arrangement of internal growth lines in combination with the orientation of aragonite crystals were used to describe the pattern of skeletal development in C. smithi. The observed pattern was verified using observations from another study on skeletal development in C. smithi, but which was based only on external observations of skeletons of living and dead specimens in different stages of development. The pattern of skeletal development in C. smithi is suggested to be subdivided into three stages, based on the deposition of specific skeletal elements during the development of the skeleton. In the first ‘juvenile’ stage, various primary skeletal elements are formed: the basal plate, the septa and a primary and secondary septotheca. The second ‘half full grown’ stage is characterized by development of apparently only an extended basal attachment, which enlarges the attachment area to the substratum. In the third ‘full grown’ stage, the edge zone of the polyp tissue is retracted from the extended basal attachment to the calice, and upward growth of the coral predominates followed by lateral thickening of the septotheca, costae, septa and columella. Internal growth lines were found throughout the skeleton and may be composed of, or resulting from the presence of organic matter. The septotheca and the extended basal attachment, which are important for a strong skeletal structure and a strong attachment to the substratum, respectively, are probably thickened faster than the other skeletal elements. Attachment scars were found in areas where attachment of the coral tissue to the skeleton is critical.

INTRODUCTION

Gladfelter (1983) suggested that describing the development of the skeleton may be important for a better understanding of calcification in corals. So far, studies have mainly been focused on the skeletal development of hermatypic corals (Vandermeulen & Watabe, 1973; Gladfelter, 1982; Brown et al., 1983; Gladfelter, 1983; Le Tissier, 1988a,b). Little is known, however, of the skeletal development of ahermatypic corals. Some studies have been undertaken in ahermatypics on the skeletogenesis of larval skeletons (Kinchington, 1980, 1981).

Ahermatypic corals are known to be slow growers, which is associated with the lack of calcification-enhancing zooxanthellae (Goreau, 1959). Also, ahermatypic corals are often found in deep cold waters, and it has been reported that at low temperatures
skeletogenesis becomes inefficient (Goreau, 1961). Therefore, studies on skeletal development deduced from incremental skeletal growth, are often more difficult in ahermatypic corals than in hermatypic corals. However, it has been observed that internal growth lines are present in the skeletons of ahermatypic corals (Sorauf & Jell, 1977; Sorauf & Podoff, 1977). To describe the pattern of skeletal development in an ahermatypic coral the growth lines and microstructure of the skeleton of the temperate coral Caryophyllia smithi Stokes & Broderip, 1828 were studied.

Caryophyllia smithi is found in both shallow and deep water, and is widely distributed in the north-eastern Atlantic (Rees, 1962; Wilson, 1975). The skeleton is subcylindrical, with the septa arranged in three cycles and the columella formed by twisted laths (Best, 1968). The theca originates from the septa and has been defined as a septotheca (Wells, 1956).

Much descriptive information is available on the microstructure of hermatypic corals (e.g. Wells, 1956; Barnes, 1970; Sorauf, 1972; Jell, 1974). An explanation of crystal growth in coral skeletons is given by Barnes (1970). The coral skeleton is formed by basic units called sclerodermites, which are three-dimensional fan systems constructed of needle-shaped aragonite crystals, radiating outwards from a centre of calcification (Barnes, 1970). Trabeculae are extended axes of calcification and are formed through vertical growth of the sclerodermites. Adjacent sclerodermites extend in a fan-like mode until they meet one another and interfere mutually in their growth. They thus continuously compete for space, causing the aragonite needles to be forced out of their fan-like growth and to become oriented almost parallel to one another (Barnes, 1970).

Relatively little is known of the microstructure of C. smithi. Vahl (1966) described the shape and orientation of aragonite crystals and their relation with the calicoblastic layer in the genus Caryophyllia. Some comments were made on the microstructure of C. smithi by Sorauf & Podoff (1977), who reported that in the genus Caryophyllia trabeculae are very small and closely packed, forming a 'dark line' when viewed in transverse section with an electron microscope. Le Tissier (1990) studied several aspects of the microstructure and the calicoblastic ectoderm of C. smithi.

In the present study, the microstructure and the arrangement of internal growth lines were studied in skeletons of C. smithi to describe the pattern of skeletal development. Wilson (1976) studied the attachment of C. smithi to different substrates, and gave a description of the skeletal development from a settled planula to a full grown coral. This was based, however, on external observations of the skeletons of several hundreds of living and dead specimens, in different stages of development. By studying the arrangement of internal growth lines in combination with the orientation of aragonite crystals the general skeletal development pattern, but also that of single specimens could be described. Wilson’s description of the skeletal development was used to verify the present description, which also completed that of Wilson (1976).

MATERIALS AND METHODS

Specimens of C. smithi were collected by scuba diving at depths of 4–20 m in the marine reserve Lough Hyne, near Skibberdeen, Ireland. Longitudinal and transverse
sections were cut through several coral skeletons with a diamond saw. Longitudinal sections were taken straight across the skeleton and transverse sections halfway down the corallite. At the apex of the corallite, a section of the septotheca was broken off to examine the external skeletal surface.

The sections were etched in 0.3 N HCl for 10 min. The samples were mounted on stubs, sputter-coated with gold, and viewed with a JEOL JSM-T3000 scanning electron microscope.

Additionally, longitudinal and transverse sections and skeletal surfaces were examined under a binocular microscope with reflected light.

RESULTS

Septotheca

Electron micrographs of longitudinal and transverse sections through the corallite revealed the microstructure and growth lines in several skeletal elements (Figure 1): septotheca, costae, septa, columella and the ‘extended basal attachment’ (Wilson, 1976).

![Figure 1.](image)

Figure 1. (A) The coral skeleton of Caryophyllia smithi: ba, extended basal attachment; ca, calice; st, septotheca. (B) Top view of the calice, showing various skeletal elements: c, costa; cl, columella; s, septum; st, septotheca.

Dark lines, formed by the closely packed trabeculae in Caryophyllia smithi, could be clearly identified in transverse sections. A central dark line ran throughout the septotheca and was crossed almost perpendicularly near each septum by radial dark lines (Figure 2A). Radial dark lines ran from the outer tip of the costae through the septotheca to the distal extremities of the septa.
They were far less numerous than those in the cohesive, sepia and collumella.

During later growth of the inner part of the septa, several growth lines (Figure 2D), defined here as an interference line, and obscuration the growth of the former. This resulted in the formation of a distinct line (Figure 2C). The latter grew uninhibited in a direction towards the septal edge, while the central dark lines were crossed at a certain point by crystals originating from the central dark septa, from Wells (1936). Crystals needles extending from the section of the radial septa have been defined as a cause for the septa to be built by extension of the septa and have thus been developed as a septal needes. The section of the central dark line in the septa, which lies between the central and peripheral needles, originates from dark lines and grow perpendicular to them.

Argonite needles originated from dark lines and grow perpendicular to them.

**Figure 2**: Transverse section through the septa (A) Electron micrograph showing the central (B) Direction of crystal needles (C) Detail of the central part of (B) Dark lines of (A) arrows indicate dark lines of (B) arrows indicate direction of crystal needles.
lumine from the central dark line (Figure 3d). The central dark line tends to separate the two neighboring cosseae, forming an intermediate line where the growing cossee are parallel, and one another, an intermediate line was

between their respective radial dark lines, they could only extend outward. Along the central dark line direction, the cossee grew towards the skeleton and crystals forming are oriented parallel to the central dark line. In transverse sections (Figure 3a), they were visible as concentric hemispheres. During this extension, growth lines were regularly formed, oriented perpendicular to the cossee. Instead of the radial dark line. As a result, growth lines from the cossee formed a radial dark line. Crystal needles were considerably oriented perpendicular to the dark line. (Figure 3a). In transverse sections, the cossee are oriented parallel to the central dark line. The cossee.

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Figure 2. Transverse section through part of the colletum. (A) Near the top of the section micro-

formation of growth lines (Figure 2B). Crystal growth was regularly interrupted by the formation of growth lines (Figure 4B). Numerous growth lines on both sides of the section indicate the direction of crystal growth. (D) A radial dark line is visible in the centre with numerous growth lines on both sides of the section. (F) Radial dark lines running through the colletum and septa. (G) Radial dark lines running through the colletum and septa. (H) Radial dark lines running through the colletum and septa.
on the lower surface of the extended basal attachment the growth lines were ex-

Figure 6: Longitudinal section through the extended basal attachment. (A) Electron micrographs
dicular to the direction of growth (Figure 6B). another, causing the interference to be replaced by a shared growth line (Figure 5B). Dashed to this junction the crystal needles from the two dark lines shared into one

extended. Continued extension broadened the extended basal attachment. Crystal
elongitudinal sections through the extended basal attachment at the skeleton/sub-

Extended basal attachment

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Single circular depressions ~10 µm in diameter (Figure 8C).

These scars sometimes fused to form larger depressions, but generally they appeared as rows (Figure 8B).

Rows of pits (Figure 8B) found at the junction of septum and septolemma. Also running downward in vertical rows, these scars were formed at the internal surface of the septolemma. The apices of the longitudinal depressions become more difficult to discern beyond the apex of the cone of the septum. These depressions are the result of the downward movement of the external skeletal wall during apparent vertical rows between conical pieces running downward from the conical rim (Figure 8A).
Figure 9. (A) Summary of observations on the lateral thickening of various skeletal elements. Arrows indicate the predominant direction of crystal growth. c, costa; st, septotheca; 1°s, primary septum; 2°s, secondary septum; 3°s, tertiary septum. (B) Schematic summary of observations on the skeletal development pattern in Caryophyllia smithi. Arrows indicate the direction of skeletal growth. The dotted line shows the approximate position of the transverse section in (A). c, costa; ccl, calcium carbonate layers (separated by growth lines); cl, columella; s, septa; ss, substratum; st, septotheca.

DISCUSSION

In the present study, the pattern of skeletal development including skeletal thickening has been described on the basis of the orientation of aragonite crystals and the arrangement of internal growth lines in the temperate ahermatypic coral Caryophyllia smithi. Tranter et al. (1982) described the spawning and post-gastrula development of planula larvae of C. smithi (under laboratory conditions), while Wilson (1976) described the skeletal development after settlement. After settlement of the planula, the basal plate and protosepta are secreted, then the septotheca and secondary septa, followed by a second septotheca, which enlarges the area of the basal plate, and tertiary septa (see Wilson, 1976, plates IA–IF). After completion of the second septotheca, the edge zone of the polyp deposits an ‘extended basal attachment’ at the base of the septotheca. During further growth of the corallite, layers of calcium carbonate are frequently laid down over the extended basal attachment, in such way forming a strong attachment between the coral and the substratum (Wilson, 1976).
Our description of the skeletal development of C. smithi, deduced from the arrangement of internal growth lines, substantiates (see Figures 7A & 9B) but also completes (see below) that of Wilson (1976), whose observations were based on the external skeleton. However, a subdivision of the development of the skeleton into three separate stages can be suggested, based on the development of specific skeletal elements during growth of the coral.

Stage one of the skeletal development may be characterized by settlement of the planula and formation of primary skeletal elements as described by Wilson (1976). This stage shows some similarities to the development of the larval skeleton of a hermatypic coral (Le Tissier, 1988a) with respect to the primary skeletal elements deposited. This stage is suggested to be defined as a 'juvenile stage', as in this stage only the primary skeletal elements are developed, which form the basis for further growth towards a 'full grown' coral.

Stage two may be characterized by the deposition of an extended basal attachment, which enlarges the attachment surface of the coral to the substratum. The layers of calcium carbonate deposited on the extended basal attachment, as observed by Wilson (1976), were distinguishable in our longitudinal sections of the extended basal attachment and were separated by growth lines. In the lower septotheca, all growth lines of the extended basal attachment ended together in a single horizontal growth line, suggesting a halt in the vertical growth of the corallite during development of the extended basal attachment. These horizontal growth lines were also found in septa at corresponding levels. Apparently, priority is given to development of only the extended basal attachment during this stage. This stage is suggested to be defined as a 'half full grown stage', as all the primary skeletal elements and the extended basal attachment have been deposited, but the vertical extension of skeletal elements, which would result in a fully-developed (full grown) coral, has apparently not yet been initiated.

Stage three of the skeletal development may be characterized by predominantly upward growth of the columella, septa, septotheca and costae, followed by their lateral thickening (see Figure 9A). Lateral thickening of these skeletal elements appears to be accomplished by continuing outward growth of aragonite crystals. In corals >15 mm in height and partly buried in sediment, Wilson (1976) observed that the edge zone was restricted to the top 3–5 mm of the coral. He suggested this to result either from deterioration of the edge zone when buried in the sediment, or, from retraction of the edge zone above the sediment. It is considered in this study that this is caused by the retraction of the edge zone, as specimens growing on cliffs (i.e. not living in the sediment) also showed the edge zone to be restricted to the calice (I.N., personal observations). This suggests that the retraction of the edge zone may be a normal event during the third stage, and that in this stage the extended basal attachment can no longer be enlarged and/or maintained. This stage is suggested to be defined as a 'full grown stage', as after the deposition of primary skeletal elements (juvenile stage) and the improvement of the attachment to the substratum (half full grown stage), skeletal development in this stage is continued by vertical extension and lateral thickening of the existing skeletal elements, resulting in a fully-developed coral with respect to its skeleton.
The subdivision of the skeletal development into three distinct stages may be used as an indication of relative age (i.e. what stage) in C. smithi. The first stage may be distinguished \textit{in situ} from the second stage by the absence of the extended basal attachment, and by the fact that the edge zone of the polyp does not yet extend over the substratum. The third stage may be distinguished from the second stage by the edge zone having been retracted after completion of the extended basal attachment.

Wilson (1976) described the pattern of skeletal development in \textit{C. smithi} from external observations of the skeletons of several hundreds of living and dead specimens. The present study shows that internal growth lines can also be used to describe the pattern of skeletal development in \textit{C. smithi}. With this method it is not necessary to collect large quantities of this relatively slow-growing coral. Furthermore, the exact skeletal development pattern of a single specimen may be determined, which can not be accomplished by studying the external skeleton of different individual corals in different stages of development as done by Wilson (1976). It is known that \textit{C. smithi} shows a wide variety of growth-forms, and both broad-based and narrow-based forms exist. The variation in the morphology of the base is probably associated with the strength of the water current and the type of substrate (Best, 1968; Zibrowius, 1970; Wilson, 1975). This method could thus also be used for comparison of the skeletal development pattern, in particular that of the extended basal attachment, between single specimens of \textit{C. smithi} living under different environmental conditions, for a better understanding of their growth and ecology.

Internal growth lines have been observed in skeletal elements of both hermatypic (Jell, 1974; Risk & Pearce, 1992) and ahermatypic corals (Sorauf & Jell, 1977; Sorauf & Podoff, 1977). Internal growth lines in \textit{C. smithi} may possibly be composed of, or resulting from the presence of organic matter, also referred to as the organic matrix (Johnston, 1977). Le Tissier (1988a) found a banding of skeleton and organic matrix in the basal plate of the hermatypic coral \textit{Pocillopora damicornis}. He suggested this may have been formed as a result of incremental growth of crystal layers. In the same species, successive rings of organic matter were found in transverse sections of extending costal spines (Brown et al., 1983). In addition, Le Tissier (1990) showed that in \textit{C. smithi} the organic matrix generally mirrored the structure of the skeleton, and that non-mineralized spaces in skeletal elements did not contain organic matter. He also suggested that the coral tissue determines the morphology of the skeleton via an organic matrix. If the internal growth lines in \textit{C. smithi} are closely associated with organic matrices, their regularity in spacing and occurrence would furthermore support the suggestion of a high degree of biological control in coral calcification (Le Tissier, 1990).

Growth lines in both the extended basal attachment and the septotheca were spaced significantly further apart than those in the costae, septa and columella. The wider spacing in the former may be caused by faster crystal growth compared to the latter. Barnes (1972) suggested that hermatypic corals are capable of faster calcification in certain thickening layers. Observations by Brown et al. (1983) on the organic matrix in skeletal spines of a hermatypic coral, inferred greater skeletal deposition at the base of the spine than in the tip, which resulted in secondary thickening of the spine. Thickening of the extended basal attachment and the septotheca is important for a strong
skeletal structure, and is particularly important in *C. smithi* as the extended basal attachment and the lower septotheca ultimately deteriorate through algal and fungal action (Wilson, 1976). Faster skeletal growth in the septotheca and the extended basal attachment could improve the skeletal structure of the lower corallite and the attachment to the substratum, respectively, before the edge zone is retracted to the calice and the extended basal attachment is no longer protected against algal and fungal attack. Faster skeletal growth in the septotheca and the extended basal attachment would also be important to survive in high-current environments. Wilson (1975) observed that corals growing in strong tidal-current areas had broad bases, whereas those growing in weak tidal-current areas had narrow bases. Zibrowius (1970) furthermore reported that broad-based specimens had thick and massive skeletal elements and that their skeletal density (determined by volume/weight ratio) was higher compared to that of narrow-based forms.

Attachment scars, similar to those found in other ahermatypic and hermatypic corals (Wise, 1970; Sorauf & Podoff, 1977), were located on both the internal and external skeletal walls, and marked the sites where the polyp tissue was attached to the skeleton (Wise, 1970; Vandermeulen, 1975). They were found in areas where attachment to the skeleton is critical, viz, at the junction between the septotheca and the septa, respectively, the costae. In *P. damicornis*, Vandermeulen & Watabe (1973) observed them to be present already at a very early stage (22 d) of the skeletal development.

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