Block-by-block and layer-by-layer growth modes in coral skeletons

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ABSTRACT

Understanding the dynamics of biomineral growth is a challenging goal of biomineralogy that can be achieved in part by deciphering biomineral structures and chemistries. The morphology, structure, and chemistry of six skeletons of Corallium and Paracorallium species (C. rubrum, C. elatius, C. johnsoni, C. niobe, P. japonicum, and P. thrinax) from the Mediterranean, the Atlantic, and the Pacific oceans have been studied by X-ray micro-computed tomography, polarized light microscope, scanning electron microscope, and electron microprobe. All species have two types of biomineral structures: an inner skeleton and sclerites that are small grains of Mg-calcite found in the living tissues surrounding the skeleton. All skeletons display a central core surrounded by an annular domain. In the species studied by electron microprobe (C. rubrum, C. elatius, and P. japonicum), the central core and the annular domains display different chemical compositions with the core richer in magnesium and poorer in sulfur than the annular domain. In terms of structure, special emphasis has been put on central cores for which little data are available. The central cores are made of sclerites and sclerite aggregates within a cement consisting of fine layers of Mg-calcite. On the other hand, the annular parts are made of fine concentric layers of calcite crystallites with only rare sclerites. These contrasting features imply two different growth modes: (1) a “block and cement” mode taking place at the apex of a branch and associated with a fast axial growth rate (~2 mm/yr); and (2) a layer-by-layer mode occurring below the apex and associated with a slow radial growth (~0.2 mm/yr). The change from a growth mode to another is anatomically controlled by the presence of a continuous network of gastrodermal canals around the sub-apical skeleton, preventing to a large extent the aggregation of sclerites. It is generally accepted that the Corallidi family exhibits different types of skeletogenesis. In contrast with this idea, we observe that all studied Corallium species display remarkable similarities in terms of skeletogenesis and a unifying growth model for the Corallium genus is proposed. Similarities and differences with previous models are discussed. The present study shows that the morphological criterion initially used to establish the genus Paracoral in the Corallidae family is inadequate.

Keywords: Corallium, rubrum, japonicum, johnsoni, skeletogenesis, block and cement, layer-by-layer, biomineral growth

INTRODUCTION

Understanding the growth modes of biomineral structures is a major and challenging goal of biomineralogy. This task is complicated by the fact that biominerals display modular organizations at different spatial scales. The presence of hierarchical levels raises important questions: Can a modular organization result from a modular construction? Is the hierarchy of structures in biominerals the result of a single or several growth mechanisms? Are these mechanisms different at nano-, micro-, and macro-scales? We address these questions through the example of the Mediterranean red coral (Corallium rubrum), and other Corallium (C. elatius, C. johnsoni, C. niobe) and Paracoral (P. japonicum, P. thrinax).

In Corallium rubrum, as in all Corallium and Paracoral species, two major biomineral structures coexist: the axial skeleton and the sclerites (Fig. 1). The axial skeleton displays a complex, often planar, arrangement of branches (Fig. 1a). The internal structure of the skeleton is composed of a central cross-shaped region (Grillo et al. 1993; Lacaze-Duthiers, 1864; Marschal et al. 2004), hereafter referred to as the central core. The central core is surrounded by an annular domain composed of crenulated concentric growth rings with tortuous interfaces reminiscent of the external surface of the skeleton. Indeed, the crenulated skeleton surface is covered with uniformly distributed microprotuberances (Grillo et al. 1993; Vielzeuf et al. 2008; Weinberg 1976). Internally, the concentric layers of the annular domain are made of submicrometer crystalline units (~80 nm). Sclerites, the second biomineral structure of C. rubrum, are small (up to 90 μm) complex-shaped grains of Mg-rich calcite (~13 mol% MgCO3) found in the living tissues surrounding the axial skeleton (Fig. 1c) (Grillo et al. 1993; Lacaze-Duthiers, 1864; Weinberg 1976). Sclerites are made of thin layers of Mg-calcite crystallites of sub-micrometer size (~80 nm) (Floquet and Vielzeuf 2011, 2012). The presence of two distinct biomineral structures in Corallium rubrum (i.e., axial skeleton and sclerites)