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Shell structure, patterns and trends of oxygen and carbon stable isotopes in modern brachiopod shells

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Abstract

This study investigates $\delta^{13}C$ and $\delta^{18}O$ variations in the shells of modern brachiopods representing all extant groups of calcite-precipitating brachiopods, collected live from 8 locations. SEM examinations determined the ultrastructural characteristics of each species prior to isotope analyses. $\delta^{13}C$ and $\delta^{18}O$ analyses of shell carbonate were carried out with samples representing disparate morphological features and ultrastructural shell layers of both ventral and dorsal valves.

Generally, $\delta^{18}O$ values from the fibrous secondary or prismatic tertiary shell layers of the articulated Terebratulida and Rhynchonellida species were in oxygen isotopic equilibrium with ambient seawater. Isotopic temperatures extrapolated from these values are close to measured annual mean seawater temperatures. $\delta^{18}O$ values were relatively unaffected by shell specialisation. The only exception was Antarctic species *Liothyrella uva*, which did not have a complete tertiary shell layer typical of this genus and had $\delta^{18}O$ values of the innermost layer strongly correlated with $\delta^{13}C$ and mostly not in oxygen isotopic equilibrium with ambient seawater. With the exception of the rhynchonellid *Notosaria nigricans*, the outer primary layer material was depleted in $\delta^{13}C$ and $\delta^{18}O$ and highly variable. Inclusion of this material even as part of a whole shell sample could lead to misinterpretation of seawater temperature, therefore only fossil secondary layer material should be used. The anomalous articulated thecideidine brachiopod *Thecidellina barretti* is composed of mainly primary shell material and was not in oxygen isotope equilibrium. $\delta^{18}O$ values from the laminar secondary layer material of the inarticulated Craniida are highly variable. Therefore, these species are not recommended for use as palaeoenvironmental proxies. This study suggests caution when employing fossil brachiopod shells with similar ultrastructures to modern craniid and thecideidine brachiopods.

The carbon isotope composition is highly variable in all of the brachiopods studied. Analysis of samples from specialised regions of the secondary shell layer show a pattern of depletion in ^{13}C relative to non-specialised secondary material. The carbon isotope variability is independent of $\delta^{18}O$ and is repeated in most of the articulated species regardless of geographical location. This is possibly a vital effect produced by metabolic prioritisation.

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1. Introduction

Lowenstam's (1961) influential study concluded that brachiopods precipitate skeletal carbonate in isotopic equilibrium with ambient seawater. Since that time, stable isotope ratio determinations from fossil brachiopod shells have been widely used as proxies for environmental changes in ancient oceans (e.g., Bates and Brand, 1991; Brand, 1989a,b; Brand and Brenckle, 2001; Bruckschen et al., 1999; Grossman et al., 1993; Marshall and Middleton, 1990; Popp et al., 1986a; Popp et al., 1986b; Qing and Veizer, 1994; Veizer et al., 1986; Wadleigh and Veizer, 1992; Wenzel and Joachimski, 1996; Wenzel et al., 2000). Recently, modern brachiopods have also been employed for contemporary environmental applications (e.g., Buening and Spero, 1996; James et al., 1997). Brachiopods are popular because the phylum is not only diverse, but also ubiquitous and continuous throughout the fossil record, ranging from Cambrian to Recent. Stable isotope analyses of their shells, therefore, have the potential to be good proxy indicators of secular changes throughout the Phanerozoic. In addition, most brachiopod species have shells composed of low-magnesium calcite (LMC); that is shells with $MgCO_3$ concentrations between 0.5 and 7.0 mol% (Brand, 1989a). This is the most stable form of skeletal carbonate and therefore is considered more resilient to diagenetic alteration (e.g., Al-Assam and Veizer, 1982; Brand, 1989a; Lowenstam, 1961). Lepzelter et al. (1983) added some weight to the equilibrium supposition with a study of $^{18}O/^{16}O$ ratios in several Recent species that were considered representative of extant brachiopods. Their study concurred with Lowenstam's (1961) findings and it was concluded that oxygen isotopes in brachiopod shells are precipitated in isotopic equilibrium with the ambient environment. The only disequilibrium noted by Lepzelter et al. (1983) was in the case of specimens taken from cold-water habitats.

Underpinning the use of brachiopods for environmental investigations is the assumption that their shells are precipitated in isotopic equilibrium with ambient seawater, a position widely accepted. However, other than the work of Lowenstam (1961) and Lepzelter et al. (1983), there have been few data provided to support this assertion. This is despite reports over many years that the potential for biological fractionations or 'vital effects' exists in many carbonate precipitating marine organisms including brachiopods (e.g., Böhm et al., 2000; Compston, 1960; Erez, 1978; Gonzalez and Lohmann, 1985; Grossman et al., 1991; Keith and Weber, 1965; McConnaughey, 1989; Ortiz et al., 1996; Popp et al., 1986b; Rosenberg et al., 1988; Swart, 1983; Weber and Woodhead, 1970). An alternative mechanism is proposed by Adkins et al. (2003) who suggest that 'vital effects' observed in deep sea corals were the result of "a thermodynamic response to a biologically induced pH gradient in the calcifying region," rather than biological effects. However, notwithstanding the mechanism, it is clear that stable isotope variation does occur in some biogenic carbonates.

The question of disequilibrium and vital effects was highlighted by Carpenter and Lohmann (1995). Mindful that the claims by Lowenstam (1961) had never been rigorously tested, Carpenter and Lohmann (1995) re-examined the issue using a variety of modern brachiopod shells from different environments. Carpenter and Lohmann (1995) concluded that the secondary layer of some taxa is precipitated close to equilibrium: therefore, some fossil brachiopods are suitable indicators of ancient seawater. However, they also reported a wide range in both $\delta^{18}O$ and $\delta^{13}C$ with differences between species at the same location as well as variations within individual specimens implying possible 'vital effects' particularly in the thin outer primary layer and specialised areas of the secondary shell.

Subsequent studies of modern brachiopods have increased the ambiguity. Marshall et al. (1996), investigated *Liothyrella uva* from Antarctica and observed that, given the narrow fluctuation of ambient seawater conditions, measured values of $\delta^{18}O$ and $\delta^{13}C$ were unacceptable as seawater proxies. Buening and Spero (1996) found $\delta^{18}O$ in *Laqueus californianus* to be in equilibrium, but could not reconcile $\delta^{13}C$ with ambient seawater. Two contemporary studies using brachiopods from the Lacepede Shelf, southern Australia came to conflicting conclusions. Rahimpour-Bonab et al. (1997) found bivalves and gastropods to be in oxygen isotopic equilibrium, while coexisting brachiopods were enriched in ^{18}O and ^{13}C. At the same location, James et al. (1997) judged brachiopods to be indicative of ambient seawater conditions. In a further study, Curry and Fallick (2002) observed different $\delta^{18}O$ values from the dorsal and ventral valves of *Calloria inconspicua* from the Otago Shelf

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