



Biogenic calcite granules—Are brachiopods different?

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ABSTRACT

Brachiopods are still one of the least studied groups of organisms in terms of biomineralization despite recent studies indicating the presence of highly complex biomineral structures, particularly in taxa with calcitic shells. Here, we analyze the nanostructure of calcite biominerals, fibers and semi-nacre tablets, in brachiopod shells by high-resolution scanning electron microscopy (SEM) and atomic force microscopy (AFM). We demonstrate that basic mechanisms of carbonate biomineralization are not uniform within the phylum, with semi-nacre tablets composed of spherical aggregates with sub-rounded granules and fibers composed of large, triangular or rod-like particles composed of small sub-rounded granules (40–60 nm). Additionally, proteinaceous envelopes surrounding calcite fibers have been shown for the first time to have a dual function: providing a micro-environment in which granules are produced and acting as the organic template for particle orientation as fiber components. In summary, these new findings in brachiopod shells reveal a complex and distinctive style of biomineralization among carbonate-producing organisms.

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1. Introduction

There are several aspects of biologically-controlled biominerals that are common to many phyla. These characteristics include the control of crystallographic orientation (e.g., [Checa et al., 2006](#); [Moreaux et al., 2010](#); [Cuif et al., 2011](#)) and the presence of component granules. In phyla such as Mollusca, Cnidaria, and Echinodermata, carbonate biomineral structures are usually composed of small (35–100 nm), sub-rounded granules (e.g., [Dauphin, 2008](#)), possibly indicating a unifying basic process of carbonate biomineral construction (see review in [Cuif et al., 2011](#)). The Phylum Brachiopoda can be included in these common trends since brachiopods exert exquisite control on crystallographic orientation in shell formation (e.g., [Cusack et al., 2004, 2010](#); [Griesshaber et al., 2007, 2010](#); [Pérez-Huerta and Cusack, 2008](#); [Pérez-Huerta et al., 2008](#); [Schmahl et al., 2004, 2010](#)) and their shells are composed, ultimately, of ‘granules’ ([Cusack et al., 2008a, 2010](#)). In spite of these observations, brachiopods are still one of the least studied groups of organisms in terms of biomineralization, despite including taxa with calcium phosphate and calcite shells ([Williams et al., 1996](#)) and their long geological history (e.g., [Cusack et al., 2008a](#)).

Recent studies of calcitic brachiopods of the Subphyla Craniiformea and Rhynchonelliformea have revealed new information, besides the crystallographic patterns and nanostructure of shells in some species, about carbonate biomineralization within this group, such as the possible presence of amorphous calcium carbonate (ACC) ([Griesshaber et al., 2009](#)) and the mechanical properties of calcite (e.g., [Pérez-Huerta et al., 2007](#); [Griesshaber et al., 2007](#); [Schmahl et al., 2008](#)). Other studies have also demonstrated the complexity of shell carbonate biomineralization (e.g., [Pérez-Huerta et al., 2009](#); [Goetz et al., 2011](#)). However, one of the most surprising findings has been the presence of large (>500 nm), triangular ‘granules’ as basic building units of calcite fibers in the rhynchonelliform species *Terebratulina retusa* ([Cusack et al., 2008a](#)). Presently, it is unknown whether these ‘granules’ are unique to this species or widespread among calcitic brachiopods.

The aim of this study is to characterize the nanostructure of calcite biominerals in brachiopod shells in order to advance our understanding of biomineralization within this group, as well as to decipher basic mechanisms of carbonate biomineral formation. In order to obtain this information, three characteristic species of rhynchonelliform brachiopods of the orders Terebratulida and Rhynchonellida with low-magnesium (~0.3–1.5 wt% Mg; [England et al., 2007](#)) calcite shells and one species of a craniid brachiopod with high-magnesium (~1–4 wt% Mg; [England et al., 2007](#)) calcite shells are analyzed. Calcite fibers and semi-nacre tablets have been studied with a combination of high-resolution scanning electron microscopy (SEM) and atomic force microscopy (AFM) for an

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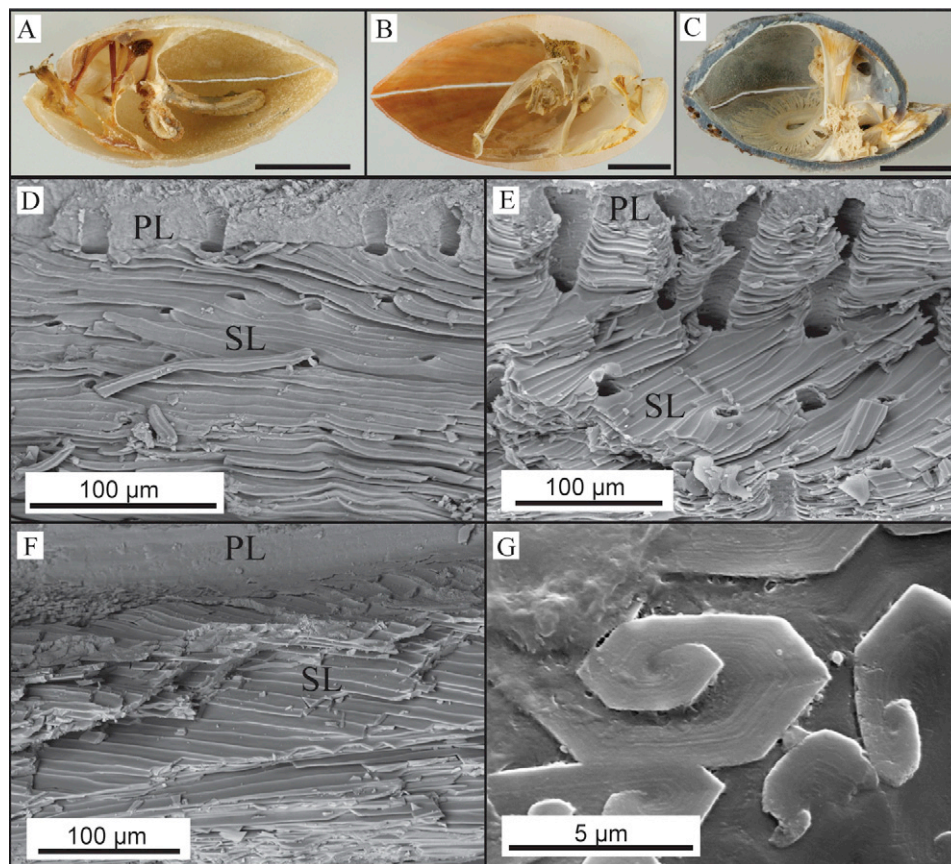


Fig. 1. Rhynchonelliform brachiopod images and shell microstructures of studied species. (A–C) Images of longitudinal sections along the plane of symmetry of *Terebratulina retusa* (A), *Laqueus rubellus* (B), and *Notosaria nigricans* (C) [scale bars = 5 cm; dorsal valve on top]. (D–F) Backscatter electron images (BSE) of the shell microstructure of rhynchonelliform brachiopods showing the primary layer (PL) and secondary layer (SL) with calcite fibers perforated by endopunctae in *T. retusa* (D) and *L. rubellus* (E) and imperforated in *N. nigricans* (F) [scale bars = 100 μm]. (G) Scanning electron microscopy (SEM) image of the semi-nacre tablets within the secondary layer of *Novocrania anomala* [scale bar = 5 μm].

Figure modified and adapted from England et al. (2007).

evaluation with previous findings and a further comparison with other carbonate biominerals, in particular calcite prisms and aragonite nacre.

2. Materials and methods

The Phylum Brachiopoda is divided into three subphyla: Linguliformea, Craniiformea, and Rhynchonelliformea, partially based on shell mineralogy (Williams et al., 1996; Cusack et al., 2010). Within the subphylum Rhynchonelliformea, the orders Terebratulida and Rhynchonellida comprise most of the living species of brachiopods, while taxa in the subphylum Craniiformea are less abundant in modern marine habitats. Two species of the Order Terebratulida, *T. retusa* and *Laqueus rubellus*, one species of the Order Rhynchonellida, *Notosaria nigricans*, and one craniiformean, *Novocrania anomala*, were chosen for this study. Living specimens of *T. retusa* and *N. anomala* were collected from the Firth of Lorn, Oban, NW Scotland, samples of *L. rubellus* from Otsuchi Bay, Japan, and of *N. nigricans* from the Otago Shelf, New Zealand (see Parkinson et al., 2005 for details).

An articulated specimen of each rhynchonelliform species was sectioned along the plane of symmetry of the valves for photography and microscopy (Fig. 1A–C). For imaging of the general shell structure by scanning electron microscopy (SEM), dorsal valves were fractured and samples were gold coated and viewed in Quanta FEI 200F (University of Glasgow) and JEOL 7000 (University of Alabama) field-emission scanning electron microscopes (Fig. 1).

High-resolution SEM imaging, using the same JEOL 7000, was carried out in central regions of the ventral valve of each species of the rhynchonelliform brachiopods, and in the anterior region of a dorsal valve of *N. anomala*. Specifics of sample preparation, including etching and coating and SEM conditions, are explained in the captions of the corresponding figures.

Atomic force microscopy (AFM) (UMR IDES Université Paris Sud) was applied to etched surfaces of ventral valves, in similar regions to those analyzed by SEM, and non-etched surfaces of dorsal valves, with specific preparations explained in the captions of the corresponding figures, using a Dimension 3100 (Veeco-Bruker) AFM in tapping mode for height, phase and amplitude, with a resolution of a few nanometers. No coating of the surface was required. Height and amplitude modes depict the topography of the surface, with amplitude images providing information on the 3D structure of the particles and granules. Phase imaging is a powerful extension that provides nanoscale information about surface structure to detect variations in chemical composition, friction, and other physical properties that contribute to the viscoelastic properties of the surface (e.g., Aoki et al., 2007).

3. Results

3.1. High-resolution scanning electron microscopy (SEM)

Rhynchonelliform brachiopods usually have a shell composed, in both dorsal and ventral valves, of an outer (primary) layer that

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