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Morphological variations of crossed-lamellar ultrastructures of *Glycymeris bimaculata* (Bivalvia) serve as a marine temperature proxy

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ABSTRACT

Bivalve shells are among the most promising archives for high-resolution seawater temperature reconstructions. However, despite major research advances in bivalve sclerochronology over the past decades, estimating water temperature from shells remains a challenging task. This is largely because the most frequently used and widely accepted temperature proxy in bivalves, i.e., the shell oxygen isotope ($\delta^{18}O_{shell}$) value, also requires knowledge of changes in $\delta^{18}O$ of the water ($\delta^{18}O_{water}$) in which the bivalve lived, which is rarely available for ancient environments. According to a few recent studies, the size and shape of individual biomineral units (BMUs) of the shell ultrastructure may serve as an independent temperature proxy that is also less vulnerable to diagenetic changes than isotope chemical proxies. However, the crossed-lamellar ultrastructure, which occurs in ca. 90% of all mollusk species, has hitherto not been investigated. Here, we evaluate the potential use of morphological properties of the BMUs in *Glycymeris bimaculata* as a proxy for water temperature. For this purpose we introduce a suitable preparation technique (immersion for 2 m in 0.001 vol% formic acid followed by 20–30 m in 3.5 vol% H_2O_2) and an automated image processing technique that tremendously speed up ultrastructure analysis (5 s versus one to 2 h image processing time with automated and manual methods, respectively) and increase the robustness of BMU measurements. *Glycymeris* is a particularly useful target taxon, because it is a cosmopolitan genus with evolutionary roots in the Upper Cretaceous, and some species of *Glycymeris* can attain a lifespan of more than two hundred years, which allows for long-term, high-resolution paleoclimate reconstructions. As in other previously studied ultrastructures, larger and more elongated BMUs formed in warmer water permitting temperature estimates with an error of 2.3 °C (1 σ). Since the new temperature proxy is unaffected by other environmental variables, including salinity, it can potentially be applied to (modern and fossil) specimens from brackish environments.

1. Introduction

Quantitative reconstruction of seawater temperatures at annual and seasonal resolution is a pressing issue in paleoclimatology (Jones et al., 2001, 2009). Such data are essential to better understand the role of the ocean in global climate change and to constrain predictive numerical climate models (Schmidt et al., 2014). One of the most promising archives that can provide such high-resolution data from nearly any part of the ocean has recently attracted considerable attention: shells of bivalve mollusks, specifically long-lived (>30 yrs-old) species (Black et al., 2008; Butler et al., 2013; Reynolds et al., 2013; Schöne, 2013). However, despite major research advances in bivalve sclerochronology, estimating water temperature from shells remains a challenging task. This is largely because the most frequently used and widely accepted proxy in bivalves, i.e., the shell oxygen isotope value ($\delta^{18}O_{shell}$), simultaneously informs about changes in temperature and the oxygen isotope signature of the water ($\delta^{18}O_{water}$) in which the shell formed (Grossman and Ku, 1986). To reconstruct temperature from $\delta^{18}O_{shell}$ data, the $\delta^{18}O_{water}$ values must be known – an information which is rarely available for ancient environments. Furthermore, diagenetic overprint can result in partial or complete change of the original geochemical properties preserved in shells (Brand and Morrison, 1987).

According to a few recent studies, morphological changes of individual building blocks (biomineral units, BMUs) of the shell ultrastructure (we prefer this term over shell "microstructure", because the latter implies a limitation of the scale to μm) may serve as an independent

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