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Review

Coccolithophore biomineralization: New questions, new answers

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ABSTRACT

Coccolithophores are unicellular phytoplankton that are characterized by the presence intricately formed calcite scales (coccoliths) on their surfaces. In most cases coccolith formation is an entirely intracellular process – crystal growth is confined within a Golgi-derived vesicle. A wide range of coccolith morphologies can be found amongst the different coccolithophore groups. This review discusses the cellular factors that regulate coccolith production, from the roles of organic components, endomembrane organization and cytoskeleton to the mechanisms of delivery of substrates to the calcifying compartment. New findings are also providing important information on how the delivery of substrates to the calcification site is co-ordinated with the removal of H^+ that are a bi-product of the calcification reaction. While there appear to be a number of species-specific features of the structural and biochemical components underlying coccolith formation, the fluxes of Ca^{2+} and a HCO_3^- required to support coccolith formation appear to involve spatially organized recruitment of conserved transport processes.

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1. Introduction

Coccolithophores are single celled marine photosynthetic protists belonging to the Haptophyte division of the chromalveolate eukaryotes. They are significant components of the marine phytoplankton with certain species, such as the cosmopolitan *Emiliania huxleyi* able to form massive blooms in temperate and sub-polar waters. Because of this their ecology, physiology and palaeontology have been well-studied. Coccolithophores also present a paradigm for the study of calcification mechanisms. The ease with which certain species can be cultured and the relative tractability of a unicellular calcification system that produces intricate calcium carbonate structures (coccoliths) allows questions relating to the biological control of crystal formation and morphology to be addressed.

Coccolithophore calcification has received considerable attention in recent years with many studies directed to the potential impacts of ocean acidification – the decrease in ocean pH associated with the dissolution of anthopogenically-derived CO_2 into the surface ocean. While these studies have generally not directly addressed questions relating to better mechanistic understanding of coccolithophore calcification, they have revealed a number of features of coccolithophore biology (e.g. strain variability, plasticity of calcification response, genetic adaptation, species differences) that are pertinent to the calcification mechanism [e.g. 1–3]. Nevertheless, important questions remain to be answered in order to fully elucidate the cellular drivers and regulators of calcification that are essential for understanding the roles of coccolithophores

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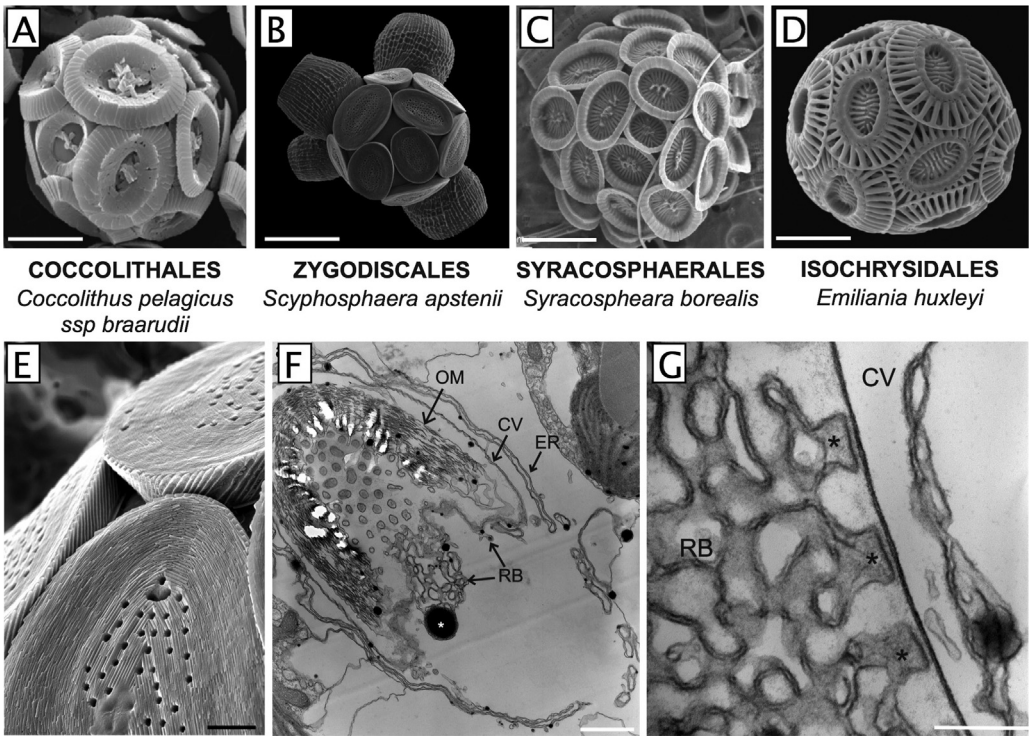

Fig. 1. (A–D) SEM images of examples of the four groups of calcihaptophytes. (E) Detail of placoliths from *S. apstenii* (B). (F) TEM section through a coccolith vesicle (CV) of *S. apsenii* showing associated endoplasmic reticulum (ER) layers surrounding the vesicle, the CV-associated reticular body (RB) and inter- and intracrystalline organic matrix (OM). (G) Ordered association of reticular body projections (*) with a base plate scale of *S. apstenii* reflecting the pattern of distribution of pores in the central region of the mature coccolith (see text for details). Scale bar 10 μm in (A, B); 3 μm in (C, D), 1 μm in (E, F), 0.25 μm in (G) (E–F reproduced with permission from [9]).

in the ecology of the oceans, predicting responses to changing ocean chemistry and realising the potential of coccolithophores for biotechnological applications.

2. The essentials of coccolithophore calcification

Well-preserved coccoliths can be found in sedimentary records 220 Ma and molecular clock studies estimate that the first calcifying haptophytes (calcihaptophytes) originated ~330 Ma [4]. This suggests that coccolithophores evolved under ocean carbonate chemistry conditions that were significantly different from those of the present day. Most studies of coccolithophore calcification mechanisms have focussed on the "model" species *E. huxleyi* which is easily isolated and cultured, with a large body of physiological data derived from culture experiments. These advantages, together with a fully sequenced genome [5] and an array of additional genomic resources have led to significant advances in understanding the biology and physiology of coccolithophores.The calcite coccoliths of diploid *E. huxleyi* cells are exquisitely sculpted complex multi-crystalline plates that are formed via crystal growth, uniquely, in an intracellular compartment, the coccolith vesicle (CV). Mature coccoliths are secreted to the cell surface where they form an outer coat (coccosphere) (Fig. 1). In many species (with the exception of *E. huxleyi*) the haploid phase produces simpler holococcoliths, formed from rhomohedral crystalline units most likely, in an extracellular space [6]. Nevertheless, the diploid heterococcolith producing life cycle stage represents the calcifying stage that is predominantly found in natural populations and dominates production of particulate inorganic carbon in the oceans.

3. The determinants of coccolith morphology

The wide range of coccolith shapes and sizes produced by different species suggests a range of functional roles as well as species-specific cellular factors that determine coccolith morphology. In order to understand the regulation of coccolith morphology it is necessary to understand the cell structures and physiology that are brought into play during coccolith development. Ultrastructural studies of *E. huxleyi* show the CV to be derived from Golgi cisternae [7]. Coccolith growth proceeds as the CV matures and completed coccoliths are secreted to the cell surface in a single exocytotic event [8]. Coccolith growth begins with the nucleation of calcite crystals with alternating orientations (V and R units) in a circular arrangement known as the protococcolith ring [7]. The coccolith matures into a distal (upper) shield and outer tube formed of V-units. The lower proximal shield, inner tube and central area elements are derived from R-units. The two unit types alternate with each other in a ring on the proximal face of the coccolith and this is interpreted to be the proto-coccolith ring locus, i.e., the location where nucleation occurred. It has been proposed that growth of the protococcolith ring initiates from an organic baseplate of alternating structure that establishes the alternating crystal orientations. In several species this baseplate has been visualized using transmission electron microscopy (TEM) [e.g. 8,9] although its organic composition remains uncharacterized. So far, the only protein known to be intimately associated with coccoliths is the so-called GPA (glutamine, proline, alanine-rich protein) that was initially isolated from a coccolith-associated polysaccharide from *E. huxleyi* [10]. Subsequently Schroeder et al. [11] identified specific sequences of a non-coding region of the *GPA* gene that correlated with specific coccolith strain morphotypes (A and B) characterized by subtle variations in degree of calcification and coccolith element dimensions. However, the GPA protein does not appear to be directly involved in determining coccolith morphology because transcriptomics studies have shown that the expression of GPA is inversely correlated with the rate of calcification [12]. For example, GPA expression was shown to be higher in non-calcifying haploid cells of *E. huxleyi* [12] and in diploid cells grown under