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Vital effects in coral skeletal composition display strict three-dimensional control

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[1] Biological control over coral skeletal composition is poorly understood but critically important to paleo-environmental reconstructions. We present micro-analytical measurements of trace-element abundances as well as oxygen and carbon isotopic compositions of individual skeletal components in the zooxanthellate coral *Colpophyllia* sp. Our data show that centers of calcification (COC) have higher trace element concentrations and distinctly lighter isotopic compositions than the fibrous components of the skeleton. These observations necessitate that COC and the fibrous skeleton are precipitated by different mechanisms, which are controlled by specialized domains of the calicoblastic cell-layer. Biological processes control the composition of the skeleton even at the ultra-structure level. **Citation:** Meibom, A., et al. (2006), Vital effects in coral skeletal composition display strict three-dimensional control, *Geophys. Res. Lett.*, 33, L11608, doi:10.1029/2006GL025968.

1. Introduction

[2] A multitude of marine organisms produce calcium carbonate skeletons that are used extensively to reconstruct water temperature variability of the tropical and subtropical oceans – a key parameter in global climate-change models [Cole et al., 2000]. Such paleo-climate reconstructions are based on observations that skeletal oxygen isotopic composition and certain trace-element abundances (e.g., Sr/Ca and Mg/Ca ratios) vary in response to changes in the water temperature [Epstein et al., 1953; Mitschuguchi et al., 1996; Smith et al., 1979]. However, it is a fundamental problem

that poorly understood biological processes introduce large compositional deviations from thermodynamic equilibrium and hinder precise calibrations of many paleo-climate proxies [e.g., Meibom et al., 2004; Meibom et al., 2003; Rollion-Bard et al., 2003b].

[3] There are substantial variations in skeletal architecture between different coral species. Yet, beyond these inter-species morphological differences, all corals build their skeleton by biomineralization of two basic structural components: centers of calcification (COC) and ‘fibers’ [Ogilvie, 1896]. The construction of new skeleton is a continuous process in which COC are formed and subsequently overgrown by fibrous aragonite [Clode and Marshall, 2003; Cuif and Dauphin, 1998; Cuif and Dauphin, 2005; Stolarski, 2003]. The fibrous aragonite gives the skeleton strength and constitutes the bulk. However, it is the spatial distribution of the COC that determines the overall architecture of the skeleton (see Figure 1). The COC are therefore not randomly distributed, but are produced repeatedly in clearly defined positions within the skeleton, overlaying previously formed COC and thereby forming essentially continuous vertical columns of COC within the skeleton [Ogilvie, 1896]. This is illustrated in Figure 1b. Thus, the COC and the fibrous skeletal components are organized in a precise geometrical distribution that requires coordination of their locations to a precision of a few micrometers.

[4] In most reef-forming corals the COC are relatively small, on the order of 5–10 micrometers, rendering precise chemical and isotopic analysis of individual COC difficult. We have circumvented this problem by analyzing COC and aragonite fibers in the zooxanthellate coral *Colpophyllia* sp., which is particularly suitable for our purpose because the COC are relatively big, on the order of 100 micrometers (Figure 1), compared with the spatial resolution of a conventional ion microprobe. We used the USGS/Stanford University SHRIMP-RG ion microprobe to carry out trace element measurements and the Cameca 1270 ion microprobe at the Tokyo Institute of Technology to carry out oxygen and carbon isotopic measurements. The specimen studied was collected live from the west coast of Barbados in 1983. For sample preparation and analytical methods see the auxiliary material.¹

2. Results

[5] Trace element analyses are presented in Figure 2 and in Figure S1. Trace element concentrations are variable in the fibrous part of the skeleton [Allison, 1996; Cuif et al.,

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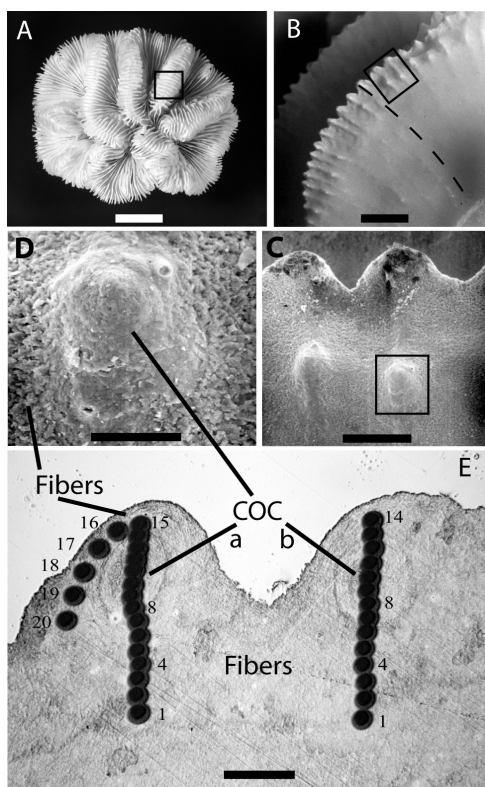


Figure 1. (a) Macroscopic view of the skeleton of *Colpophyllia* sp. after removal of the cell-layer. Scalebar is ~2 cm. (b) Enlarged view of the black frame in Figure 1a showing a side-view of an individual septa. Within the septa, the COC form continuously along precisely defined growth axes (one is delineated by a dashed line). In the grow process, the COC are produced and subsequently overgrown by layers of fibrous aragonite. The precise alignment of the COC requires strong spatial control over the growth process. Scalebar is ~1 mm. (c and d) Secondary electron microscopy (SEM) images of individual COC protruding from the septa. The COC are surrounded by fibrous aragonite. Region shown in Figure 1c corresponds to the black frame in Figure 1b. Scalebar is ~300 μm . Region shown in Figure 1d corresponds to black frame in Figure 1c. Scalebar is ~100 μm . (e) Reflected light image of the polished and gold coated *Colpophyllia* sp. specimen analyzed. The cut is parallel to the plane of the septa. Ion microprobe spots are visible with numbers corresponding to the trace element analyses shown in Figure S1. Lighter upper part of the image is epoxy. COC labeled 'a' and 'b' are visible as ellipsoidal objects. Both COC and adjacent fibrous aragonite are traversed by the ion microprobe. Scalebar is ~100 μm .

2003; Hart and Cohen, 1996; Meibom et al., 2003]. More importantly, the COC are characterized by significantly higher concentrations of all trace elements. Strontium, which is in solid solution in the aragonite crystal structure [Allison et al., 2005], increases by 10–15% in the COC; from ~9 mmol Sr/mol Ca in the fibrous part to a maximum concentration of about 10.4 mmol Sr/mol Ca in the COC, which is higher than expected for equilibrium with seawater [Cohen and McConnaughey, 2003]. Sodium concentrations in COC (data not shown) are similarly 15–20% higher than

in the fibers. All other measured trace elements show significantly higher concentrations in the COC compared with the surrounding fibrous aragonite: Mg is higher by a factor of ~1.5–2.0, Ba by a factor of ~2, B by a factor of 1.7 to 1.8 and S by a factor of 1.6 to 1.8 (Figure S1). Recent results suggest that S is present primarily in the form of highly sulfated, acidic polysaccharides [Cuif et al., 2003]. The primary observation arising from the trace element analyses presented in Figure 2 and Figure S1 is that fibrous aragonite and COC are distinctly different in terms of all trace elements.

[6] This conclusion is reinforced by carbon and oxygen isotopic analyses (Figure 3). In general, the bulk skeletal C and O isotopic ratios in scleractinian corals (here represented by the fibrous aragonite analyses) are shifted toward lower values compared to aragonite in equilibrium with seawater [Weber and Woodhead, 1970]. The precise magnitude of this shift is difficult to access for our analyses because the data required to estimate the aragonite equilibrium composition are not available (i.e., water temperature, salinity and $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of dissolved inorganic carbon).

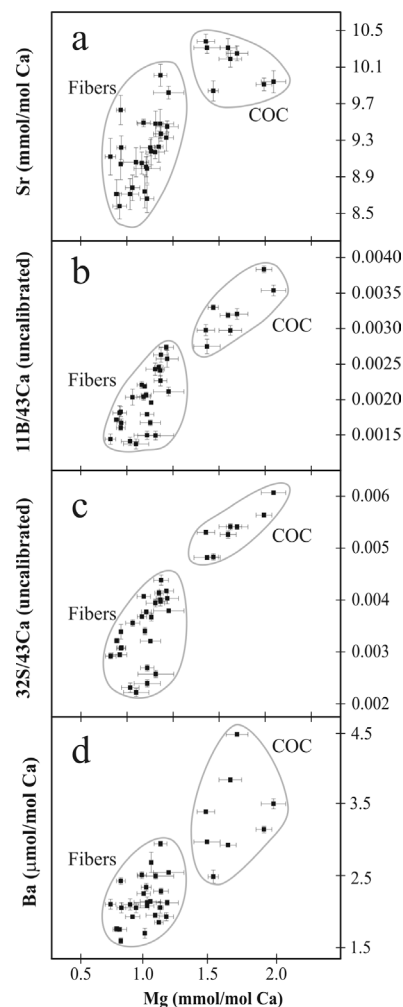


Figure 2. Trace elements compositions of fibers and COC (see Figure S1). The measured Mg/Ca ratios are plotted against (a) Sr/Ca, (b) B/Ca, (c) S/Ca, and (d) Ba/Ca. COC have distinctly higher concentrations of all trace elements compared with adjacent fibrous skeleton. Error bars are $\pm 1\sigma$.

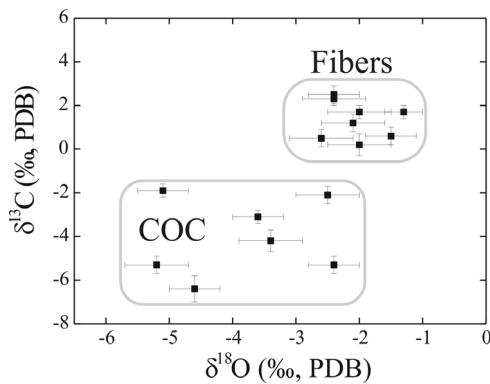


Figure 3. Carbon and oxygen isotopic compositions measured in fibers and COC, expressed as $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$; the permil level variation relative to the international PDB standard. The COC and fibrous skeleton have dramatically different isotopic compositions. COC are characterized by the lightest isotope compositions. Error bars are $\pm 1\sigma$.

More importantly, however, the COC are characterized by dramatically lighter and more variable isotopic compositions compared with the fibrous skeleton (Figure 3). The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in the fibrous part of the skeleton vary by less than 1.5‰ and 2.5‰, respectively, whereas the COC display variations as large as 3.5‰ and 5‰ in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, respectively. The total range in isotopic composition ($\sim 4\%$ in $\delta^{18}\text{O}$ and $\sim 9\%$ in $\delta^{13}\text{C}$) is comparable to the maximum total stable isotopic variability previously observed within a single zooxanthellate or azooxanthellate coral [Adkins et al., 2003; Rollion-Bard et al., 2003a; Rollion-Bard et al., 2003b]. Overall, the COC and the fibrous part of the skeleton are demonstrably out of chemical as well as isotopic equilibrium with each other.

3. Discussion

[7] Typical linear extension rates for *Colpophyllia* sp. are about 0.5–1 cm per year [Huston, 1985]. The skeletal structures analyzed here have linear dimension of about 100 micrometers (Figure 1) and are formed within a few days, during which changes in external environmental parameters, including water temperature and composition, were very limited. The strong chemical or isotopic variations observed within COC and fibrous skeleton (Figures 2 and 3) cannot be ascribed to changes in environmental conditions. These variations result from biological processes during skeletal formation and are, therefore, ‘vital’ effects.

[8] Our data require a compartmentalized interface between the calicoblastic cell-layer and the skeleton. Only a distinctly compartmentalized organization of the calicoblastic cell-layer can allow the formation of skeletal components that differ so dramatically in terms of chemistry and isotopic composition. Furthermore, only a precisely compartmentalized calicoblastic cell layer that is fixed relative to the skeleton, can allow the formation of COC with the observed degree of spatial, three-dimensional control (Figure 1b). This conclusion is supported by recent observations of the interface between the skeleton and the calicoblastic cell-layer. There is a very tight physical contact between the calicoblastic cell-layer and the surface of the growing skeleton

[Clode and Marshall, 2002, 2003; Muscatine et al., 1997]; maintained by ubiquitous desmocyte cells that anchor the calicoblastic cell-layer to the skeleton [Muscatine et al., 1997]. The interface is characterized by a one-to-one correspondence between the morphology of the skeletal ultra-structure and the morphology of the calicoblastic cell-layer. Importantly, the newly formed COC, which become increasingly overgrown by fibrous aragonite, protrude like columns from the skeleton (Figures 1b–1d) and have clearly defined morphological counterparts in the form of depressions in the cell-layer (Figure S2). The COC are formed by calicoblastic cells at the bottom of these depressions in the cell layer.

[9] Presently, there is no evidence for the existence of different cell types in the calicoblastic layer. However, histological observations of *Porites* sp. and *Diploria* sp. (both massive zooxanthellate corals) have shown that the calicoblast cells, which are generally flattened and interdigitated, display different and essentially cuboidal shapes with filopodial extensions into the skeleton in regions of enhanced calcification [Domart-Coulon et al., 2006]. Furthermore, observations of *Stylophora pistillata* show that cell layers over the COC have different histological organization compared with cell layers over the fibrous skeleton. Over the COC, the cell layers are characterized by an absence of zooxanthellae and endodermal cells (E. Tambutté et al., Tissue-skeleton interactions in the concept of coral biomineralization, submitted to *Coral Reefs*, 2006). The analytical techniques traditionally applied to the study of the histology of the calicoblastic cell-layer (e.g., optical microscopy and transmission electron microscopy) are unlikely to be capable of detecting differences in cellular function. Molecular techniques, such as protein profiling (proteomics) and micro-analytical techniques such as confocal microscopy and NanoSIMS [Meibom et al., 2004; Peteranderl and Lechene, 2004], which allow imaging of labeled compounds at sub-cellular length scales, might provide key information about specific differences in cellular function or mechanisms. We predict that differences in cellular function must exist within the calicoblastic cell layer.

[10] Our observations necessitate modifications to existing geochemical models that currently attempt to explain ‘vital’ effects in coral skeletal composition by invoking only a single ‘reservoir’. This reservoir is classically envisioned to exist between the calicoblastic cell-layer and the skeleton, and is often referred to as the ‘extra-cellular calcifying fluid’. In existing geochemical models, precipitation of the entire skeleton is assumed to take place from this reservoir [Adkins et al., 2003; Cohen and McConnaughey, 2003; Goreau, 1977; McConnaughey, 2003; Swart and Leder, 1996]. Such models are not supported by our observations. Models, in which COC are ascribed solely to nighttime precipitation in near-thermodynamic equilibrium with ambient seawater [Cohen and McConnaughey, 2003] are also not consistent with our observations. COC do not seem to exhibit trace element or isotopic equilibrium with seawater. Furthermore, the observed compositional and isotopic differences between COC and fibers are not explained by kinetic effects alone. Many of the processes and kinetic fractionations invoked in current geochemical models [Adkins et al., 2003; Cohen and McConnaughey, 2003; Goreau, 1977; McConnaughey, 2003; Rollion-Bard et al., 2003b; Swart and Leder, 1996] are undoubtedly relevant

and important. However, future work on coral skeletal 'vital' effects should not be restricted to skeletal chemistry or isotopic composition. Skeletal ultra-structure, the organization of the calicoblastic cell-layer and the corresponding cellular processes are key parameters. Knowledge of cellular pathways and molecular mechanisms involved in transport and production of the skeletal constituents, including organic molecules, is sparse [Allemand *et al.*, 2004]. However, it is increasingly clear that coral skeletal formation is a highly dynamical process that is under strong biological control. Thus, only with a strong focus on the biology of corals can we understand better the 'geochemistry' of their skeletons. This will allow more precise paleo-environmental records to be extracted from these beautiful, living archives.

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