



# Assessing foraminifera biomineralisation models through trace element data of cultures under variable seawater chemistry

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## Abstract

The process by which foraminifera precipitate calcite from seawater has received much attention, in part because a mechanistic basis for empirical calibrations between shell chemistry and environmental parameters is desirable given their widespread application in palaeoceanography. The incorporation of fluorescent membrane-impermeable molecules into the shell demonstrates that seawater, transported by vacuolisation, is present at the site of calcification. However, recent discussion has focused on whether the calcium required for chamber formation is sourced predominantly by transmembrane Ca transport (TMT), with seawater vacuolisation playing a passive role, or vice versa. This debate has arisen in part because of the need to explain the low Mg/Ca ratio of most foraminifera compared to inorganic calcite. Here, we present trace element data of *Operculina ammonoides* and *Globigerinoides ruber*, a high-Mg shallow benthic, and low-Mg planktonic species respectively, cultured under variable seawater carbonate and elemental chemistries. We find that Mg incorporation in high and low-Mg species is characterised by an opposite response to the carbonate system, demonstrating that the negative relationship between Mg/Ca and pH or  $[\text{CO}_3^{2-}]$  in several low-Mg foraminifera is not an intrinsic feature of calcite precipitation. Therefore, any biomineralisation model must be able to explain why the mechanism by which seawater Mg/Ca is reduced is impacted by the carbonate system. Moreover, we show that trace element incorporation in *G. ruber* is consistent with Rayleigh fractionation from unmodified seawater except for Mg-removal, but in very poor agreement with a biomineralisation site [Ca] substantially elevated above that of seawater as required by the TMT hypothesis. In addition, any biomineralisation model must explain the nonlinear relationship between seawater and shell Mg/Ca, and the large number of seawater vacuoles observed in some species. Although there are important inter-species differences in biomineralisation, evident from the observed range of shell Mg/Ca ratios, we argue that these differences are mechanistically related to the degree of Mg exclusion prior to chamber formation. Indeed, whilst our data for both low-Mg and high-Mg species are consistent with biomineralisation via ions sourced through seawater vacuolisation, it is difficult to reconcile many of these observations with a model based on significant transmembrane Ca transport.

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## 1. INTRODUCTION

Geochemical proxy data from foraminifera forms the basis of much of our knowledge of palaeoceanography and past changes in Earth's climate (e.g. Lear et al., 2000;

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Elderfield et al., 2012; Rosenthal et al., 2013). Furthermore, this group of unicellular organisms is responsible for a large proportion of oceanic  $\text{CaCO}_3$  production (Schiebel, 2002), and thus has resulted in a virtually continuous archive of planktonic and benthic species throughout the Cenozoic and beyond. As such, a considerable amount of research has focused on understanding the biomineralisation process in foraminifera (e.g. Erez, 2003; Bentov and Erez, 2006; de Nooijer et al., 2014; Toyofuku et al., 2017; Fehrenbacher et al., 2017). One principal goal of this work is to underpin empirical proxy calibrations between environmental conditions and shell geochemistry with a theoretical basis. Understanding how and why foraminifera modify the chemistry of seawater prior to calcification may improve the accuracy of foraminifera-derived palaeoclimate reconstructions and enable the identification of environmental conditions under which empirical calibrations may require adjustment. For example, the incorporation of Mg in planktonic foraminifera is sensitive to both temperature and the carbonate system (Russell et al., 2004; Evans et al., 2016b; Gray et al., 2018), yet correcting fossil Mg/Ca measurements for secular shifts in ocean carbonate chemistry remains challenging because it is unclear which carbonate system parameter(s) modulate calcification rate and shell Mg uptake (Bach, 2015; Allen et al., 2016; Henehan et al., 2017). Constraining how different foraminifera source and concentrate the inorganic carbon necessary for calcification may address this problem, whilst also providing invaluable information regarding the likely response of this important group of marine calcifiers to ocean acidification.

There is currently no consensus within the community on the fundamental mechanism by which foraminifera source the calcium and carbon necessary for mineralisation, highlighting the challenge of observing and analysing organisms typically less than a millimetre in diameter. Moreover, it indicates that different foraminifera may have evolved different biomineralisation strategies (ter Kuile et al., 1989; de Nooijer et al., 2014), especially between the very diverse benthic species which produce  $\text{CaCO}_3$  with a wide range of Mg/Ca ratios and chamber wall structures (e.g. Reiss, 1958; Bentov and Erez, 2006; Evans et al., 2015b; van Dijk et al., 2017). This contribution focuses on the rotaliid (hyaline or perforate) foraminifera, on which most palaeoceanic reconstructions are based.

Direct observation of intracellular processes poses obvious challenges, and as such much recent work has focused on inferences from the isotopic and elemental composition of foraminifera shells (e.g. Segev and Erez, 2006; Zeebe et al., 2008; Raitzsch et al., 2010; Vigier et al., 2015; Evans et al., 2016b). The justification for such studies is a relatively large body of literature on trace element and isotope incorporation into inorganic calcite, which forms the basis of inverse modelling the conditions at the site of calcification. A simple illustration of this is the observation that the Mg/Ca ratio of planktonic foraminifera is approximately twenty times lower than inorganic calcite precipitated from seawater (Mucci and Morse, 1983), providing strong evidence that some species possess a mechanism of excluding Mg before final precipitation of the shell. Based

on both direct observation of cellular processes, and inferences such as this, two principal biomineralisation mechanisms have been proposed, briefly summarised here.

(1) The seawater vacuolisation model (SWV), in which ions are predominantly sourced from seawater vacuoles. This model is based on the observation that hyaline foraminifera, in particular *Amphistegina lobifera*, endocytose large quantities of seawater that are transported to the site of chamber formation in vacuoles (e.g. Bentov et al., 2009). Numerous experiments culturing foraminifera in seawater containing membrane-impermeable fluorescent markers such as calcein (623 Da) and FITC-dextran (10 kDa) demonstrates that seawater is present at the site of calcification (e.g. Erez, 2003; Dissard et al., 2009; Evans et al., 2015b). Furthermore, ‘pulse-chase’ experiments have been conducted by placing foraminifera into seawater containing FITC-dextran or calcein for a period of time, followed by a chase period in normal seawater (Bentov et al., 2009). Material precipitated during the chase period was strongly labelled, demonstrating that the seawater present at the site of biomineralisation must be derived (in part or entirely) from internal seawater vacuoles. Research utilising fluorescent pH indicators has shown that the pH of these vacuoles is increased to  $\sim 1$  unit above seawater (Bentov et al., 2009; de Nooijer et al., 2009), suggesting that they play an important role in concentrating carbon. Providing support for this is earlier experimental work using  $^{14}\text{C}$  tracer uptake to demonstrate that the hyaline species *A. lobifera* does indeed have a large inorganic carbon pool (ter Kuile and Erez, 1987; ter Kuile and Erez, 1988). The mechanism of the foraminifera carbon concentrating mechanism was later revealed through confocal microscope observations. Specifically, raising the pH of the vacuole would increase the DIC and  $[\text{CO}_3^{2-}]$  by promoting  $\text{CO}_2$  diffusion directly from acidic vesicles in the cytosol, or possibly from the surrounding seawater (Bentov et al., 2009). Variations of this model invoke vacuole pH elevation through  $\text{Na}^+\text{-H}^+$  active transport (pumps), which would also modify the vacuole [Li] and  $\delta^7\text{Li}$  given that Na pumps are unlikely to be completely selective for  $\text{Na}^+$  over  $\text{Li}^+$  (Erez, 2003; Vigier et al., 2015). Therefore, this process may be associated with a minor modification in seawater elemental chemistry. A long-standing challenge of the model is that seawater vacuolisation alone does not explain how many species of foraminifera are able to form calcite shells with a Mg/Ca ratio 1–2 order of magnitude lower than inorganic calcite (e.g. Lea et al., 1999; Erez, 2003; Rosenthal et al., 2011). Therefore, an additional mechanism is required to remove Mg in the seawater vacuolisation model before final precipitation of the shell. This process has been variously suggested to relate to (i) active Mg removal through channelling and pumping (Erez, 2003; Bentov and Erez, 2006), (ii) uptake by mitochondria (Bentov and Erez, 2006; Spero et al., 2015), (iii) precipitation and removal of Mg-rich phases (Bentov and Erez, 2005; Khalifa et al., 2016), (iv) precipitation through an amorphous or metastable precursor phase (Jacob et al., 2017). Of course, two or several of these processes may act together.

(2) The Ca trans-membrane transport (TMT) model posits that the majority of the calcium required for

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