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Coral biomineralization: From the gene to the environment

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ABSTRACT

In this review we discuss the present knowledge on the biological and environmental control of biomineralization (calcification) in hermatypic corals. We describe first the anatomy of the coral, discussing the soft tissues followed by the hard tissues at both the macro- and micro-scales. We then discuss the tissue-skeletal interface, the extracellular calcifying medium and the processes responsible for skeletal formation. Concerning the biological control of coral calcification, we discuss different models from the literature with respect to the major biomineralization steps and the current state of knowledge on the organic matrix and ion supply for calcification. Finally we discuss the effect of environmental factors such as nutrients, light, temperature and pCO_2 on coral calcification as well as the role of coral calcification in the global carbon cycle.

Contents

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1. Introduction

The science of Biomineralization is the study of the formation, structure and properties of inorganic solids deposited in biological systems (Mann, 2001). The result of coral biomineralization is the formation of the coral skeleton, a composite structure, called biomineral, made of an organic fraction embedded in calcium carbonate ($CaCO_3$) in the form of aragonite. As the coral skeleton is made of calcium, the term calcification may be alternatively used to describe the process of coral skeletogenesis.

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, which cover an area of about 284300 km^2 (Spalding et al., 2001). Coral skeletons not only serve as the 3D-framework for reef building but may also play indirect physiological roles such as light scattering to enhance light absorption by symbionts (Enriquez et al., 2005). In addition, coral skeletons are used for paleoclimate reconstruction and as bone implants. Although the study of coral calcification started with the study of coral biology more than 150 years ago (Dana, 1846), our knowledge remains patchy, with only a handful of species used in multiple studies. Fig. 1A-F show the cumulative number of publications published on major topics in the field of coral biomineralization (for details see supplemental data). Our knowledge in the different areas: histology, ion transport, organic matrix biochemistry, genomics/proteomics has been acquired on different coral families (see Fig. 2) and different coral species (see supplemental data), impairing an integrated understanding and, in these 4 domains, very few species have been the subject of more than 5 papers (*Acropora cervicornis*, *Galaxea fascicularis*, *Pocillopora damicornis*, *Favia stelligera*, *Stylophora pistillata*). The species that appears the most studied in the different areas is *S. pistillata*. Most of our knowledge was acquired during the last 30 years, due both to the development of techniques for studying structural and molecular organization of biominerals (atomic force microscopy, genomics, proteomics…) and an increased number of teams (Fig. 1F). Nevertheless, a lot of questions remain unanswered, some specific to coral calcification such as the importance of biological control on skeleton formation (see below, Section 4), some more general to the field of biomineralization such as skeleton morphogenesis. However, this lack of knowledge on coral calcification is not so surprising since even in bone biology, basic questions such as the nature of the bone mineralization process, active *vs* passive, remain debated (Schinke and Amling, 2007).

This review is focused on reef-building corals, *i.e.* shallow-water, hermatypic corals (Schuhmacher and Zibrowius, 1985). Broadly speaking coral calcification involves at least two ions that react following reaction (1) to form calcium carbonate.

$$Ca^{2+} + CO_3^{2-} \Leftrightarrow CaCO_3 \quad (1)$$

The favorability of the formation of calcium carbonate from solution is commonly expressed as the 'saturation state' (or Ω), which is defined as follows:

$$\Omega = [Ca^{2+}] * [CO_3^{2-}]/K_{sp}$$

where K_{sp} is the solubility of the calcium carbonate phase precipitated — when discussing corals, this is usually the solubility of aragonite. Saturation states in excess of one indicate that precipitation is thermodynamically favored, values less than one indicate dissolution is favored. Calcification may directly precipitate carbonate from seawater (reaction 1), however, carbonate ions may be formed from bicarbonate ions or from CO_2 hydration, thus the net reaction proceeds *via* reactions 2 and 3. In both cases, reactions involve a third ion, H^+, that needs to be removed from the site of calcification.

$$Ca^{2+} + HCO_3^- \Leftrightarrow CaCO_3 + H^+ \quad (2)$$

$$CO_2 + H_2O + Ca^{2+} \Leftrightarrow CaCO_3 + 2H^+ \quad (3)$$

After a presentation of both soft and hard tissues involved in coral calcification and their interface, we will discuss the present knowledge on the biological and environmental control of calcification as well as the role of coral calcification in the global carbon cycle. For more details in specific areas, the reader is referred to previous reviews (Allemand et al., 2004, 2011; Cohen and McConnaughey, 2003; Gattuso et al., 1999a).

2. Soft tissues: epithelial layers and calicoblastic cells

2.1. Epithelial layers

This section will synthesize the terms used to describe coral anatomy and histology with a diagrammatic representation (Figs. 3 and 4) to aid comprehension of the vocabulary used in the following sections. Briefly, the anatomical unit of a coral is the polyp which consists of a sac-shaped structure with a central mouth surrounded by a ring of tentacles and a column as the main body. Except for a few corals such as fungiids which are solitary and only consist of one large polyp, all reef-building corals are colonial organisms. Colonial corals are constituted of polyps, linked together by a tissue named the coenosarc. While extracellular, the skeleton is not directly exposed to the surrounding seawater, but is covered by the polyps and coenosarc. The tissues forming the polyps as well as the coenosarc consist of two epithelial layers named epidermis and gastrodermis, referring to the adult epithelia, or ectoderm and endoderm, referring to their embryological origins (Fautin and Mariscal, 1991; Galloway et al., 2006). However in the literature, ectoderm and endoderm are classically used for coral adult epithelia and these terms will be used in this paper. The two epithelial layers are separated by a connective layer of extracellular matrix called mesoglea. The mesoglea is highly hydrated (Bouillon and Coppois, 1977) and in corals as in other anthozoans, it is primarily composed of collagen fibers (Young, 1973). From studies on other Cnidarians it can be inferred that the mesoglea also contains non-collagenous elastic fibers such as described in jellyfish (Shaposhnikova et al., 2005). The tissue facing seawater is the oral tissue also referred to as the surface body wall (Galloway et al., 2006) whereas the tissue adjacent to the skeleton is the aboral tissue also referred to as the basal body wall (Galloway et al., 2006). The oral tissue is usually thicker than the aboral tissue (Johnston, 1980; Tambutté et al., 2007a). Resident intracellular photosynthetic dinoflagellates (genus *Symbiodinium*) commonly called zooxanthellae are only found in the endoderms, and mostly in the oral endoderm. The aboral ectoderm in contact with the skeleton is often referred as the skeletogenic tissue, the calicoblastic ectoderm, or simply the calicodermis as recently proposed by Galloway et al. (2006).