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Species-specific foraminiferal ultrastructures modulate surfaces available for diagenesis

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The Earth's long history with climate change has in large part been revealed through the application of the oxygen isotope paleothermometer on fossil foraminifera tests. However, from the moment a foraminifer dies and is buried under progressively thicker layers of sediment, its original isotopic and elemental composition begins to change by diagenetic processes, even if imperceptible to optical or scanning electron microscopy (SEM) (Bernard *et al*., 2017; Chanda *et al.*, 2019). The reaction rate, i.e. diagenetic susceptibility, for wide ranges of biocalcites has been directly related to the size of their constituent carbonate crystals (Walter and Morse, 1985; Constantz, 1986). Rotaliid foraminifera, on which the majority of palaeoceanographic reconstruction are based, are fundamentally composed of roughly spherical grains of calcite measuring 10–100 nm in diameter (Dubicka *et al.*, 2018; Cuif et al., 2010). The susceptibility of the high surface-area of this ultrastructure to pore fluid penetration and geochemical alteration must be investigated in order to determine the reliability of foraminifera as paleo-environmental proxies.

To understand where and how pore fluids exchange with foraminiferal calcite we performed experimental simulations of diagenesis. The textures and geochemistry of three species of modern foraminifera (*Ammonia sp.*, *Haynesina germanica* and *Amphistegina lessonii*) were compared before and after exposure to calcite-saturated ^{18}O-enriched artificial seawater at 90 °C for 4 hours or 6 days. We utilized optical, SEM, transmission electron microscopy, and NanoSIMS in combination with bulk isotope measurements to characterise the fluid-mediated diagenesis in each species. SEM imaging showed that tests, before and after experiments, were texturally equivalent, yet NanoSIMS images revealed heterogeneous but ubiquitous ^{18}O enrichment across the entire calcitic test. This demonstrated that fluids penetrated and exchanged with all parts of the test down a length scale smaller than the lateral resolution of the NanoSIMS (i.e. ~ 120 nm). Additionally, the ^{18}O-highest enrichment was correlated to two ultrastructural features present in all species of foraminifera: organic linings and cogwheel structures. Bulk isotope measurements showed that isotopic exchange with pore water is species-specific and clearly correlated with the density of these ultrastructural features.

These results demonstrated that during burial, calcitic tests of benthic foraminifera can be penetrated by and exchange with oxygen from ambient pore-fluids down to the ultrastructural level. Additionally, species-specific ultrastructures modulate the surface area accessible for fluid penetration and demonstrate a species-level predisposition to diagenesis. This indicates that foraminifera-based single-species and multi-species paleoclimate compilations are highly susceptible to isotopic exchange during diagenesis.

Until these processes are better understood and quantified, the existing paleoseawater temperature reconstructions based on, e.g., the O-isotopic compositions of biogenic calcites cannot be considered unbiased.

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