



Testing the biomineral archive: microstructural patterns of modern brachiopod shells

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Biominerals, such as marine macroinvertebrate shells, represent valuable archives for the reconstruction of recent and past environmental conditions. Brachiopod shells are among the most reliable high-resolution biomineral archives of climate and environmental change, as they resist diagenetic alteration due to their low-Mg calcite composition, are abundant and widespread in the fossil record, and precipitate shell material close to isotopic equilibrium with ambient seawater, with limited vital effects. Studying modern brachiopod shells is therefore key to assessing their potential as reliable archives to reconstruct past dynamics of species and ecosystem changes at different scales from decades to millions of years.

Previous research has focused extensively on the micro- and nanostructure of modern brachiopod shells, yet our understanding of their mesoscale structural patterns remains limited. Moreover, few studies have investigated the relationship between shell microstructure and geochemical variation, and existing results are often contradictory; in this context, mesoscale patterns may provide a means to assess potential microstructural control on geochemical signatures. This study examines the organization, arrangement, and thickness of different shell fabrics (i.e., primary dendritic, secondary fibrous, and tertiary columnar) to identify systematic patterns of variation at interspecific, intraspecific, and intra-shell levels and how these relate to geochemical variation. A microstructural analysis of several two- and three-layered modern brachiopod shells was performed using a scanning electron microscope (SEM). Specimens belong to eight terebratulid and rhynchonellid species from different settings and water depths.

Results reveal differences between the three-layered species: *G. vitreus* exhibit a more regular and well-organized microstructure, whereas *L. neozelanica* has frequent intercalations of fibrous and columnar fabrics. The two species differ in their posterior shell region, where *G. vitreus* is dominated by the tertiary layer, whereas *L. neozelanica* is composed almost entirely of fibers. In both species, the tertiary layer is thickest in the central portion of the shell and progressively thins toward the anterior margin, where it eventually disappears. These results suggest that microstructure does not exert a primary control on geochemistry, as similar isotopic patterns reported by Crippa et al. (2025) are observed in both species despite their microstructural differences. Two-layered species exhibit interspecific variation while maintaining the typical shell architecture composed of an external thin primary layer and an inner fibrous fabric. Although *L. uva* is typically classified as a two-layered species, small prism-like elements resembling tertiary

columnar structures were observed intercalated with fibers, particularly toward the interior of the shell. Layers of calcitic pads were observed at the anterior margin of *L. uva*, forming when a rapid mantle retraction temporarily halted secretion, after which carbonate deposition resumed at new sites.

Future research should integrate these mesoscale structural patterns of modern brachiopod shells with high-resolution geochemical analyses to advance our understanding of brachiopod biomineralization and further assess their reliability as environmental proxy archives.

References:

Crippa, G. et al. (2025). Brachiopods as archives of intrannual, annual, and interannual environmental variations. *Limnology and Oceanography Letters*, 10(3), 390-402.