Letter to the editor:

We received two reviews to our manuscript entitled *"A new model for biomineralization and trace-element signatures of foraminifera tests"* and would like to thank the reviewers for their good work.

We would like to point out that we show in our manuscript for the first time that the commonly accepted notion, which clearly has acquired the status of dogma, that the calcification of foraminifera is based on seawater vacuolization is demonstrably wrong in the species investigated by us. The reviewers do not doubt our data at any point but still claim that some processes e.g. the isotopic fractionation of Boron can be explained by vacuolization, neglecting that our data are clearly showing that there is no significant seawater vacuolization. We acknowledge that species-specific differences exist. In fact, the major strength of our model is the ability to deal with these differences. Far from ruling vacuolization out, our model gives this process, formerly regarded as the main source of shell-calcite building blocks, a modulatory role. The latter can vary in importance, which represents, in our view, the origin of species-specific differences. Therefore, our model provides a new view on biomineralization in foraminifera, which will prove constructive in the development of proxy-understanding.

It is also important to realize that our paper only indicates the direction in which further research can develop, but does not pretend to represent "the universal biomineralization model". Our findings are an important piece of this puzzle and we hope that you will agree that it deserves publication in the present form to encourage the community to break new ground in this field of research.

The reply to the reviewer's comments you will find below.

Best regards,

Gernot Nehrke

Interactive comment on "A new model for biomineralization and trace-element signatures of foraminifera tests" by G. Nehrke et al.

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The work done presented an elegant set of experiments, which have resulted in a nice set of data about the calcium transport in forminifera. The data and calculations made could show that endocytosis cannot be the only method for calcium transport and suggest that a trans-membrane transport and a passive transport must exist.

I have some major remarks and concerns about the conclusions drawn from the results obtained; For calcification to take place, the saturation state must be increased.

Reply: Increased with respect to what? If the reviewer means "with respect to seawater", the answer is: not necessarily, because seawater is supersaturated with respect to calcite. Supersaturation also implies precipitation of calcite from a fluid. We do not know through which pathway the calcite in foram tests is produced. Perhaps amorphous calcium carbonate is involved, in which case the concept of supersaturation becomes irrelevant.

This can be done by increasing the concentrations of calcium and carbonate at the site of calcification through the transport processes and by increasing the pH. To be able to do this, the organism must isolate the site of calcification from the seawater, otherwise, there will be no build up for the concentrations of the needed ions and also there will be no control on the pH.

Reply: We agree insofar that the organism has to isolate the site of calcification from seawater. This assumption is, by the way, included in all conceptual calcification models for foraminifera and coccolithophores. Our model is no exception. We do, however, consider the possibility that the seal is not perfect, and that unfractionated Ca, Mg, and Sr from seawater can arrive at the site of calcification. We made that point very clear and give numbers to illustrate that the fraction of inter-pseudopodial ion flux (if existent) or vacuole-transported seawater components is rather small.

The authors said that passive transport (PT) is achieved by diffusion of cations through gaps in the pseudopodial network and by vacuolization of seawater. This cannot be true, because the suggested pseudopodial network is not able to control the diffusion of ions to and from the site of calcification, which is a function beyond the capability of a network to achieve. Rather a selective membrane is needed. It is highly unlikely that the pseudopodia can seal the site of calcification. Also, the pore size created will be too big to control the diffusion of ions.

Reply: The assumption that the pseudopodia can seal off rather effectively the site of calcification is not our invention but is also a feature of the now classical model of Erez

(2003). This assumption must largely be true, because otherwise one will not be able to account for any control over chamber formation as indeed exerted by foraminifera.

If, as the authors suggested, that passive diffusion is allowed to the site of calcification, then the diffusion will be against the calcification process and not supportive at all as the model said. This is because the concentration of ions at the site of calcification must be higher than that in the seawater, and therefore the diffusion of ions will be from an area of higher concentration to an area of lower concentration. This free diffusion will lead to dissipation of the concentration built-up and will lead to decreased saturation state. When this happens, calcification will stop.

Reply: Again, we do not know through which pathway the calcite in foram tests is produced. The above comment is based on the notion of physiochemical precipitation from seawater, to which we do not subscribe. But even if the calcite did precipitate from seawater, the ion concentrations would not have to be higher because seawater is already supersaturated with respect to carbonate.

The authors suggested the presence of trans-membrane transport of ions, but they could not show this by the set of experiments done. There is nothing written about the nature of this TMT!

Reply: On page 9803, lines 10-14 we mention the relevant key features of trans-membrane Ca-transport.

Based on the above mentioned points, I think that the work done cannot predict a new model for biominiralization in foraminifera. The data obtained can only show that the endocyosis is not the only method of ion transport. The conclusions made are not based on actual data. I believe that the research team needs conduct further experiments to fully characterize the ion transport methods in forams. My personal feeling is that the mechanism of calcification in foraminifera is very much like that in other calcifying organisms in the sea, such as corals.

Reply: The inferred element-to-calcium ratios of all conceptual foram biomineralzation models are drawn from different features of trans-membrane transport proteins (this holds true also for the classical Erez-model as well; please remember 'selective Mg-removal'). The transport proteins, which are crucial in our model, are Ca-channels and Ca-pumps. These transport-proteins are ubiquitous within the realm of eukaryotes and it was shown that at least Ca-channels of various, evolutionary distinct (e.g. seed plants and nematode worms), organisms share certain features when analysed by means of electrophysiological methods. One of these features is the strong fractionation of a typical Ca-channel against Mg. Since Ca-transport proteins are very old in evolutionary terms and their basic features highly conserved, it is absolutely reasonable to assume that these basic features will be present in

some organisms not yet investigated electrophysiologically. This is what we have done. It might be worth mentioning that this is also what researchers in the coccolithophore community have done. In the latter community this step has led to a new conceptual model of trace element fractionation, by means of which previously unresolved problems could be tackled. Moreover, a full characterization of ion transport in foraminifera is a task, which has to be undertaken by more than one research team. Just to put that task in context, please remember the huge amount of great work done by Jonathan Erez and co-workers over many years. Without this contribution and the contribution of many people working over decades in the coccolithophore community we could not have come up with our proposition. We feel that we have convincingly argued for a new model, which hopefully will serve as springboard for more sophisticated research.

Interactive comment on "A new model for biomineralization and trace-element signatures of foraminifera tests" by G. Nehrke et al.

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I have the same concerns as the other referee concerning this study. In particular, I wonder how this model could explain the d11B data obtained in foraminifera, i.e. indications of pH variations that were interpreted as different pH in seawater vacuoles. I think that this is something that should be discussed. I'd like also that the authors show how their model works with other trace element and isotopic ratios that were measured in foraminifera. What would be the implications of your model on the isotopic compositions of Mg in forams? What are also the main implications for paleo-reconstructions of environmental conditions? This aspect is mentioned in the introduction, but was not developed after that.

Reply: Reply: The focus of this paper is to show that the dogma of sea water vacuolization as the source for biomineralization of all foraminifera is not true. The issue of d11B is a good illustration why this paper is so important. In the case of coccolithophores for example *it was shown that the B/Ca ratio of coccoliths in response to seawater carbonate chemistry changes can be explained by assuming trans-membrane transport only. The fact that a model gives the correct results does not mean that it is correct. However, it will be the task of future research to decipher how trans-membrane transport leads to the element/isotope signatures we measure in foraminifera. Even if it will be difficult to find an explanation it is not possible to ignore the fact of a strong contribution of trans-membrane transport in the biomineralization process of foraminifera, as clearly shown in our study*

I have few more comments:
L18 (9799): the reference 'Bentov and Erez (2006)' should be added.

Reply: Will be done in a revised version of the manuscript.

Results section: Could you give some ideas about the distribution of the total number of vacuoles volume for the specimens studied? Is this a continuous distribution? Here we just know the maximum volume.

Reply: The question is not quite clear to us, but the volume of vacuoles is a highly dynamic parameter that can vary between almost no vacuoles to the maximum values quoted in the manuscript.

L14 (9802): It seems that there is also some new layer formed inside all the previous chambers (figure 2C). How is it explained?

Reply: As can be seen from the SEM picture, this is related to the morphology of the test. It does not show the inside but the outside of the test because the test is not sectioned perfectly through the central plane.

L23-26 (9805): It was, for example, done in Segev and Erez (2006), so the results could be used to test the different assumptions about Mg pathways.

Reply: Yes, we cite the Segev and Erez study and state in line 17 – 20 and wrote "This is in qualitative agreement with currently available data from two species (Segev and Erez, 2006), but similar data on other species would further validate our model."