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Exploring the biomineral morphology of crossed-lamellar bivalve shells as a water temperature proxy

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Bivalve shells serve as excellent high-resolution archives of marine paleoclimate. Recently, ultrastructural features of the shells were investigated as potential temperature proxies that can overcome the limitations of the stable oxygen isotope method (i.e., missing data on past seawater oxygen isotope signature and diagenetic overprint). According to previous studies, the size of individual biomineral units of prismatic, nacreous and crossed-lamellar ultrastructures in cross-sections along the axis of maximum growth was solely related to water temperature. Despite being present in 90% of all mollusks, the crossed-lamellar ultrastructure was only studied for environmental relationships in one species (*Glycymeris bimaculata*) until now. To determine whether this new proxy can be applied to other bivalves with crossed-lamellar ultrastructure, further studies are needed.

We analyzed the shells of other Glycymerididae collected at near-shore and shelf environments (*G. nummaria* and *G. pilosa*: Adriatic Sea, Croatia; *G. glycymeris*: Iroise Sea, France; *Glycymeris* sp: Southern Pacific, New Zealand) by means of SEM, using a previously developed automatic image analysis procedure. Morphological changes of the biomineral units of the shells were assessed for relationships with temperature, salinity and food availability. Additionally, the crossed-lamellar architectures of phylogenetically more distantly related taxa (*Venus verrucosa* and *Callista chione*: Adriatic Sea, Croatia) were assessed.

Our results show that all studied Glycymerididae species, irrespective of environmental setting and locality, formed larger biomineral units in warmer waters. However, biomineral properties of ontogenetically old shell portions are more difficult to interpret, because declining growth rates condense the shell record and aggravate ultrastructural analyses. The crossed-lamellar shell layers of *V. verrucosa* and *C. chione* exhibited hierarchical organizations very similar to those of the Glycymerididae. The ultrastructural temperature proxy can therefore be applied to crossed-lamellar shells of bivalves from a wide range of coastal settings, preferably in ontogenetically young shell portions.