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The biomineralization mechanism in foraminifera and its implications for the incorporation of paleoceanographic proxies to their shells

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A new framework for the interpretation of stable isotope fractionations and trace element distribution coefficients in foraminiferal shells is presented in view of the biomineralization processes in foraminifera. Using special cellular preparations of non-calcified foraminifera and employing confocal laser microscopy, microelectrodes electron probe and SIMS analyses and culturing experiments of live foraminifera we propose the following scheme for the biomineralization process in forminifera:

1. Perforate (calcitic radial) foraminifera precipitate two types of $CaCO_3$ that are completely different in their mode of calcification and in their chemical and possibly isotopic composition. Primary calcite is precipitated in close association with the organic matrix, it is enriched in Mg, S, Na and shows low δ^{18}O values. On both sides of the primary calcite secondary calcite is precipitated by a seawater vacuolization mechanism (see below). The secondary calcite, (roughly 95 % of the calcite in the shell), forms th calcitic radial texture, and it is composed of low-Mg calcite with low concentrations of S and Na, and higher δ^{18}O values. The proportion between the two calcite types may change with environmental parameters(e.g. temperature).

2. The supply of Ca^{2+} and CO_3^{2-} for calcification of the secondary calcite is by large (macropinocytotic) vacuoles that bring seawater to the site of calcification. The vacuoles are modified to increase their internal pH, absorb $CO_{2(aq)}$ from the cytosol, and thus form a large internal dissolved inorganic carbon (DIC) pool. Cytosolic $CO_{2(aq)}$ comes from respiration (with low δ^{13}C) and also from small acidic seawater vacuoles.

In species with symbiotic algae, there is a competition for this $CO_{2(aq)}$ between the host's basic vacuoles needed for calcification and photosynthesis by the symbionts. The close nature of the DIC reservoir may lead to internal recycling of carbon and oxygen, low photosynthetic fractionation of the symbiotic algae and hence the overall effect on the δ^{13}C of the shell may be small.

3. The pH and CO_3^{2-} at the calcification site has been measured with microelectrodes showing values of 9.4 and 1200 μM, respectively, and the Ca^{2+} concentration is similar to that of seawater ($\sim$11 mM). The DIC concentration is $\sim$ 4 mM (much higher than that of seawater). The supersaturation for calcite under these conditions is very high and the organism may have a special mechanism to prevent spontaneous precipitation of calcite.

4. Many of the perforate foraminifera (especially the planktonic and the deep benthic ones), must have a special mechanism to remove Mg^{2+} from the calcification site. This may start at the vacuoles stage and continue at the calcification site. Mg may be removed by a channel that allows passive diffusion into the cytosol and removal from the cytosol to the surrounding water by a specific Mg^{2+} pump.