



Microstructural patterns of modern terebratulid brachiopod shells: *Gryphus vitreus* and *Liothyrella neozelanica*

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Introduction

Biominerals, such as those forming marine macroinvertebrate shells, serve as archives for reconstructing environmental conditions in the recent and distant past. 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 in near equilibrium with ambient seawater (Ye et al., 2018; Simonet Roda et al., 2022).

Previous research has focused extensively on the micro- and nanostructure of recent brachiopod shells (e.g., Ye et al., 2018; Simonet Roda et al., 2022; Crippa et al., 2025), yet a gap remains in our understanding of mesoscale structural patterns. Moreover, the observation of Crippa et al. (2025) of an intra-shell geochemical trend highlights the need to further explore the relationship between microstructure and geochemistry.

This study investigates the organization, arrangement, and thickness of different shell layers (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.

Materials and Methods

The microstructural analysis was performed on three-layered shells of *Liothyrella neozelanica* (New Zealand) and *Gryphus vitreus* (Mediterranean Sea) (Tab. 1), using a JSM-IT500 SEM (JEOL Ltd.) at the University of Milan.

Shells were sectioned along the main growth axis and prepared following the procedure of Crippa et al. (2016). SEM images were merged using Adobe Photoshop and the relative thicknesses of the secondary fibrous and tertiary columnar layers in both dorsal and ventral valves were measured (Tab. 2). Three shell regions (i.e., posterior, central, and anterior) were analyzed to assess intra-shell variation.

Table 1. List of analyzed species, shell layers, specimen IDs, valves, sites of collection, water depths, temperatures, and salinity. I: Primary layer, II: secondary layer, III: tertiary layer. ¹Analyzed in Crippa et al. (2025). Sampling site data from Crippa et al. (2025).

Species	Shell layers	Specimen ID	Valve	Locality	Water depth (m)	Temperatures (°C)	Salinity (PSU)
<i>Liothyrella neozelanica</i>	I, II, III	#67 ¹	Ventral and dorsal	Doubtful Sound (New Zealand) 45° 20' S, 167° 02' E	18	11.2-17.4	34-35
<i>Gryphus vitreus</i>	I, II, III	#5V ¹ #66D	Ventral Dorsal	Montecristo (Italy) 42° 26' N, 10° 04' E	140-160	13-17	38-39

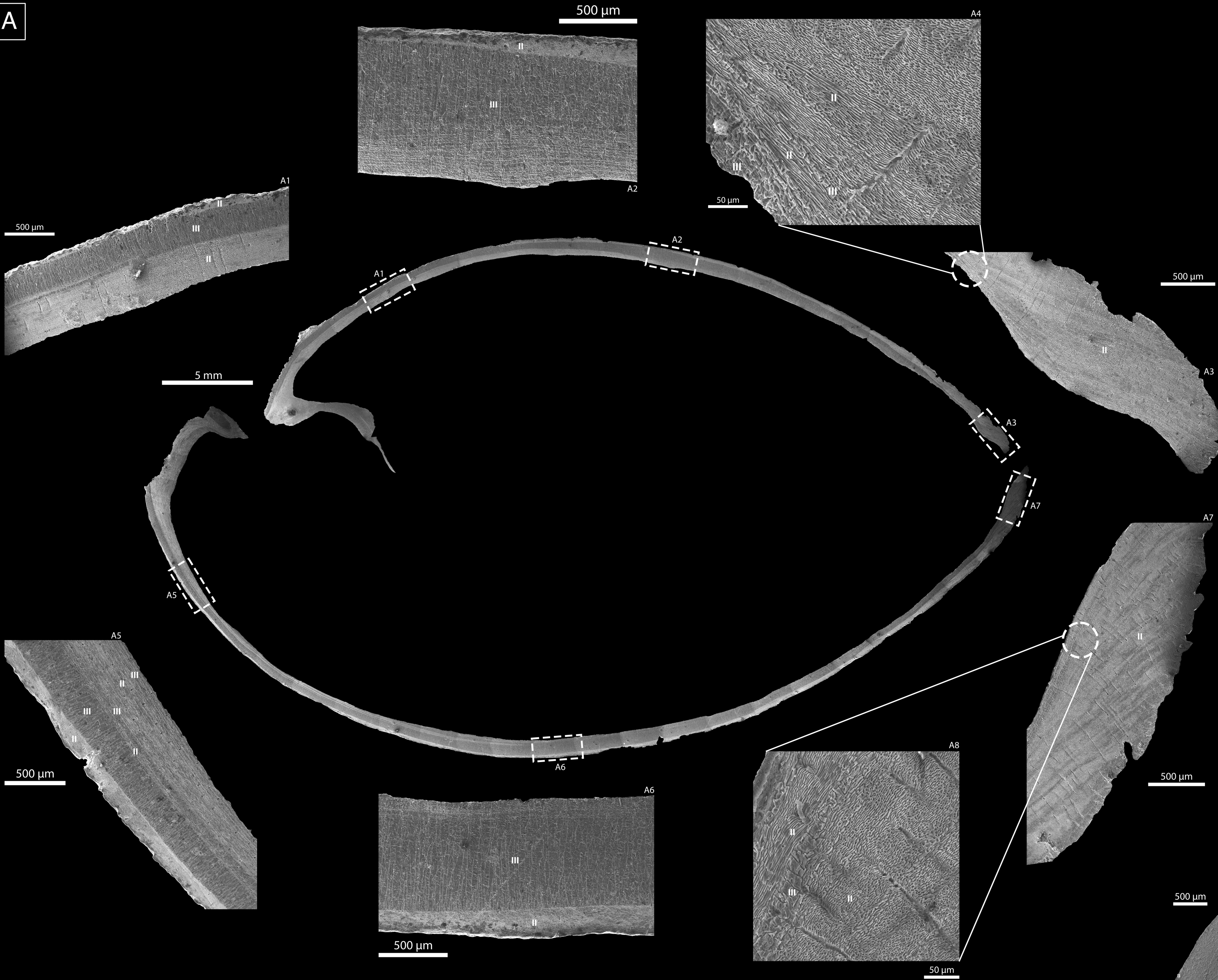


Figure A. Specimen of *L. neozelanica* (Thomson, 1918) (#67). Shell sections: dorsal valve (D; above) and ventral valve (V; below). (A1) Posterior region (D): irregular intercalations of fibrous secondary and columnar tertiary layers. (A2) Central region (D): dominant tertiary layer. (A3) Anterior region (D): thinning of the tertiary layer; dominant secondary layer with changes in fiber orientation. (A4) Close-up of the anterior zone (D) where the tertiary layer ends. (A5) Posterior region (V): several intercalations of secondary and tertiary layers. (A6) Central region (V): maximum thickness of the tertiary layer, dominating over the secondary. (A7) Anterior region (V): thinning of the tertiary layer; dominant secondary layer with fibers changing orientation. (A8) Close-up of the anterior zone (V) where the tertiary layer terminates.

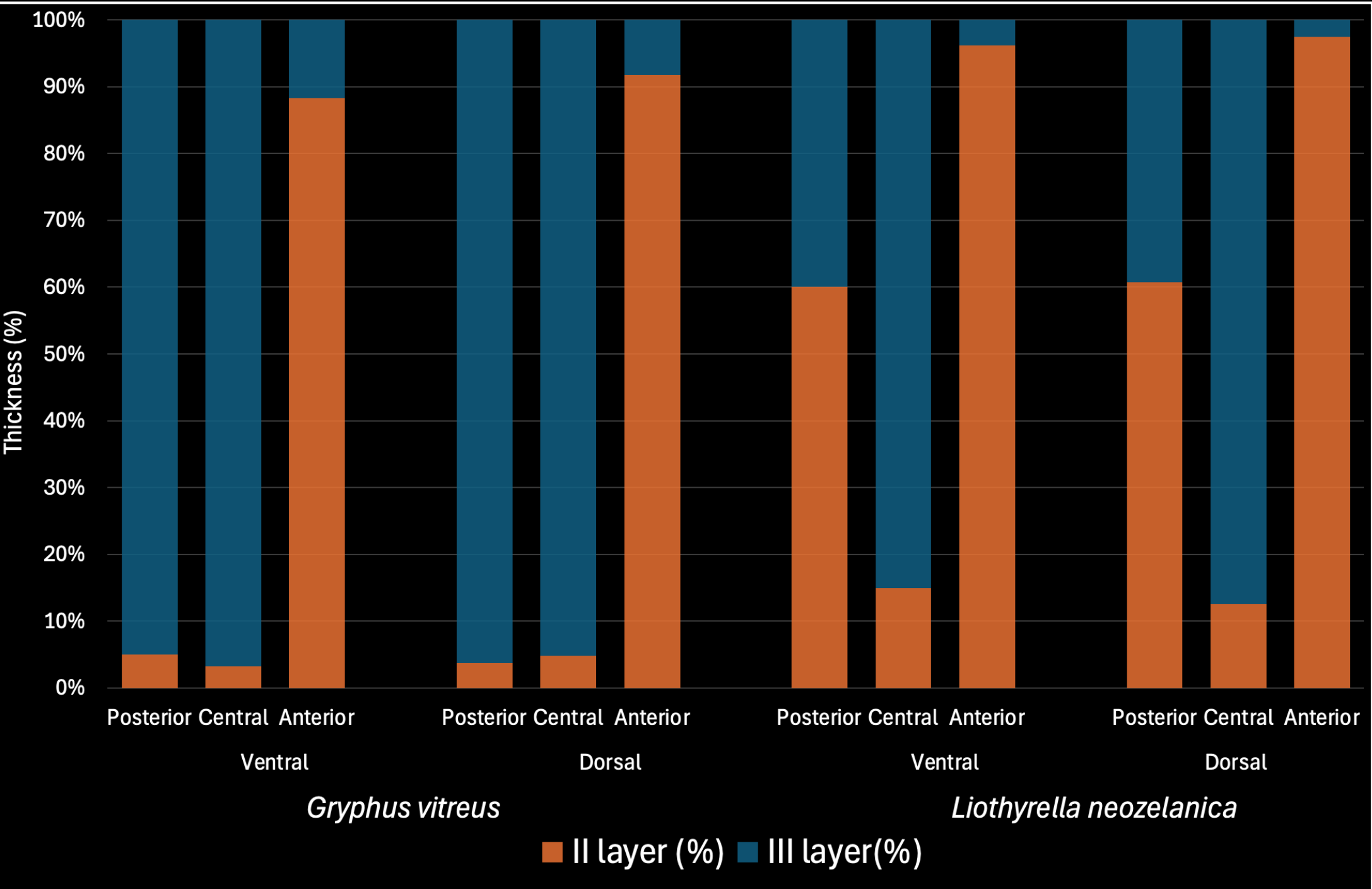


Table 2. Thickness (%) of fibrous secondary (II) and columnar tertiary (III) shell layers in the three-layered shells of *Gryphus vitreus* (specimens #5V, ventral valve; #66D, dorsal valve) and *Liothyrella neozelanica* (specimen #67, ventral and dorsal valves).

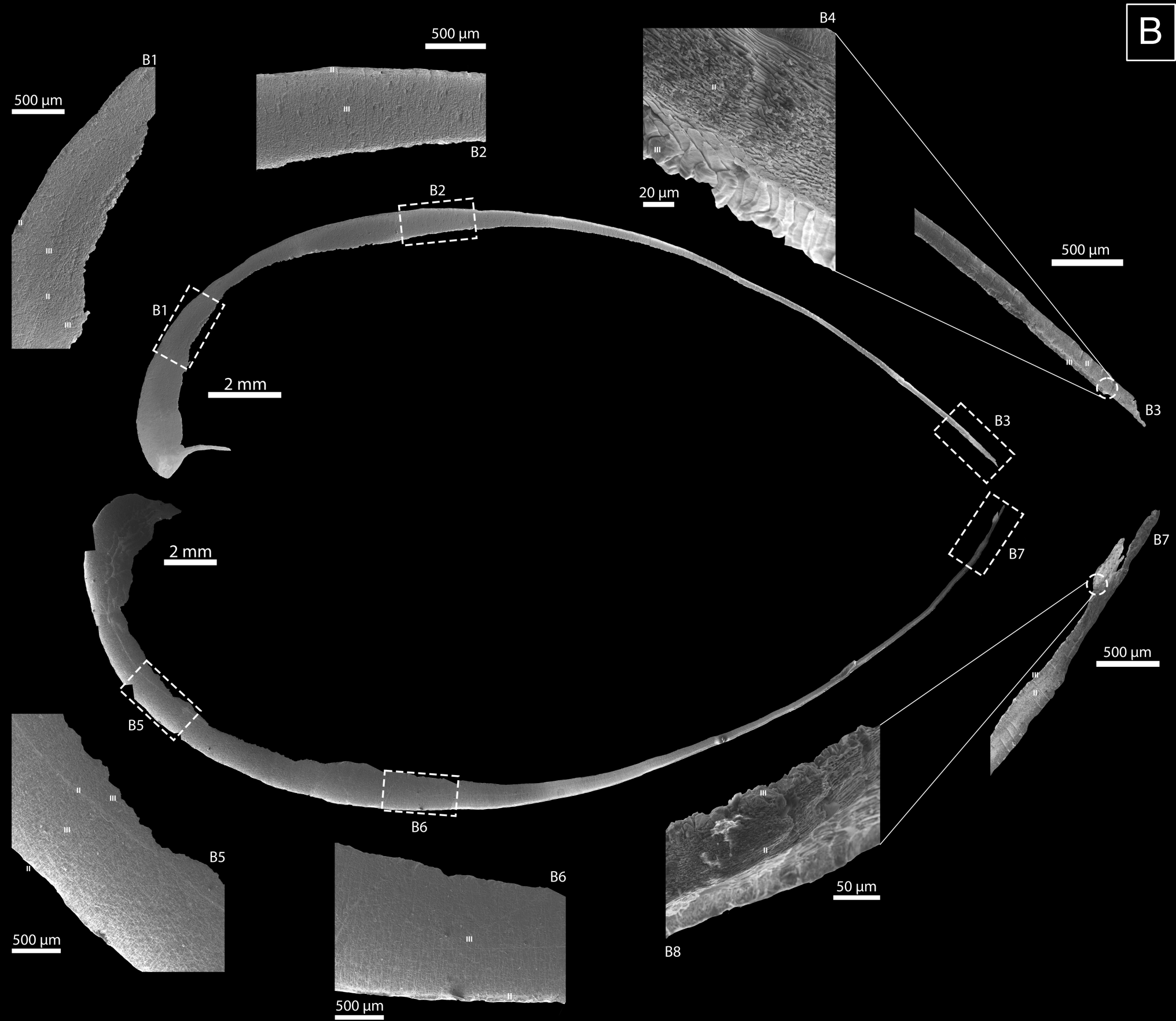


Figure B. Specimens of *G. vitreus* (Born, 1778): #66D dorsal valve (D; above) and #5V ventral valve (V; below). (B1) Posterior region (D): fewer and thinner intercalations of fibrous secondary and columnar tertiary layers compared to *L. neozelanica* (#67). (B2) Central region (D): dominant tertiary layer. (B3) Anterior region (D): thinning of the tertiary layer; dominant secondary layer. (B4) Close-up of the anterior zone (D) where the tertiary layer terminates. (B5) Posterior region (V): thin intercalation of fibers within the tertiary layer. (B6) Central region (V): maximum thickness of the tertiary layer. (B7) Anterior region (V): thinning of the tertiary layer; dominant secondary layer. (B8) Close-up of the anterior zone (V) where the tertiary layer terminates.

Conclusions

G. vitreus displays a more regular and ordered microstructure, whereas *L. neozelanica* has frequent intercalations of fibrous and columnar layers. In both species, the tertiary layer is thicker and regularly arranged in the central shell portion, but thins toward the anterior margin until disappearing. However, the posterior region is quite different in the two species, the tertiary layer being much thicker than the secondary in *G. vitreus*, but it is thinner and with irregular patterns in *L. neozelanica*. No significant differences in the arrangement and thickness of the two layers were observed between the ventral and dorsal valves.

Future studies should include additional specimens of *G. vitreus* and *L. neozelanica* to assess whether intraspecific patterns of variation are present. Other modern brachiopod species should also be comprised, and the data integrated with geochemical analyses to more robustly evaluate their potential as archives of environmental change.

References

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