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Review

Coral biomineralization: A focus on intra-skeletal organic matrix and calcification

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ABSTRACT

In the recent years several papers and some reviews have dealt with characterization, localization and influence on the precipitation of calcium carbonate, of the organic matrix from scleractinian corals. In fact, it has been well established that coral calcification is a biological controlled process orchestrated in space and time by the organism also trough the secretion of organic matrix molecules because it has been well established that coral calcification is a biological controlled process, and thus is orchestrated in space and time by the organism also through the secretion of organic matrix molecules. In this review is presented a scientific path on the biomineralization of corals having as focusing point the intra-skeletal organic matrix, the molecules that are associated with mineral (aragonite). The review starts with a an overview on coral tissue, skeleton and tissue skeleton interface, describes the intra-skeletal organic matrix putting attention mainly on the proteins associated to aragonite and finally describes the *in vivo* and *in vitro* calcium carbonate precipitation experiments carried out aimed to evaluate the role of the organic matrix. The last paragraph reports studies on the role of the organic matrix in controlling calcification when corals are subject ocean acidification effects. The readers are expected to find a source of inspiration for new studies on the biomineralization of corals that are organic matrix addressed and merge diverse scientific disciplines.

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1. Overview

Biomineralization is the science that studies the formation, structure and properties of minerals deposited by organisms, usually referred as biominerals [1–3].

Corals play an important role among mineralizing organisms (Fig. 1). They lead to a production of calcium carbonate ($CaCO_3$) of about 10^{12} kg year^{-1} [4]. Beside this, coral calcification is a globally important biological and geochemical process as it allows the tiny polyps of coral colonies to build the most important bioconstruction of the world, coral reefs [5]. Coral skeletons not only serve as the 3D-framework for reef building, but may also play indirect physiological roles such as light scattering [6]. In addition, coral skeletons are used for paleoclimate reconstruction [7] and as bone implants [8].

Hard corals, the Scleractinian order, which accrete exoskeletons are distinguished from soft corals (*Octocorallia* and *Antipatheria*). Scleractinian corals can host symbiotic algae, or zooxanthellae, in

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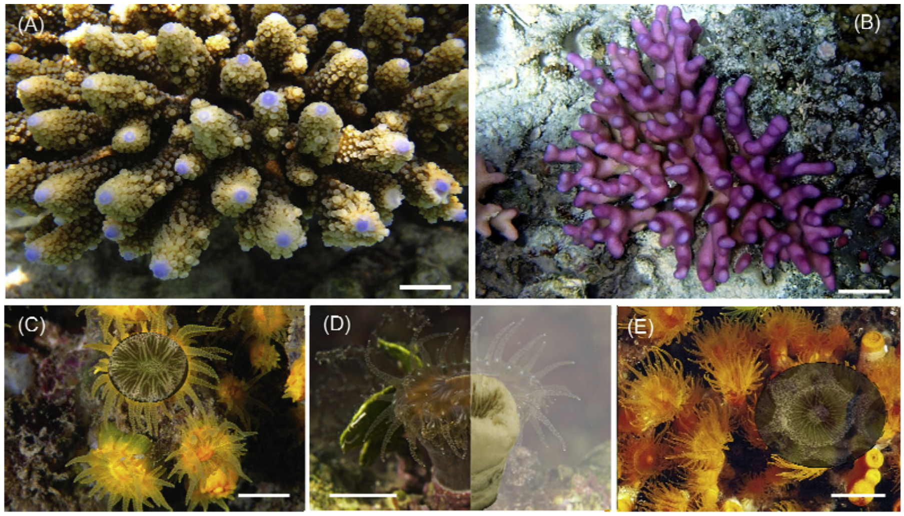

Fig. 1. *In situ* camera pictures of the scleractinian coral. *A. digitifera* (A) and *S. pistillata* (B) are among the most common studied species from the reef. *L. pruvoti* (C), *B. europaea* (D) and *C. caespitosa* (E) are Mediterranean species for which the role of OM in calcification was recently investigated. A shadowed image of the skeleton is inserted in the pictures (C)–(E). Scale bar: 1 cm.

the polyp tissue, or not have zooxanthellae. Coral can be also colonial, the reef building, or solitary.

The reef building corals are hermatypic on the opposite of the ahermatypic ones. In several reviews details on the structure of scleractinian corals are available [9–15].

The study of coral calcification started more than 150 years ago [16]. Nevertheless, the knowledge still remains patchy and multiple studies have involved only few species. Skeleton formation was initially considered as a mineralogic process where the basic element of the skeleton – that is, the fiber – was described as a single orthorhombic crystal of aragonite formed without biological involvement [17]. Proposed biomineralization mechanisms in scleractinian corals range from biologically induced, that is, precipitation regulated primarily by physico-chemical and environmental parameters [18–22], over combinations of both abiotic and biotic processes [23–31], to strict biological control highly regulated with an organic matrix component [*e.g.* 32–47]. This debate, which is not restricted only to coral biomineralization [48,49], is partly the result of difficulties in defining clear criteria (morphological, structural, crystallographic and chemical) for addressing biomineralization pathways.

2. Tissue and skeleton

The scleractinian corals are organisms composed of polyps covering the skeleton. In colonial corals the polyps are linked together by a tissue, the coenosarc that is missing in solitary corals. The exoskeleton (extracellular) is located at the base of the coral tissues. In this section a brief, and not exhaustive, introduction to tissue, skeleton and tissue skeleton interface features is presented.

The oral tissues are in contact with seawater, whereas the aboral tissues are facing the skeleton and cover it almost completely. Tissues consist of two epithelial layers, an ectoderm and an endoderm, separated by a connective layer called mesoglea [50,51]. The aboral ectoderm in contact with the skeleton, the calicoblastic ectoderm, has a topography that exactly complements the growth surface of the skeleton [32,52]. Calicoblastic cells are long (10–100 μm), highly interdigitated, and overlap each other, their form is species specific and changes during the diverse stages of the skeletongenesis. The calicoblast cell secretes the organic matrix (OM) and control the flux of ions leading to the formation of the aragonitic skeleton [*e.g.* 37,39,51,53].

Regarding the coral skeletal microarchitecture the main building units are the Early Mineralization Centers (EMCs) and the fibrous aragonite crystals that radiate from around these centers (Fig. 2). These basic building blocks are structurally similar in hermatypic (reef building) and ahermatypic corals [54–58]. The spatial arrangement of the centers and the incremental zonation of the fibers vary among taxa [59] (Fig. 2). The EMCs have a high organic content [60] in which $CaCO_3$ grains are embedded and the crystallinity of the $CaCO_3$ within the EMZ is lower than in the aragonitic fibers [61]. The fibrous aragonite crystals comprise the bulk of the coral composition and, in contrast to the EMCs, have a low organic concentration of about 1% by weight [62] while the entire skeleton contains at least 3% by weight organic material [63]. Also the distribution of trace and minor elements is not uniform throughout the skeleton [64]. The EMCs contain higher concentrations of magnesium [40], strontium, and barium than the fibers [41]. Heterogeneity in strontium concentration occurs both within and between the EMCs and the fibers [54,65–67]. The distribution of trace and minor elements and stable isotopes [42–45,68,69], has been used to evaluate the degree of biological control and contributed to the interpretation of climate proxies [*e.g.* 70]. This information has strongly contributed to the (sometimes contradictory) debate on the degree of biological control over the calcification process and the influence of environmental parameters.

The skeletal microarchitecture of EMCs, and mainly of the fibers, ends up in a diversity of skeletal morphologies that is species specific. This has been historically used for classification of scleractinian corals, [71–73] and recently it has been generally confirmed by modern molecular methods [54,74]. Thus, skeletal morphology is a characteristic of species and is under a genetic control and needs to be dictated by the organism during the skeletongenesis. However, despite this biological control, coral morphology can vary with environmental parameters [*e.g.* 75].

The appearance of coral skeleton morphology is due to the mineral growth process, for which diverse mechanisms, associated to the extent of biological control over calcification, have been proposed [11,14 and references therein]. A well accepted mechanism of growth is that *via* a two-step matrix-mediated process [38]. Such growth process is based on cyclic secretion of mineralizing compounds by the tissue basal ectoderm. These biochemical components are repeatedly produced resulting in a stepping growth mode of fibers and a layered global organization of coral