

Biogeosciences Discuss., author comment AC3
<https://doi.org/10.5194/bg-2021-67-AC3>, 2021
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Reply on RC2

Thore Friesenhagen

Author comment on "Test-Size Evolution of the planktonic foraminifer *Globorotalia menardii* in the Eastern Tropical Atlantic since the Late Miocene" by Thore Friesenhagen, Biogeosciences Discuss., <https://doi.org/10.5194/bg-2021-67-AC3>, 2021

Response to "General comments"

Comment: "The manuscript 'Test-size evolution of the planktonic foraminifera *Globorotalia menardii* in the Eastern Tropical Atlantic since the Late Miocene' present a size record of *M. menardii* over the last 8 million years. Most notably, it shows an increase in size to a 'giant' *G. menardii* type in the last 2 million years. The manuscript explains this size change by investigating three possible hypotheses: influx of giant specimens from the Indian Ocean by Agulhas Leakage, a local evolutionary event or a response to oceanographic conditions. I have several major concerns regarding the methods and data interpretations."

Response: I thank the anonymous referee for the critical comment. Some of the reviewer's concerns may be caused by some unclear formulations in the script, others may be solved by clarifying that all the presented hypotheses are working hypotheses, which need to be further investigated in future studies. Detailed responses to the reviewer's critiques and suggestions are given below.

Comment: "The dataset is not suitable to test the first two hypotheses (Agulhas Leakage and Local Evolution), and evidence for the third hypothesis is inconclusive."

Response: The scope of this initial study is not to definitively prove or dismiss one of the three presented hypotheses, but to discuss the possibilities of these hypotheses as explanations, especially of the Agulhas Leakage hypothesis (ALH), and to identify directions for further investigations. In this context the very similar patterns of size evolution at 667A (eastern Atlantic) and 925B (western Atlantic), thousands of kilometres apart, are one argument in favour of the ALH. This pattern of similar size evolution within the tropical Atlantic as well as the Caribbean Sea was not known before.

Comment: "Additionally, the characteristics used for species identification (number of chambers in final whorl) are not sufficient to tell Menardiform species apart. There is a possibility that the size record presented here consists of multiple Menardiform species

and any changes in size could therefore be the result of a change in species composition, rather than a species-specific evolutionary event.”

Response: This comment is most likely based on an unclear formulation in the manuscripts’ Material and Methods chapter 2.4. As mentioned by the reviewer, there are several other menardiform species like *G. exilis* and *G. pertenuis* with 5 to 9 chambers in their last whorl. These species are easily separable from *G. menardii*, *G. limbata* and *G. multicamerata* and had been previously removed from the applied dataset for this study. The reason for the removal of *G. exilis* and *G. pertenuis* is that (1) their occurrence is too rare and sporadic to be investigated in this study and (2) their removal facilitates the investigation of the *G. menardii*-*G. limbata*-*G. multicamerata* branch.

These points will be discussed in detail in the section ‘Response to “Methods”’.

Response to “Specific comments – Interpretation”

Comment: “The link between AMOC strength and size, which is presented as the best explanation for size increase at 2.0 Ma in *G. menardii*, is weak.”

Response: The reviewer’s comment revealed that some passages about the AMOC hypothesis may be misunderstandable. As written in the Conclusion, this hypothesis represents one possible explanation for the size evolution from 8 to at least 3 Ma due to the covariation of the AMOC strength (Dausmann et al., 2017 and as a new additional reference Karas et al., 2017) and the test-size evolution. However, during the Gelasian I postulate that the dispersal of a new *G. menardii* type via the Agulhas Leakage is the most likely cause for the observed substantial test-size increase. Text passages which may cause the unintended impression of the AMOC hypothesis being the favoured explanation for the test-size increase around 2 Ma, will be modified accordingly.

Comment: “The covariation between ϵNd and size is not significant at Site 925 and explains very little variation in the size record of Site 667 (Figure A8).”

Response: I am aware of the fact that the statistical significance of the covariation is low, but one cannot dismiss a certain similarity between ϵNd and the pattern of the maximum test-size evolution over larger time as is shown in Fig. 10 and Fig. 12 of the manuscript. The hypothesis was formulated as a working-hypothesis. A detailed discussion about the covariation is given further below.

Comment: “If Atlantic water column restructuring had a strong influence on size through accumulation of nutrients we would expect this effect to be visible everywhere in the Tropical Atlantic.”

Response: In my opinion, the effect is visible in the tropical Atlantic, shown by the very similar pattern in size evolution of *G. menardii* in the western and eastern tropical Atlantic as well as in the Caribbean Sea (Fig. 12).

The proposed AMOC and thermocline hypotheses are an attempt to explain the observed test-size pattern within the Atlantic Ocean, but it is clear that further work and studies are needed to test these hypotheses. *Globorotalia menardii* is known to thrive within the thermocline and the chlorophyll maximum zone (e.g. Ravelo et al., 1990), so that a

relation between the food availability and the test size can be proposed.

Comment: "Additionally, if size increased due to nutrient accumulation in the thermocline we would expect to see a size increase in all thermocline dwelling species at the same time. For as far as I know, no such increases are known for any other species."

Response: To my knowledge there is no quantitative study available that relates nutrient enrichment with size evolution in PF and none - besides these mentioned in the manuscript - which investigates the test-size evolution of any other PF in geological timescales in the tropical Atlantic Ocean which may give further evidence or reject the thermocline hypothesis. If the reviewer knows of any studies which could help to prove or disprove the hypothesis, I would be very interested and grateful, if the reviewer could share these.

Furthermore, if other thermocline PF species show another size evolution through time compared to *G. menardii*, this does not automatically mean that the thermocline hypothesis is wrong. Other thermocline species may well react in different manners to the respectively experienced ecological conditions. For example, they may have different diets, a different ontogenetic development and different lifetimes. Due to their ecological preferences, it is rather likely that they will react in different manners to AMOC-strength induced changes in the water column than *G. menardii*.

In addition, the AMOC is mostly likely not the exclusive environmental factor influencing the test size of *G. menardii*.

Comment: "Finally, if ϵNd and *G. menardii* size are linked we would also expect an increase in size in the interval 3.5-5.5 Ma, when ϵNd values were comparable to those of the interval with giant specimens. As *G. menardii* reached minimum size values in this interval, I am not convinced there was a strong link between ϵNd and size."

Response: I disagree with the reviewer. In the time interval from 3.5 to 5.5 Ma, a size increase at ca. 4 Ma is clearly observed, which parallels the ϵNd values. The impression of an opposite evolution of the AMOC strength and the test size between 4 Ma and 5 Ma is probably an artefact of the lower resolution of the ϵNd record by Dausmann et al. (2017) and the approach of linear interpolation of this record used in this manuscript. The stable isotopic record in Figure 3c of Karas et al. (2017) suggest a relatively weak and stable AMOC from 4.5 to 5 Ma (see attached Fig. 1), precisely the time interval in which *G. menardii* shows a relatively small maximum size at Site 667 and 925. These results complement the data of Dausmann et al. (2017) and support the AMOC hypothesis. They will be integrated/added to Fig. 12 of the manuscript according to the attached figure 1.

A correlation between AMOC strength and the test-size evolution, even if not 1, is still recognizable. The system, however, is not strictly mechanistic and there are a multitude of subtle interrelationships between ecology and test size of *G. menardii*. A visual similarity between the ϵNd -trends and the test-size evolution cannot be denied.

In order to explain the missing strict, linear and cause-effect relationship, one may reason the following hypotheses:

- It is assumed that the younger giant *G. menardii* type/form (0-2 Ma) may have occupied a (slightly) different ecology (ecological niche) in comparison to the ancestral Miocene/Pliocene form (2-8 Ma). It is a non-analogous situation. The younger type thus might have not been affected in the same way by changes of the AMOC strength than the older form.

Evidence for this explanation is given by a modified form of Fig. A8a (see attached Fig. 1). It shows the correlation between linearly interpolated ϵNd values and the maximum size from Hole 667A for the time interval from 0-2 Ma (blue points) and 2-8 Ma (orange points), which fall into two groups. Fig. A8a and A8b will be modified according to attached figure 2.

- Due to the closure of the Central American Seaway, the Atlantic's hydrography and oceanography altered and the AMOC strength changed significantly (Haug and Tiedemann, 1998; Haug et al., 2001) which can explain the distribution of points in the attached figure 2.

Although the correlation seems weak, there is a visual correlation between ϵNd – trends and the test-size evolution from 3 and 8 Ma (Fig. 10, 12), which in my opinion is worth to be mentioned and to be tested in future studies.

Comment: "In the Agulhas Leakage hypothesis giant *G. menardii* are transported from the Indian Ocean, around South Africa into the tropical Atlantic Ocean. Although a giant form existed in the Pacific, no existing or new data is presented to suggest that giant forms also evolved in, or migrated to the Indian Ocean. A record of Indian Ocean *G. menardii* size is needed before the Agulhas Leakage hypothesis can be tested."

Response: I agree with the reviewer that data from the Indian Ocean are needed to check, if the ALH is possible. As mentioned in the manuscript at L385-386, a second study is currently in progress which investigates the test-size evolution in the Mozambique Channel.

At the moment, we have to rely on the data from Site 503 in the eastern tropical Pacific. The description of a second core would go beyond the scope of this paper. The present study is of preparatory nature, whose results are discussed in terms of the three hypotheses described in the manuscripts. It is a precondition for testing the ideas presented.

Passages in the text will be revised which may be misunderstood in a way that the data of this study can prove the ALH.

Comment: "The Local Evolution hypothesis discusses whether the giant *G. menardii* evolved locally through punctuated evolution. The resolution of the record presented here, with a sample resolution of 0.1-0.2 million years, is too low to test for sudden evolutionary events taking place in as little as 50,000 years (line 397). A much higher resolution record of the interval around (suspected) speciation is necessary to test for sudden punctuated evolution. A higher-resolution record could also help distinguish between the Agulhas Leakage and local evolution hypotheses: local evolution is likely a single interval with increasing maximum size, whereas leakage of eddies could have

resulted in the sudden appearance of fully formed giant *G. menardii* several times. A higher resolution record with sample spacing of 5-10 kyr might be able to detect these differences.”

Response: The reviewer is right: the data presented here cannot test this hypothesis, but please note that the dataset is not primarily intended to test a punctuated-evolution event. The hypothesis of a punctuated, evolutionary event was proposed by Knappertsbusch (2016) as an alternative hypothesis, which may explain the size increase in case the ALH fails (personal communication). The idea of this local evolution can only be validated by an additional, more detailed high-resolution record within the Gelasian stage, but is beyond the scope of the present work.

Please note that the cited literature examples for punctuated evolution in the paper rely exclusively on single cores and neglect the regional/geographical aspect of evolution. As far as I know, none of them tested their results in additional cores from different locations. Sudden changes in the morphology of a species may equally be caused by an immigration event from another location and so mimic rapid evolution.

Response to “Methods”

Comment: “The Methods describe species identification based on the number of chambers in the final whorl. However, chamber number alone is not enough to distinguish Menardiform species. The species descriptions in the Neogene planktonic foram atlas (Kennett & Srinivasan, 1983) state that *G. menardii* has 5-6 chambers in the final whorl, *G. limbata* has 6-8 and *G. multicamerata* has 8 or more. Additionally, *G. exilis* and *G. pertenuis* have 5-7 and 6-8 chambers in the final whorl, respectively. Therefore, specimens with 6 or fewer chambers, which the manuscript calls *G. menardii*, could be either *G. menardii*, *G. limbata*, *G. exilis* or *G. pertenuis*. The *G. menardii* size record presented in the manuscript could thus be a composite of several species, and any changes in size could reflect changes in relative species abundance rather than an evolutionary event.”

Response: Please see the comments on page 1 and 2. Chapter 2.4 of the manuscript will be revised according as follows:

All menardiform specimens were identified on species level by illustrations in Kennett and Srinivasan (1985), Bolli et al. (1985) and in comparison with the reference collection to “49 Cenozoic planktonic foraminiferal zones and subzones prepared by Bolli in 1985 – 1987”. This included also the identification of *G. exilis*, *G. pertenuis*, *G. miocenica*, *G. pseudomiocenica*, *G. tumida*, *G. merotumida*, *G. plesiotumida* and *G. unguata*, which all are easily to distinguish from *G. menardii*, *G. limbata* and *G. multicamerata*. Diagnostic features included the size, the outer wall structure (porcelaneous appearance due to finer perforation), number of chambers in the last whorl and the δX and δY ratio. After species determination, forms like *G. exilis*, *G. pertenuis*, *G. miocenica*, *G. pseudomiocenica* and the *G. tumida* group were sorted out and not included in the present morphometric study. Thus, the dataset presented herein only contains specimens of *G. menardii*, *G. limbata* and *G. multicamerata*.

I am aware of the problem to distinguish *G. menardii*, *G. limbata* and *G. multicamerata*. The apparently most distinctive morphological character of *G. limbata*, its limbation of the chamber sutures on the spiral side (Kennett and Srinivasan, 1983), is difficult to recognise and is also observed in *G. menardii* and *G. multicamerata* (Knappertsbusch, personal communication; personal observation). In order to crystallise a possible cladogenetic pattern between *G. menardii* and *G. limbata*, the present study experimented with the

pragmatic discrimination that *G. limbata* has only 7 chambers in its last whorl. In the absence of other taxonomically clearly distinguishable parameters this approach is to be understood as an experiment, which seems to work well. *Globorotalia limbata* became extinct at ca. 2.4 Ma (Wade et al., 2011), which falls together with the observation that the abundance of 7-chambered *G. menardii*-like specimens drastically decreased and are only rarely found from 2.5 Ma to present (Knappertsbusch, 2007, 2016; this study). Another point favouring this definition is observed in Figure 5, 6 and 7 in the manuscript, which show that 7-chambered *G. menardii*-like specimens have an intermediate position between *G. menardii* and *G. multilocamerata* and indicate a cladogenetic trend within the time interval from 5 to 4 Ma.

Comment: “*G. exilis* and *G. pertenuis*, which evolved from *G. limbata* are not mentioned in the manuscript, even though both were present in the tropical Atlantic at the time of the study interval (e.g. Chaisson & Pearson, 1997; Chaisson, 2003). These two species became extinct around 2.0 million years ago, around the time that *G. menardii* size increased.”

Response: *Globorotalia exilis* and *G. pertenuis* were present but show exclusively episodic occurrences and were rare in number. Only the assemblage of the sample at 2.3 Ma was monospecifically composed of *G. exilis* and *G. pertenuis* specimens. For these reasons and to make morphological patterns more readable, these species were excluded from this study. The inclusion of these species would have gone beyond the scope of this paper and must be reserved to a separate high-resolution study.

Comment: “I wonder if this size change could in part be explained by a removal of smaller Menardiform species in the assemblage.”

Response: I am not entirely sure if I understood the intention of this comment correctly. All intact specimens >63 µm of *G. menardii*, *G. limbata* and *G. multilocamerata* were included in this study, as was described in section 2.3 and can be seen for example in figure 8 of the manuscript at 2.057 Ma.

In case the reviewer intended a different thread, I ask the reviewer to specify his comment.

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Please also note the supplement to this comment:

<https://bg.copernicus.org/preprints/bg-2021-67/bg-2021-67-AC3-supplement.pdf>