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# Biostratigraphy of large benthic foraminifera from Hole U1468A (Maldives): A CT-scan taxonomic approach

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Swiss Journal of Geosciences

# Biostratigraphy of large benthic foraminifera from Hole U1468A (Maldives): A CT-scan taxonomic approach

--Manuscript Draft--

| | |
|---|---|
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| **Abstract:** | Large benthic foraminifera are important components of tropical shallow water carbonates. Their structure, developed to host algal symbionts, can be extremely elaborate and presents stratigraphically-significant evolutionary patterns. Therefore their distribution is important in biostratigraphy, especially in the Indo-Pacific area. To provide a reliable age model for two intervals of IODP Hole U1468A from the Maldives Inner-Sea, large benthic foraminifera have been studied with computed tomography. This technique provided 3D models ideal for biometric-based identifications, allowing the upper interval to be placed in the late middle-Miocene and the lower interval in the late Oligocene. |
| **Response to Reviewers:** | See attachment |

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06 December 2017

Prof. Wilfried Winkler
Editor-in-Chief
Swiss Journal of Geosciences

Dear Prof. Winkler,

I wish to submit our manuscript entitled ′ **Biostratigraphy of large benthic foraminifera from Hole U1468A (Maldives): A CT-scan taxonomic approach**′ for consideration for the Swiss Journal of Geosciences, **Swiss Sed Special Volume**.

Our study defines a reliable age model for two intervals (middle Miocene and late Oligocene) dominated by shallow-water material retrieved in IODP359 Hole U1468A, from the Maldives Inner-Sea. Our biostratigraphy is defined by the large benthic foraminifera (LBF) assemblages with their biometric-based, species identification established from data obtained through computed tomography as opposed to the classical thin section approach. As LBF have significant stratigraphic importance, this study contributes to the knowledge of LBF biostratigraphy in the shallow-water environment. In addition our use of CT-scanning and establishment of a concise and reliable mounting mechanism for LBF is extremely beneficial for palaeontologists, biostratigraphers and sedimentologists alike as it makes LBF biometry accessible for a wider audience.

With the present letter, we confirm that none of the submitted data has previously been submitted or published elsewhere. This research was funded under the Swiss National Foundation project number 200021_165852 / 1.

Thank you for the consideration.

With our best regards,
Giovanni

Click here to download Authors' Response to Reviewers' Comments Anwers to reviewers.doc

**Answer to Reviewer 1 (Alberto Collareta)**

First of all I would like to sincerely thank you for your dedicated and patient work on the manuscript and for your useful suggestions. Pleas find below the answers to your comments on the initial version of the paper.

**Comments on the annotated manuscript (the lines indicate the lines of the original manuscript)**

**Lines 20-21** (I don't know how many keywords are allowed by the journal, but perhaps a couple of them could be dedicated to the utilized methodology (e.g., Computed Tomography scanning, micro-CT...):

The journal allows up to 6 keywords, therefore I have removed morphology, which is far too generic, and included Microtomography.

**Line 37** (I would use LBFs as plural form.):

Although the form LBFs is also used, most of paper uses LBF, and is always intended as plural.

**Line 59** ("...further difficulties in correlation.": references would be useful here.):

According to your suggestion I have included in this sentence a reference to Renema 2015. In the paper the author discuss in detail the heterogeneity of the evolutionary process and the difficulty to make assumptions in this regard.

**Line 70** (The last sentence of the Introduction is quite long and awkward: please cut and/or rephrase.):

According to your suggestions in the new version of the manuscript I have rephrased this sentence.

**Line 88** ("...became restricted to narrow bands at the respective most oceanward areas": correct, but not promptly comprehensible. Please, reconsider and reformulate.):

According to your suggestion I have reformulate this sentence.

**Line 92** ("mbsf" is "meters below sea floor", isn't it? So that's not water depth! Please correct (and explain the meaning of mbsf if needed).

Yes it is, I am sorry this is a typo. In a draft version of the manuscript the final depth of the hole was included. However, it was removed later, but unfortunately mbsf was left behind. I have corrected this mistake in the new version of the manuscript.

**Line 117** (What measurement does "5 cm" stand for? Specify.):

5cm is the length of the shaft, I have rephrased the sentence in order to describe more clearly the sample holder.

**Line 192** ( "remarkably" is a bit weird here... "largely" instead?):
I have revised the manuscript according to your suggestions.

**Line 269** (Hofker (1933) originally described *Planoperculina heterosteginoides* as a species within the genus *Operculina*. Therefore, parentheses would be needed here. Please check this way every singles species you cited: I suppose that several parentheses would be needed here and there enclosing author-year pairs.):

Thank you for your correction. I have checked the manuscript to correct similar problems.

**Line 362** (Take care of italicizing completely specific names (here and later), and nothing more.):

Thank you for your correction. I have checked the manuscript to correct this problem.

**Lines 381, 383 and 398** (Here and in a few other instances in the rest of the manuscript: commas should be uniformly avoided between subject and verb.):

I hopefully corrected this mistake.

**Line 405** ("the paper". What paper? Specify.)

In this instance I was intending one of the figure of Betzler et al. 2017 (which is the IODP report of hole U1468A). In order to deal with the request of an other reviewer I have removed this paragraph entirely.

**Line 412** (I would strongly advice not to include references to "in prep." works. Use "pers. obs." rather than "in prep.".):

In the revised version of the manuscript I tried to reduce as much as possible the reference toward the oncoming work on the detailed plankton stratigraphy of Hole U1468A.

**Line 447** (Although something has already been written at line 127, it would be very interesting if you could make explicit here how much time was spent on each working phase versus expected working time spent using "classical" methods - just a couple of reliable estimates, nothing more.):

I have included in the discussion more or less how much time we spent on each working phase. While the 12 hours of scanning is a good estimate, the 72 hours of post-processing and the 48 for the measures are probably “rounded down” estimates. There were three of us working on the data, and it took us more or less three days for the post processing, working all day long (and part of the night). More or less three other days were necessary for the measurements, but in this case there was some spare time. From the beginning to end, if you are alone and have no other distractions I

think you can do 100 specimens in a week.
Comparatively speaking you can do probably even twice as many thin section samples in a week (not considering the measurement phase) but your success rate (I define success as a perfectly orientated equatorial section) is going to be a lot lower. With this CT scanning method the success rate is 100%.

**Line 478** (Add referees and editor, if you like.)

I will for sure.

**Lines 746, 763, 776 and 790** (Please make the name of the genera explicit the first time you mention them in a caption.):

I have revised the captions according to your suggestion.

**Line 804** (Please, provide a new version of figure 8 with italicized generic and specific names.)

Figure 8 has been revised. The new version is characterized by a less condensed font. The latter was the cause of the visual lack of italicization in the names.

**Line 811** (Please, provide PDF versions (rather than DOCX versions) of Online resources 1, 2, 3, and 4.)

According to your suggestion the revised version of the supplementary material are in .PDF.

**Answer to Reviewer 2 (Anonymous)**

I would like to thank you for your revision work, you suggestions and your advices that improved the manuscript by tackling some of the major issue of the initial version. Please find below the answers to the your comment on the original version

**Answer to the comments included in the letter**

**1** (Unfortunately, the main papers using growth-independent and growth-invariant characters for nummulitids, heterosteginids and Cycloclypeus have not been used, especially the first paper in the list below, which was published in 2011!!
Hohenegger, J. 2011: Growth-invariant meristic characters. Tools to reveal phylogenetic relationships in Nummulitidae (Foraminifera). Turkish Journal of Earth Sciences, 20, 655-681, 10.3906/yer-0910-43.
Hohenegger, J., Torres-Silva, A.I., 2017. Growth invariant and growth-independent characters in equatorial sections of Heterostegina shells relieve phylogenetic and paleobiogeographic interpretation. Palaios, 32, 30-43.
Torres-Silva, A.I., Hohenegger, J., Ćorić, S., Briguglio, A., 2017. Biostratigraphy and evolutionary tendencies of Eocene Heterostegines in Western and Central Cuba based on morphometric analyses. Palaios, 32, 44-50.):

Following your suggestions and for the purpose of helping future researchers interested in the taxonomy of *Heterostegina* and the other nummulitids, I have include in the revised version of the manuscript Proloculus size and Deuteroloculs ratio.
Unfortunately, at the time of preparing this paper, I was unaware of Hohenegger (2011). However, I was acquainted with these parameters as I have studied detail the Hohenegger (2000) paper and I have read both the Hohenegger-Torres Silva papers on Heterostegina. I find in particular Torres-Silva et al. (2017) extremely helpful for their clear and unambiguous way of naming the parameters of the embryo (PW, PH, DW, DH). An oversight on my part, unfortunately, was that the paper was not cited in the manuscript. This has been corrected in the revised version. Furthermore, to my knowledge, this the first paper (excluding those in which the creator of the parameter itself J. Hohenegger is an author) in which the back-ward bending angle is measured and its importance highlighted. It was an extremely useful parameter to clearly separate, on a numerical basis, almost symmetrical specimens of *Amphistegina* from involute nummulitids. The latter feat is simple with recent material, but on battered and partially recrystallized specimens is much more difficult (impossible with just the external morphology).
The additional parameters proposed in Hohenegger (2000) were not used in this manuscript for practical reasons. The specimens are far too broken for the parameters to be applied. The specimens in the nummulitids group (excluding *Heterostegina*) have, on average, a diameter of 600 µm and they have, on average, two whorls preserved. Using for example the charts with radius vs revolution angle (Hohenegger 2000; Hohenegger 2011) the vast majority of the specimens examined fall in a small field close to the origin of the axis where it is impossible to separate the different genera. The same problem is encountered with thickness vs marginal radius. Additionally, using chamber base length vs chamber number was problematic and in the majority of cases impossible. Finally, as most of my specimens are incomplete and abraded, at best I had up the 30$^{th}$ chamber present, most of the data presented in Hohenegger 2011 refers to chamber numbers above the 30$^{th}$ chamber and thus could not be applied.
I recognise that these problems could have been solved by scanning many more nummulitids to obtain a larger dataset. In this way, I could have found more well preserved specimens in the samples, however, their presence in the samples is not guaranteed. I feel as the main aim of the

paper was the biostratigraphy of Hole 1468A, and the whole *Nummulites*/*Operculinella*/*Operculina*/*Planostegina*/*Amphistegina* group is not particularly helpful in this regard, it was not necessary to focus more on this matter. Due to the overall poor preservation of the specimens, I initially scanned these specimens as from their external morphology their genus was indistinguishable. Regardless of their poor preservation, we were still able to measure a number of parameters and thus they were included in the manuscript. This was done to not only provide a clearer picture of the entire assemblage present in the samples but as they could also be useful for future researchers interested in the distribution and the taxonomy of these foraminifera.
Concerning *Heterostegina*, I did not use most of the parameters proposed in Torres-Silva et al. (2017) and in Hohenegger and Torres-Silva (2017) because they are used to characterize Eocene to early Oligocene *Heterostegina* from Cuba. My samples include late Oligocene *Heterostegina* from the Indo-pacific, in comparison a different time-frame and different bioprovince. Of course, if the aim of this paper was the taxonomy and phylogenesis of *Heterostegina* I would have applied more detailed analyses including all the classic biometric parameters (number of undivided chambers, number of chamberlets in 3$^{rd}$, 4$^{th}$ ,5$^{th}$ chamber etc.) and growth-invariant parameters. The purpose of the paper, however, was mostly stratigraphic and most of the *Heterostegina* species are identified just on the basis of the classic parameters, I have just applied the classic biometry.

**2** (In the chapter about Systematic Paleontology, the use of 'exemplum intercentrale (ex.interc.)' is doubtful, because the statistical prove (using analyses of variance etc.) of positions between two types are not given. If these are real continuous lineages, then an arbitrary interruption is not possible and clear differences in a more or less continuous line has to be named by subspecies, not by species, as done by Less et al. in his work on Eocene heterosteginids.) & (The data are well presented by their distribution parameters, but statistical comparison between types and the intermediate forms are completely lacking.):

In the paper the use of exemplum intercentrale follows the methodology of Ozcan et al. 2009 (Oligo-Miocene foraminiferal record (Miogypsinidae, Lepidocyclinidae and Nummulitidae) from the Western Taurides (SW Turkey): Biometry and implications for the regional geology). The limits for the population are those from Van Vessem 1978 which is focused on the study area. *N. ruttenii* is separated by *N. martinii* on the basis of the number of auxiliary chambers, the mean is 6.3 and the limit between the two species is 6.5. The mean of the population is closer than 1 standard error from the limit of the two species.
*N. isolepidinoides* and *N. sumatrensis* are separated on the basis of the degree of embracement and the number of auxiliary chambers. For our sample the mean number of auxiliary chambers of the population is within the limit of *N. isolepidinoides*. The mean degree of embracement is 43 and its standard error 2.33. Taking into account that the limit is 40, and that the examined population is small, I think it is safe to use the ex. interc. notation even in this case.

**3** (Further, short diagnoses of the genera should be presented.):

According to your suggestion short diagnoses of the genera have been included in the revised version of the manuscript. Genera diagnoses were not included in the original version of the paper because the journal has strict length-rules. Each page, starting with the 13$^{th}$, is directly charged to the authors. In order to have more space for the plates I tried to keep everything else to the essential.

**4** (The remarks on Operculinella (lines 294 to 298) are incorrect, the classification relies on internal features (see Hohenegger et al. 2000).):

I apologize for this mistake. The distinction between recent *Nummulites* and recent *Operculinella* is indeed problematic. According to Hohenegger (2000) *Operculinella cummingi* is characterized by the test developing an expansive, flat last whorl, while *Nummulites venosus* shows this construction only in very large specimens. Following Hohenegger (2000) transverse trabeculae, marking the branches of sutural canals on the surface, are diagnostic for the genus *Nummulites*. However, according to Renema 2018 trabeculae are not a good character, yet the author does confirm the importance of the morphology of the last whorl. Since my specimens are broken and in most instances without the last whorl ( in actual fact a large portion of the whorls were missing), in the revised manuscript, I have identified them as Nummulitidae sp.

**5** (The discussion about the stratigraphic position seems to be o.k., but must be supported by nannoplankton data!!! These investigations are lacking!!):

In the original version of the manuscript the independent age control systems used to verify and integrate LBF-based stratigraphy, I acknowledge, were not presented in a very clear way. In the revised version of the paper I have rephrased the last paragraph in order to clearly separate the LBF-based stratigraphy from the planktonic-foraminifera-based stratigraphy (which is from Betzler et al. 2017 and Spezzaferri et al. In prep). I have also included information on nannofossils (from Betzler et al. 2017) which further support the LBF stratigraphy. Finally I have modified the final figure to include all the information on biostratigraphic framework of the two studied intervals of Hole U1468A.

**Answer to Reviewer 3 (Willem Renema)**

Dear Prof. Renema, I would like to thank you for your work on this manuscript. Your suggestions greatly improved the overall structure of the paper and were extremely useful for the taxonomy of *Heterostegina*. I am sorry for the extremely long letter of answers, but I took this opportunity to discuss some problematic points. I am really grateful for your help. Please find below the answers to the comment you have included in the letter and to the comments directly referring to lines of the original manuscript.

**Answer to the general comments included in the letter**

**1) I think the style of writing can be improved. There is often unclarity because too many messages are included in a single sentence:**

The manuscript has been reviewed in this sense especially by the second author who is native English speakes.

**2) For these kind of works: Independent age control is needed:**

I agree, an external age control is extremely important in biostratigraphic works.
In this instance we already have a preliminary framework which is provided by Betzler et al. 2017 and is based on both planktonic foraminifera and calcareous nannoplankton. The planktonic foraminifera stratigraphy is currently being updated (Spezzaferri et al., in preparation). In the previous version of the paper information, on the external age control, was presented in a confusing way. In this revised version I have revised the discussion and the last figure to clearly separate our information on LBF stratigraphy from those based on other fauna.
According to planktonic foraminifera the first interval of this paper can be placed in zones M9 to M11 since we have *Fohsella fohsi* that appears in sample 71-CC and *Paragloborotalia mayeri* that disappears in sample 8-CC. This information is present in table T2 of Betzler et al. 2017 and is confirmed by the ongoing work of three of our authors (S. Spezzaferri, D. Kroon & S. Stainbank quoted in the paper as Spezzaferri et al. in prep.). Additionally, according to calcareous nannoplankton Interval One of this paper should span from zone NN6 to NN15 (M4 to M12), this information is also included in Betzler et al. 2017 (Biostratigraphy_Calcareous Nannofossils_Interval B). Both the planktonic foraminifera and nannoplankton stratigraphies are thus in agreement with LBF which suggest a M9 to M10 age. However, since this interval is dominated by LBF there are few planktoninc foraminifera and few calcareous nannofossils and therefore LBF are very useful and informative.
The top of the second interval (sample 107-CC), according to planktonic foraminifera, is in zone O7 due to the FO of *Paragloborotalia pseudokugleri*. An older age is suggested for the rest of the interval because both *Chilogumbelina cubensis* and *Paragloborotalia opima* occur in samples 108-CC and 109-CC suggesting an O4 to O5 age. Again, this information is from the ongoing work of three of our authors (S. Spezzaferri, D. Kroon & S. Stainbank quoted in the paper as Spezzaferri et al. in prep.). Betzler et al. 2017 report the first occurrence of *Paragloborotalia kugleri* in sample 105. This event marks the top of zone O7. Furthermore, according to calcareous nannofossils the top of this interval (sample 107-CC) is younger than 27.27 Ma and, therefore, it corresponds to upper zone O6 to O7 of Wade et al. 2011. This information is included in Betzler et al. (2017). Once again LBF are in substantial agreement since they suggest an upper zone O7 for sample 107 and an older age (O4 to O7) for the other samples. As this interval is also dominated by LBF, plankton stratigraphy is limited by scarce occurrences of key species , but the planktonic foraminiferal

stratigraphy is in sufficient agreement with the LBF stratigraphy.

**3) Detailed morphological data are needed. This means not only morphometrics, but also presence/absence or difficult to quantify characters are needed (e.g. coiling, presence of alar prolongations, alar prolongations divided into chamberlets or not etc)**:

The characteristics of alar prolongations is indeed an important character for *Heterostegina* and is useful from a biostratigraphic point of view. Therefore, we have investigated the models more carefully. Unfortunately, most of the times the preservation is far from optimal. However, in the best preserved specimens of *Heterostegina*, it was clearly possible to see the division of the alar prolongations into chamberlets. This supports their placement into the *Vlerkina* sub-genus. The importance of these structures has been addressed in the revised version of the manuscript.
It must be stressed that the purpose of this paper was supporting the age model of the hole by providing data on large benthic foraminifera, which were initially not considered as a possible instrument for dating in the original report of the Hole (Betlzer et al. 2017). Therefore the paper was mostly focused into identifying the age diagnostic species.
The preservation of the material, as mentioned above, is far from perfect, this is presented in Betzler et al. (2017) (fig. F5B and fig. F7B). The large majority of the specimens appear as small lenses of calcite with no clear external structures or ornamentation. The large majority of the specimens are also broken so most of the time the later whorls are lost. *Cycloclypeus annulatus* most of the time was reduced to just the central umbo and was basically identical to the *Amphistegina*/*Operculina*/*Operculinella-Nummulites* group. Recrystallization and glauconitization was also fairly common in the Oligocene interval. Therefore, even though our focus was biostratigraphy and we were only interested in a few genera, we had to scan a large number of specimens to have a decent amount of good material.
The scanning procedure itself was designed to produce a large number of good 3D models rather than a few exceptional reconstructions. This was achieved by scanning a larger number of specimens using a shorter scanning time. We never had the aim to enter the taxonomy of most of these groups, nor do we have the proper material (for example most of the growth-independent parameters used by Hohenegger in its 2000 paper on nummulitids require complete specimens to see differences between the groups, but most of our specimens have two whorls at best; we have also tried some reconstruction with Avizo but the results were questionable).
However, I thought it would have been a waste of material to not describe and document the large number of scanned nummulitids and A*mphistegina*. I thought it could have been useful for future researchers. On the other hand I also restrained myself to do more detailed analyses on the non-age diagnostic groups because it was outside the aim of the paper. Probably a series of papers, each focused on a single genus, would be necessary to properly address the problem with sufficient precision.
Furthermore, most of the taxonomy of fossil specimens is still based on simple 2D parameters, since, aside from a few recent papers, most of the literature is based on thin sections. Therefore, for many groups, more detailed analyses would not produce more accurate identifications because there are no references in literature. This is the case for example for lepidocyclinids. Most of the papers base their identifications on the embracement of the protoconch, the number of chamberlets on the deuteroconch and the pattern of equatorial chambers. In recent papers some species of *Lepidocyclina* have been characterized on the basis of the distribution of the pillars and the characteristics of the cubicula (e.g. Boudagher-Fadel & Wilson 2000 _ A revision of some large foraminifera of the Miocene of SE Kalimantan_ Micropaleontology 46, 153-165). But the authors do not provide a taxonomic keys for these characteristics. Furthermore most of the identification are based on the description of the characteristics (e.g., Dark finely micro-granular pillars; Dark thick pillar of finely microgranular calcite; Club-shaped pillars; Club-shaped hyaline pillars; Strong pillars), which is extremely subjective especially because they do not provide a comparative table of

these characteristics.
There is a series of interesting papers from Schiavinotto (Schiavinotto 1993 Neanic stage biometry in *Nephrolepidina praemarginata*_ Bollettino della Società Geologica Italiana 112: 805-824; Schiavinotto 1992_Neanic stage of *Nephrolepidina tourneri* biometry and biostratigrafic implications_Bollettino della Società Paleonotologica Italiana 31: 189-206; Schiavinotto 2010_ Neanic stage biometry in Nephrolepidina from the Upper Oligocene of Lonedo (Lugo di Vicenza - Northern Italy)_Bollettino della Società Paleontologica Italiana, 49: 173-194). In his work, the author discusses the possibility to use a series of 2D parameters, related to the shape of the neanic equatorial chambers of *Nephrolepidina*. He provides a lot of information and explains clearly how to do the measurements. However, the results are not incredibly beautiful (useful?), and they require a really large number of measurements for each individual. But the major problem is that they are used only by Schiavinotto who worked in the Western Tethys in a couple of localities.
This problem occurs with most of the papers based on the 3D approach as the reference material is patchy And the bulk of information is still in 2D.
We thus see the importance of expanding the knowledge on the basis of 3D measurements and this is addressed in the revised manuscripts discussion. But establishing a new LBF taxonomic based on advanced 3D analyses is not the purpose of this paper and is far above our skill.

**Answer to the punctual comments in the letter (the lines indicate the lines of the original manuscript, as indicated in the letter itself)**

**Line 37** (LBF have not been present since the Paleozoic. In several time periods since the Carboniferous different groups of benthic forams evolved gigantism.):

My sentence was specifically referring to Fusulinidae. I honestly am not an expert of the group and I have always relied and take for granted the general information delivered during paleontology lessons which describe them as large, symbiont bearing foraminifera. There are actually papers that support this view (e.g. Groves J.R., Pike M., Westley K., (2012) – A test for the possibility of photosymbiosis in the extinct fusuline foraminifera: size and shape related to depth of habitat. Palaios, 27: 739-752. “ The trend is not likely the result of hydrodynamic adaptation, postmortem size sorting or size decrease along a bottom oxygen gradient. It most likely reflects geometric optimization for photosymbiosis”). It was an honest mistake, I apologize for it and I have changed the sentence in the revised version of the manuscript.

**Line 40** (I am also not convinced that 'adaptive strategy and evolution are relatively well known' (line 40). Part of the LBF community place all their findings in the context of nepionic acceleration, ie within lineages the initial chambers get progressively larger, test size increases, and test complexity increases more rapidly, but especially cross-correlation over longer geographic distances is needed to test these assumptions.):

Following your suggestion in the revised version of the manuscript. I have tried to present this concept in a more correct way, highlighting that there is still a lot of research that needs to be done. The problem is also discussed in the final paragraph of the discussion in the new version of the manuscript.

**Line 49** (I think Renema 2018 is a better citation for this, it ads terrestrial influence to this equation, as well as provides much more details about the diversity pattern. With respect to the diversity

pattern Langer and Hottinger (2001) should be cited as well.):

Thank you very much for these suggestions! It is a real pity that your 2018 paper was published online only in mid December (we submitted this paper in the first week of December), its taxonomic scheme is very clear and complete, it would have helped us a lot (an awful lot actually!) for the nummulitids and the *Amphistegina* species. Thank you very much!

**Lines 50-52** (Renema, 2006 would be a better citation here, as I actually describe the contribution of LBF to the sediment in the interreef area. Here I show that in the Spermonde and Berau archipelago LBF can make up substantial parts of the sediment. Although not quantified, by looking at the grainsize distributions (as well as additional analyses) LBF can make up a large part (>50%) of the sediment in these environments. Furthermore, on Pacific atolls LBF (especially calcarinids) are the dominant producer of sediment as well (see refs in Renema, 2018).
With respect to the GBR: I do not provide original data on the GBR in the Renema et al 2001 paper, but cite Tudhope and Scoffin, 1988, who similar to the findings in Indonesia, found that LBF can be dominant in the inter reef sediment, and that they are the second important carbonate producers in the GBR system (second to calcareous algae), when next to the reefs also the lagoon is incorporated.):

Thank you very much also for these suggestions, I have included this paper in the revised manuscript.

**Line 56-59** (It is true that in the time that LBF were the (almost) only easy tool for biostrat in (sub) tropical shallow settings, independent age control was difficult to obtain. When this was looked for these were mostly planktonic forams. However, in recent times numerous additional tools became available, including cacl. Nannoplankton and Strontium Isotope Stratigraphy. Integrating these data challenges some of the paradigms on LBF evolution (Renema, 2015)):

In the revised version of the manuscript I have changed the title paragraph 6.2 into “CT-scan and LBF biostratigraphy” to try to address the existing knowledge gap and suggestions for the future. In the introduction paragraph I have removed the the part of the sentence focused on planktonic foraminifera.

**Line 133 and further** (I would suggest to name characters similar to other studies, for example, PW=DII in van Vessem):

You are highlighting a major problem of the LBF biometry in my opinion:
Van Vessem (but also Schiavinotto in his various papers) for example uses DII for the diameter of deuteroconchh measured perpendicular to the medio embrionic line.
Chaproniere 1980 measure DII <u>along</u> the medio embrionic line.
Ozcan and Less 2009 call the diameter of the deuteroconch (measured perpendicular to the medio embrionic line) simply D. On the other hand they use P for the diameter of the protoconch measured perpendicular to the medio embrionic line.
Furthermore:
P is also used for the protoconch measurements of *Heterostegina* by Daya and Biginot 2005, whereas for Torres-Silva et al 2017 is PW (always speaking of *Heterostegina*)

The same value is measured two different ways and called in countless different ones. And this is just a result of a quick search. The same problem occurs with most parameters. Auxiliary chambers are the worst. They are counted, and defined in countless different ways. Even within the papers of the same author (Schiavinotto) you can find two different methodologies!

I have tried to find a common ground between the different papers, but it was hopeless and frustrating. For protoconch and deuteroconch parameters I have tired to follow the naming system used by Torres-Silva et al. 2017. I think is more clear to have P for the protoconch and D for the deuteroconch and use W and H to differentiate width and height respectively, instead of using again DII which is ambiguous.
However, I will leave to you the final decision and I am open to further suggestions on the subject.

(**furthermore, for clarity, I would suggest to name NX Nx (N subscript X) (and in other characters where measurements are taken per whorl).) & (I find the name Nx for the number of chambers in whorl x confusing, as N is usually used to indicated number of specimens**):

In this instance I have followed Bendetti et al. (2017) and I have capitalized everything in to conform with the other parameters.
Following your suggestions, I have used subscripts andchanged NX in $NC_X$. Consequently I have changed the diameter of the whorl from DX into $D_X$.

(**I would suggest to make the order - coiled, - heterosteginids, - cyclclypeus, lepidocyclinids as that is more following morphotypes (the former are mostly all nummulitids (and Amphistegina), the latter only lepidocyclina.**):

I have changed the text according to your suggestion. Consequently I have also modified the order of the schematic drawings of figure 3. All this part has been included in Figure 3 in the revised version of the paper.

(**I find it very confusing that X is not used consistently with other studies (here number of Operculine chambers, in other studies the number of Operculine+Heterostegine chambers (=N preannular chambers, for this Y is introduced.**
**Perhaps following the naming of a single paper (e.g. Chaproniere who also includes both lepidocyclinids and nummulitids) is a more consistent solution than inventing a naming scheme of characters on your own (my X = your Y = pc (number of precyclic chambers, eg Fig 4. 5 in Chaproniere (1980)) & (For Cycloclypeus I would include the proloculus and deuteroloculus in X, like Chaproniere (1980, 1984) and Renema (2015). In this definition X= number of pre-annular chambers, and the number of chamberlets per chamber also can be directly compared. This would mean that X=3 in line 239 rather than 1.**):

For *Cycloclypeus* I have mostly followed Ozcan and Less (2009) (which also has *Lepidocyclina*, *Heterostegina*, *Cycloclypeus* and nummulitids). I have also chosen to use X, because in Benedetti et al. (2017) (which is focused on *Heterostegina*) X was defined in this way.
Following your suggestions I will include the two embryonic chambers in X. I will also use PC for precyclic chambers.

**Line 138-141** (A single line is described for the orientation, whereas the equatorial plane is defined by two lines. How was the other direction oriented in to represent the optimal section? Again, one of the strengths of CT scanning is that you do not have to determine this orientation, but can work in a reference frame independent of orientation which often results in additional noise in the measurements. Furthermore, several taxa (including lepidocyclinids and Cycloclypeus) are often not perfectly flat, but wavy or saddle shaped in the equatorial plane. These could be the reason to find radiate structures in Nephrolepidina.):

This paragraph was perhaps a bit ambiguous. Due to the problems in the measuring system of the protoconch and deuteroconch diameters I thought it would have been more clear to state that all the embryo-related measurements were done using the medio embrionic line as reference.
The equatorial section was identified by moving the cutting plane and rotating the model in Ct vox. Often for there was not a perfect equatorial section and I made the measurements moving through slightly different sections. This was actually pretty common for *Cycloclypeus*. This method was also necessary to access the correct number of auxiliary chambers in *Lepidocyclina*.
In the revised version I have removed this paragraph. It is more straightforward to introduce the first parameter involving the medio embrionic line and then explain the medio embrionic line.

**Line 167** (would be useful to provide illustrations of this here. Four different types are already figured in fig. 3, so adding the 5th and a legend would be sufficient):

You are absolutely right. The F parameter is used quite often but the comparative chart is only present in Chaproniere's 1980 work, a complete legend would be really useful. I have created a drawing similar to those of Van Vessem for F=3.I have also included the F value in the caption of the figure in the revised manuscript.

**Line 181**: number of specimens is not provided for the averages provided in the SOM. I would also suggest to provide the underlying measurements (ie, measurements per specimens) in the SOM.

I have included this numbers in the SOM.

**Line 183 and further** (I think the descriptions are very brief, and missing some critical data to evaluate the findings, especially in the nummulitids.):

The brief descriptions are partly a matter of necessity. The journal has a strict policy of a maximum number of 12 pages (including figures) for papers. A page charge is applied from the 13$^{th}$ page onward. Since the space was an issue I had to choose between plates and descriptions, I opted for the former. Actually the paper has 4 full page plates for a total of 96 panels. This is the main reason why the description are extremely short. As you have correctly highlighted the importance of the morphology of alar prolongations and the degree of involution in the distinction of nummulitids in general and Heterostegina in particular (in this regard I really have to thank you for your paper on the Heterostegina lineage. Together with Banner and Hodgkinson it was incredibly helpful for me). Therefore, in the revised manuscript I have included a more information of these key features in the nummulitids.

(**Also, it would be nice to provide information on in which samples the species was found, how many specimens were examined etc to provide some context to better follow what is discussed.**):

According to your suggestions and those of Rev2 I have included the number of examined specimens in the table of the supplementary material with the complete set of biometric parameters. It must be stressed that although we examined about 160 models in total a lot of them were horribly preserved and were unusable. Other specimens were so poorly preserved that only the embryo was recognizable. Most of the nummulitids were also fragmented, so while it was relatively easy to measure the number of chambers in the first whorl the subsequent whorls were often partially or completely broken. Therefore, for each parameters there is a different number of examined

specimens
The distribution of all the different species is included in Table 1.

**Line 241** (unclear 'embryo is generally surrounded by five additional precyclical chambers subdivided into chamberlets': you mean, next to the P&D there are 5 pre-annular chambers (X=7))

I totally agree that the sentence is extremely convoluted and confusing, therefore I have rephrased it. (Actually X=8 (X sensu Renema 2015) there are 5 chambers divided into chamberlets following the embryo and the undivided third chamber.). In the revised version it is more straightforward and hopefully clearer.

**Line 260** (Heterostegina sp1 should be compared to H. pleurocentralis and H. assilinoides).

Following your suggestion I have tried a comparison with the two species based on the description provided by Banner and Hodgkinson 1991. Consequently I have included this comparison in the remarks of the species.
*H. assilinoides* has a slightly larger proloculus (140 to 200µm), a significantly larger number of chamberlets in the 10$^{th}$ chamber and also just a single undivided chamber after the deuteroconch (compared to the 2 to 4 of *H*. sp 1).
*H. pleurocentralis* has a much larger proloculus (up to 400µm). The latter is also reniform in shape. Additionally it is characterized by a large number of chamberlets in the 4$^{th}$, 5$^{th}$ and 10$^{th}$ chamber. We have relatively few specimens well preserved specimens of this species (in the Oligocene samples in general the preservation was terrible and most of the examined ones were just battered remnants of something that was once an *Heterostegina*). But this morphology (small protoconch, many undivided chambers, very few chamberlets) was quite constant and well separated from *H. borneensis*.

**Line 267** (Planorperculina This is a dubious genus name (see discussions in Loeblich and Tappan, Banner and Hodgkinson, ***). The specimen illustrated definitely does not match with the extant species P/O heterosteginoides. (see illustrations in Hohenegger et al 2000; Renema, 2006, 2018):

I totally agree. I had quite a lot of problems with this species because of the different definition that are available in literature.
Not to mention the actual pictures:

Ercan Özcan, György Less, Mária Báldi-Beke, Katalin Kollányi 2010 – Micropaleontology - Oligocene hyaline larger foraminifera from Kelereêdere Section (Muê, Eastern Turkey) ;
Plate 4 specimen 26, identified as *O. complanata* and presenting incomplete division of the chambers.

Andrea Benedetti, György Less, Mariano Parente, Johannes Pignatti, Bruno Cahuzac, Ana I. Torres-Silva & Dieter Buh – 2011 – Journal of systematic Paleontology Heterostegina matteuccii sp. nov. (Foraminiferida: Nummulitidae) from the lower Oligocene of Sicily and Aquitaine: a possible transatlantic immigrant ; Figure 14 I, K rare but definitely present incomplete divisions of the chambers, once again identified as *O. complanta*.
Since I understood that the taxonomic picture was quite confused during the preparation of the paper I decided to use Hohenegger (2000) definitions, because that scheme was clear (I honestly prefer Renema 2018, which is far more clear, but it was not available when I was preparing the paper).

I am aware that my specimens are quite different by those represented in Hohenegger (2000), Renema (2006) and Renema (2018). The latter have a more open spiral and above all they have a lot of incomplete partial septula. My specimens have a more close spiral and much less incomplete septula. I think it makes sense since we are comparing recent specimens with Oligocene specimens. Therefore I have identified the specimens as *Operculina* cf *heterosteginoides* highlighting these points in the remarks.

**Line 320** Sphaerogypsina (It would be good to explicitly discuss the difference between sp1 and sp2, and its potential taxonomic relevance):

The differences between the two species have been highlighted in the remarks of *Sphaerogypsina* sp.2. However, I must say that we have analyzed very few specimens of *Sphaerogypsina* since it was not useful for the biostratigrafic framework. Therefore I have restrained myself from extensive taxonomic considerations because they are outside the purpose of this paper and the dataset is far too limited.
From what I have observed the main difference between the two species is in the embryo. The Miocene specimens has a trochospiral embryo while the Oligocene has a bilocular embryo. This possibility was already highlighted in a master thesis of 1962 (Wayne C. Horton, Foraminifera of the Cenozoic and recent genus *Sphaerogypsina* Galloway, Missouri Scholars'Mine). The text is available online and I think is one of the few (if not the only) work that tries to investigate morphology and taxonomy of *Sphaerogypsina*. I was unable to include the work in reference list since it is not a paper. The author highlights the presence of three embryo type: single chamber, two chambers and trochospiral. He also notes that the internal organization of the chambers is variable (regular column, no regular column; a lot of disorganized chambers around the embryo, no disorganized chambers around the embryo). This variability suggests that "*Sphaerogyspina*" includes a lot of species and probably more than one genera. As already stated, these kinds of considerations were well beyond the purpose of this paper and will require the analysis of a large number of specimens from different time periods and different areas. Additionally, I acknowledge that this foraminifera is so common in the geological record that resolving this group does require more attention.

**Line 380-395** (because of the inconsistency in the taxonomical boundaries between the papers that are discussed, it is no wonder that the stratgraphic ranges differ markedly between these studies. This is further emphasized because all studies use different ways to place the samples in stratigraphic context (from SIS, plankton forams, to LBF biostrat):

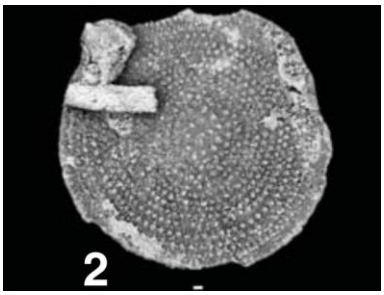
Indeed. It would have been nice to have single general and clear stratigraphic chart but most of the information are inconsistent. Therefore, I have preferred to present all the meaningful data on which I have based my conclusions, and they clearly point toward a late middle-Miocene age. I have also tried to use also the lineage proposed by Boudagher-Fadel and Prince (2010) on Journal of Foraminiferal research, but unfortunately the authors do not present the range of the parameters of the species. Furthermore, it uses a parameter P/E without explaining how it is calculated. It is clearly related to the embracement of the protoconch but how? Maybe area of the protoconch over the total area of the embryo?
However, taking into account all the information I am confident that a M9 to M11 age is a correct hypothesis for these *Nephrolepidina* species.

**Line 396** (I would say that the morphology of C. annulatus is closer to the early part of its range than the later part of its range, see Renema, 2015):

You are definitely right. I have read the graph with insufficient accuracy. I apologize for this and I have corrected the manuscript accordingly.

**Line 403-404** (unclear (identified on the basis of the image included in the paper). Does this mean it is figured in the Betzler et al paper? This is the site report of the cores in the current paper, so why is it in there, and are there no specimens of C. carpenteri included in this study? It is relatively easy to identify from C. eidae: the proloculus is twice as large and X much smaller. For stratigraphical reasons it is highly useful if it can be figured, and ideally morphologically described. The proloculus size of C. annulatus is very small for the top part of its range (Renema, 2015). I think the Renema et al 2015 paper referred to should be Renema, 2015, the former is mostly about Late Miocene and younger):

First of all, I have corrected the citation and referred instead to Renema et al. (2015)
Concerning *C. carpenter,* below is the image




This is the specimens reported in Betzler et al. 2017, identified as *Cycloclypeus*. But none of the *Cycloclypeus* we have measured had this ornamentation (nor a large protoconch). Since I have not observed its internal morphology I think it will be wiser to remove this paragraph. As you stated in you 2015 paper "specimens occur with variable surface ornamentation, but similar internal morphology" therefore guessing the identification of a just single specimens purely on the basis of its external ornamentation is wrong and against the methodology proposed in the paper itself: "Species identifications were done, wherever possible, based on biometric parameters."

**Line 423** (Hallock et al 2006 is 2004 in refs (which makes more sence)):

I have corrected the reference in the text, it was Hallock, P., Sheps, K., Chapronière, G., and Howell, M., 2006. Larger benthic foraminifers of the Marion Plateau, northeastern Australia (ODP Leg 194): comparison of faunas from bryozoan (Sites 1193 and 1194) and red algal (Sites 1196–1198) dominated carbonate platforms. In Anselmetti, F.S., Isern, A.R., Blum, P., and Betzler, C. (Eds.), *Proc. ODP, Sci. Results*, 194. I apologize for the mistake.

**Line 429** (what is meant with the 'only age diagnostic species remainng is H. borneensis? N. isolepidinoides is generally younger, but Nephrolepidina has a FO in Indonesia in the Middle Rupelian, so finding H. borneensis with Nephrolepidina is no surprise.)

The sentence probably needs to be reorganized because it is confusing. With the "only age diagnostic species" I was intending that in sample 109-CC *H. borneensis* is the only species with a biostratigraphic significance, while the others, like *A. mammilla*, are unhelpful from a biostratigraphic point of view. I have revised this paragraph and this sentence.

**(H. borneensis: see the discussion on its range and evolution in Java/Indonesia in Lunt and Renema (2014). There H. borneensis is most abundant in the middle Chattian, and younger**

**populations develop secondary chamberlets**.):

I have included this remark in this paragraph. Once again thank you for the suggestion.

**Line 446-458** (See earlier remarks. I think a comparison between traditional and new methods is needed for this to be a meaningful discussion. Only the characters that can be observed are included, and a discussing should be presented on preservation and the limits of the methods. Maybe it works well in these kinds of deposits, but also lepidocyclinids are completely filled in with calcite in Late Oligocene- Early Miocene carbonate platform deposits.):

In the revised version of the manuscript we have expanded this paragraph including a more detailet discussion on the limits and the benefits of this approach, a comparison with traditional methods.

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# Biostratigraphy of large benthic foraminifera from Hole U1468A (Maldives): A CT-scan taxonomic approach

**Running title**: Biostratigraphy of large benthic foraminifera

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**Keywords**

Microtomography; *Nephrolepidina*; *Cycloclypeus*; *Heterostegina*; *Amphistegina*; nummulitids.

**Abstract**

Large benthic foraminifera are important components of tropical shallow water carbonates. Their structure, developed to host algal symbionts, can be extremely elaborate and presents stratigraphically-significant evolutionary patterns. Therefore their distribution is important in biostratigraphy, especially in the Indo-Pacific area. To provide a reliable age model for two intervals of IODP Hole U1468A from the Maldives Inner-Sea, large benthic foraminifera have been studied with computed tomography. This technique provided 3D models ideal for biometric-based identifications, allowing the upper interval to be placed in the late middle-Miocene and the lower interval in the late Oligocene.

## 1 Introduction

Large Benthic Foraminifera (LBF) are important component in tropical carbonate platforms, major sediment producers and powerful tools for stratigraphic and environmental studies (Hottinger 1977; 1983; Schaub 1981; Lee and Hallock 1987; Pignatti et al. 1998; Serra-Kiel et al. 1998; Beavington-Penney and Racey 2004; Boudagher-Fadel 2008). Their tests present complex internal architectures, related to the presence of algal symbionts, that coupled with their external morphology, are fundamental for their taxonomy (Tan 1932; Loeblich and Tappan 1964; Haynes, 1965; Hottinger 1977). Their distribution is controlled by temperature, light intensity, water energy, substrate type, nutrient availability and detrital input (Hohenegger 1994, 2000; Langer and Hottinger 2000; Renema et al. 2001; Beavington-Penney and Racey 2004; Renema 2007, 2018). LBF are particularly common and diverse in the Indo-Pacific, where, from the Paleogene to present-day, they massively contributed to carbonate production (Hallock 1981; Tudhope and Scoffin 1988; Renema et al. 2001;

Renema 2006). Because of their high abundance, stratigraphy based on LBF represents a powerful dating tool (Van der Vlerk and Umbgrove 1927; Adams 1970; Chaproniere 1984; Boudagher-Fadel and Banner 1999; Boudagher-Fadel and Lokier 2005; Renema 2007). However, the correlation between carbonate platforms and the adjacent basin is challenging when independent age-controls are not available. LBF lineages can be regional, leading to further problems (Renema 2015). Specimen preparation is problematic in itself since perfectly oriented thin sections are necessary for reliable identifications (Briguglio et al. 2014). This approach is time consuming and destructive, making it impossible to obtain axial and equatorial sections of the same specimen (Briguglio et al. 2013). Computed tomographic scanner (CT-scan) overcomes these limitations, giving 3D representations of both external and internal structures along every possible section (e.g., Benedetti and Briguglio 2012; Hohenegger and Briguglio 2014; Briguglio and Hohenegger 2014; Briguglio et al. 2016).

Aim of this study is to provide a preliminary biostratigraphy for two intervals from Hole U1468A, drilled by the International Ocean Discovery Program (IODP) in the Inner Maldivian Sea, using LBF assemblages. Species identification follows a morphometric approach based on the results of the CT-scanning. Obtained ages are correlated with planktonic foraminifera and nannofossil distributions to provide independent age controls

## 2 Geological Setting

The Maldivian archipelago is a pure carbonate depositional system composed of two rows of atolls, separated by channels and surrounding the Inner Sea (Fig. 1; Aubert

and Droxler 1992). Carbonate platforms surround the atolls, while periplatform ooze sedimentation, locally accumulating as drift deposits, occur in the Inner Sea (Droxler et al. 1990; Betzler et al. 2013). The sedimentation started between the early Eocene and Oligocene. At first it was restricted to narrow bands on the oceanward areas, leading to the formation of a double row of atolls. Subsequently, platform margins prograded toward the Inner Sea and current-related, clinoform bodies characterized the region from the late middle-Miocene (Betzler et al. 2017). In one of the channels connecting the Inner Sea to the ocean, IODP Expedition 359 drilled Hole U1468A (4°55.98′N, 73°4.28′E, water depth of 521 m; Fig. 1). The recovered succession features eight units, among them Units II, VII and VIII are characterized by shallow-water carbonates and a rich LBF fauna (Unit II, 45.7–192.5 mbsf, 6H to 30F; Unit VII, 817.5-854.7 mbsf, 106X to 109X; Unit VIII, 854.7-865 mbsf, 110X to 111X; Betzler et al. 2017)

## 3 Methods

The first analyzed interval includes four regularly spaced samples spanning Unit II: 29F-CC; 22F-CC; 15F-CC and 7H-CC. The second interval consists of four samples covering Units VII-VIII: 110X-CC; 109X-CC; 108X-CC and 107X-CC. **S**amples were soaked in water, then washed through a 32 µm sieve and dried. In each sample LBF were selected, based on their external morphology, to represent the entire assemblage. 160 specimens were mounted with standard clear nail polish at distinct levels, 5 mm apart, around cylindrical Polyether ether ketone (PEEK) sample holders (Distrelec stock no. 148-21-756). Sample holders, manufactured in-house, were 6 cm in length, comprising a 5 cm length shaft (4 mm of diameter) and a 1 cm length base

(6.4 mm of diameter; Fig. 2). The base serves for easy mounting into the Bruker SP-1212 and SP-1213 CT stage extenders. The shaft allowed the fixation of 5 - 8 specimens at each level, depending on size (Fig. 2). Similarly sized individuals were mounted at each level (Fig. 2). Specimens were scanned with a multi-scaled Bruker X-ray nano-computer tomographic scanner SkyScan 2211, using an open X-ray source with a diamond-window target at energies of 60 kV and currents of 350 µA. Images were acquired on a 11Mp cooled CCD detector resulting in a voxel resolution of 2 µm. 180 degree scans were taken with a rotation step of 1° (25' of acquisition time for each level). Images were subsequently reconstructed with InstaRecon applying Gaussian smoothing, beam hardening and ring artifact corrections. Reconstructed images were analyzed with CTAn, CTVox and Avizo (FEI). After scanning, LBF specimens were removed from the PEEK sample holders with acetone. The biometric study focused on equatorial sections integrating different procedures proposed in literature (Fig. 3; Tan 1932; Van der Vlerk 1959, 1963; O'Herne 1972; Matteucci and Schiavinotto 1977; Van Vessem 1978; Schiavinotto 1978; Chaproniere 1980; Hohenegger et al. 2000; Less et al. 2008; Özcan et al. 2009; Hohenegger 2011; Renema 2015; Benedetti et al., 2017; Torres-Silva et al. 2017). Species identifications were mostly based on biometric parameters. Following Özcan et al. (2009), the notation exemplum intercentrale (ex. interc.) was used whenever the mean value of the identifying parameter of a group of specimens fell very close to the limits of two contiguous species of the same lineage. The complete biometric dataset is provided online (Online resources 1-4).

## 4 Systematic paleontology

Family Lepidocyclinidae SCHEFFEN 1932

Genus *Nephrolepidina* DOUVILLE 1911

Test discoidal, biconvex with a distinct layer of equatorial chambers and lateral chambers on each side. Megalospheric stage with a protoconch only partially embrached by the deuteroconch.

*Nephrolepidina* ex. interc. *rutteni* VAN DER VLERK 1924 -*martinii* SCHLUMBERGER 1900; Fig. 4a-n; Online resource 1

Test biconvex, symmetrical and rounded. Surface with common, randomly distributed pustules representing the outer termination of thick pillars. Remnants of a collar can be observed along the equatorial plane. Embryo of megalospheric specimens small (PW= 105µm; DW= 185µm), with a rounded to slightly rectangular protoconch which is largely embraced by the deuteroconch (Ai= 61%). The wall enclosing the embryo is thick, while the wall dividing the two initial chambers is thin. No ACI observed on the protoconch, NPAC= 2. External surface of the deuteroconch almost completely covered by ACII (NACII= 6.3). Chambers on the equatorial plane disposed in a wavy concentric pattern (F= 4).

Remarks

The average number of ACII observed in the examined specimens suggests a positioning between *N. martini* (6.5>NACII>4.5) and *N. rutteni* (NACII> 6.5; Van Vessem 1978). No remarkable variability observed among the samples, B∑ACII is rather constant.

*Nephrolepidina transiens* UMBGROVE 1929; Fig. 4o

Test biconvex, symmetrical and rounded. Surface with common, randomly distributed pustules. Remnants of a collar can be observed along the equatorial plane. Embryo of megalospheric specimens large (PW>250 μm; DW>350 μm), with an irregularly shaped deuteroconch. Wall of the embryo thick and surrounded by a large number of irregularly-shaped auxiliary chambers. Equatorial chambers disposed in a wavy concentric pattern (F= 4).

*Nephrolepidina* ex. interc. *isolepidinoides* VAN DER VLERK 1929 -*sumatrensis* BRADY 1875; Fig. 4 p-x; Online resource 1

Test biconvex, symmetrical and rounded. Surface characterized by common pustules. Remnants of a collar can be observed along the outer surface of the equatorial plane. Embryo small (PW= 130μm; DW= 200μm), composed of a rounded protoconch and a kidney-shaped deuteroconch, the latter only slightly encloses the protoconch (Ai= 43%). Wall enclosing the embryo as thick as the wall separating the first and second chambers. NPAC= 2 and NACII= 1.8, no ACI observed. Chambers on the equatorial plane disposed with an intersecting curve pattern (F= 1).

Remarks

The low NACII observed in this population, coupled with the low Ai value, places these specimens between *N. isolepidinoides* and *N. sumatrensis*. The former is characterized by an Ai<40% and NACII<2.25, while the latter has an Ai>40% and NACII>2.25 (Van Vessem 1978). Both Ai and NACII are higher in the specimens from 107X-CC and lower in those from 108X-CC.

Family Nummulitidae DE BLAINVILLE 1827

Genus *Cycloclypeus* CARPENTER 1856

Test large, circular, with a central umbo and a narrow periphery. Megalospheric stage has a central embryo composed of two chambers follwed by a short nepionic spire composed at first by undivided chambers and then by chambers divided into chamberlets by secondary septula. This nepionic spire is followed by annular chambers divided into chamberlets.

*Cycloclypeus annulatus* MARTIN 1880; Fig. 5a-i; Online resource 2

Test large and flat, with a central area surrounded by annular inflations as thick as the umbo (the test between the annuli is thin and fragile). Outer surface lacking evident ornamentations. Embryo consisting of a circular protoconch and a large kidney-shaped deuteroconch (PW= 195µm; DW= 245µm). The first two chambers are followed by a third undivided chamber (X= 3) and this entire structure is surrounded by a thick wall. The wall separating the three chambers from each other is thin. Specimens generally characterized by 7 to 8 precyclical chambers (PC= 7.8; S4+5= 10.7).

*Cycloclypeus eidae* TAN 1930; Fig. 5J-n

Specimens poorly preserved, broken and bioturbated. Test large and flat thicker at the center and thinner towards the edges. Outer surface granulated. Embryo composed of a small and rounded protoconch (PW 70 to 90 µm) and a hemispherical deuteroconch. One or two undivided chambers (X≈3-4) and two whorls of nepionic chambers follow the embryo, after which annular growth starts.

Genus *Heterostegina* D'ORBIGNY 1826

Subgenus *Vlerkina* EAMES, CLARKE, BANNER, SMOUT & BLOW 1968 emended BANNER & HODGKINSON 1991

Test lenticular, biconvex, planispiral and involute. Embryo of megalospheric specimens composed of two chambers, followed by a variable number of undivided chambers. Later chambers are divided into chamberlets by secondary septula. Alar prolongations generally subdivided into lateral chamberlets. In axial section it present a single layer of lateral chamberlets is present for each whorl of the spire.

*Heterostegina* (*Vlerkina*) *borneensis* VAN DER VLERK 1930; Fig. 5o-x; Online resource 3

Test, involute, planispiral, flat and thicker at the center. Some specimens seems to have pillars in the central part of the test, but the external surface is generally abraded and bioturbated, therefore, it is unclear whether or not ornamentations were present. Alar prolongations are narrow and divide into a single layer of lateral chamberlets. Embryo large and composed of a rounded protoconch followed and a kidney-shaped deuteroconch (PW= 210µm; DW= 250µm). This structure is followed by one undivided chamber (X= 3; S3+4= 3.9; S4+5= 7; S10= 7).

*Heterostegina* (*Vlerkina*) sp. 1; Fig. 6a-g; Online resource 3

Test large, planispiral, involute and thick. Outer surface unornamented. Alar prolongations narrow and divided into lateral chamberlets. A single layer of lateral chambers is present for each whorl. Protoconch and deuteroconch small; two to three undivided chambers follow them (PW= 105µm; DW= 110µm; X= 5.5). Compared to *H.* (*V.*) *borneensis* the subsequent chambers have less subdivisions (S3+4= 2; S4+5= 2.8; S10= 3.3).

Remarks

This species differs from *H. (V.) borneensis* by its smaller protoconch, more undivided chambers after the embryo, and less chamberlets in the first divided chambers. It also differs from other coeval *Heterostegina* (*Vlerkina*) species of the Indo-Pacific. The protoconch is smaller than both *Heterostegina* (*Vlerkina*) *pleurocentralis* and *Heterostegina* (*Vlerkina*) *assilinoides*, it has more undivided chambers and less chamberelets in the 3$^{rd}$ , 4$^{th}$, 5$^{th}$ and 10$^{th}$ chambers of the spire (Banner and Hodgkinson 1991).

Genus *Operculina* D'ORBIGNY 1826

Test lenticular, planispiral, from evolute to almost completely involute, with a lax spire. Septa can be regular or folded and can present partially developed septula.

*Operculina complanata* (DE FRANCE IN BLAINVILLE 1822); Fig. 6i-q; Online resource 4

Test planispiral, entirely evolute and very flat, with a granulated surface. Alar prolongations absent. Protoconch small and rounded (PW= 42µm). Deuteroconch small and kidney-shaped (PW= 23µm). Septa are quite regular and they do not have septula.

*Operculina* cf. *heterosteginoides*; Fig. 6h-k; Online resource 4

Test planispiral, entirely evolute, very flat, with a smooth outer surface. Alar prolongations absent. Embryo small and composed of a rounded protoconch and a hemispherical deuteroconch (PW= 60µm; DW= 60µm). Subsequent chambers partially divided by incomplete septula.

Remarks

This species has a lax spire and fewer incomplete septula than the extant *Operculina heterosteginoides*. Evolute nummulitids with incomplete chamber divisions are have a complex taxonomic history (Renema 2018). Since their revision is beyond the purpose of this paper we simply compare this species with the extant *O. heterosteginoides*, the most similar living representative of the group.

*Operculina* sp.1; Fig. 6r-x; Online resource 4

Test planispiral, moderately thick and involute with a smooth outer surface. Alar prolongations long and narrow. Embryo composed of a small rounded protoconch and kidney-shaped deuteroconch (PW= 35µm; DW= 29µm). Septa often bent and irregular as the main wall of the spire.

Nummulitidae sp. 1; Fig. 7a-f; Online resource 4

Test planispiral, thick, lenticular and completely involute. Alar prolongation long and narrow, not extending over the center of the test. Embryo characterized by a small protoconch and a narrow, kidney-shaped, deuteroconch (PW= 48µm; DW= 39µm). Septa starting straight and slightly bending backwards close to the intersection with the wall of the subsequent whorl (BBA=19).

Remarks

*Nummulites* and *Operculinella* are both involute nummilitids. They are distinguished mainly by shape of the last whorl (Hohenegger et al. 2000; Renema 2018). The presence of trabeculae on the surface is also considered important by some authors (Hohenegger et al. 2000), as well as the number of chambers in each whorl and the

BBA (Hohenegger et al. 2000; Renema 2018). Since the examined specimens were always broken and abraded, estimate the number of chambers per whorl, studying the last whorl and the superficial features was unfeasible. Thus, straightforward species identification was impossible.

Family Amphisteginidae CUSHMAN 1927

Genus *Amphistegina* D'ORBIGNY 1926

Test low trochospiral, involute to partially evolute and unevenly to almost uniformly biconvex. Chambers of the spire strongly curved backward at the periphery.

*Amphistegina lessonii* D'ORBIGNY 1926; Fig. 7h-m; Online resource 4

Test trochospiral, involute, lenticular, slightly asymmetrical and thick, with a smooth surface. Alar prolongations long and narrow. Protoconch and deuteroconch very small (PW= 30µm; DW= 22µm). Chambers subdivided by strongly backward bending septa (BBA=41). Coiling with a low expansion rate and few chambers per whorl.

*Amphistegina mammilla* (FICHTEL AND MOLL 1798); Fig. 7n-u; Online resource 4

Test trochospiral, involute, slightly to remarkably asymmetrical, moderately thick, with a smooth surface. Dorsal side more convex than the ventral side. Alar prolongations long and narrow. Protoconch spherical and small, deuteroconch small and hemispherical (PW= 42µm; DW= 45µm). Septa of the chambers strongly bending backwards (BBA= 55).

Family Acervulinidae SCHULTZE 1854

Genus *Sphaerogypsina* GALLOWAY 1933

Test globular to somewhat irregular. Constructed of numerous layers of polygonal to squared chambers arranged in column and radiating from the center. Outer surface characterized by a chessboard pattern of raised and depressed chambers. Embryo located at the center of the test, surrounded by an area of unordered chambers.

*Sphaerogypsina* sp. 1; Fig. 7v

Test small and spherical, with a mean diameter of 800 μm. Outer surface displaying the characteristic chessboard pattern. Embryo small and trochospiral. Embryonic area followed by a few rings of unordered chambers, which in turn are surrounded by chambers arranged in a more or less regular pattern of radial columns.

Remarks

It is indistinguishable from *Sphaerogypsina globula*. The lack of clear characteristics to separate the species within this genus prevents an accurate identification.

*Sphaerogypsina* sp.2; Fig. 7w-x

Test small and almost spherical (diameter of 750 μm). Outer surface exhibiting the characteristic chessboard pattern. Embryo bilocular, composed of a small elliptical protoconch and kidney-shaped deuteroconch. Embryonic area followed by a few rings of unordered chambers, which in turn are surrounded by chambers arranged in a regular pattern of radial columns.

Remarks

In contrast from *Sphaerogypsina* sp.1 exhibits a bilocular embryo. Additionally, the radial column of chambers are more regularly arranged. Such a major differences clearly suggests that they are separated species and has substantial taxonomic implications. Since the taxonomy of *Sphaerogypsina* is beyond the purpose of this

biostratigraphic paper the subject is not further investigated. *Sphaerogypsina* sp.2 also fits perfectly within the broad definition of *S. globula*, but the lack of clear characteristics for species separation prevents an accurate identification.

## 5 Discussion

### 5.1 Biostratigraphy

In the first interval (Unit II, Samples 7H-CC to 29F-CC), LBF specimens are poorly preserved with evidence of abrasion and fragmentation. The assemblage is quite uniform with *N*. ex. interc. *ruttenii-martinii* and *C. annulatus* occurring in all examined samples (the latter is particularly poorly preserved and many specimens only possess the central part of the test; Tab. 1). *Nephrolepidina*. ex. interc *martini-ruttenii* suggests at late middle-Miocene to early late-Miocene age (Adams 1970; Van Vessem 1978; Boudagher-Fadel 2002; Sharaf et al. 2005). Van Vessem's (1978) regards *N. ruttenii* as a more evolved species developing within the same lineage of *N. martini* and places this transition within Zone M11 (sensu Wade et al. 2011). Chaproniere (1984) places these two species within the same lineage and their transition between Zones M9 and M10. Adams (1970) and Sharaf et al. (2005) consider *N. martini* and *N. ruttenii* two separate species, with overlapping stratigraphic ranges. For Adams (1970) *N. martini* is restricted to the middle Miocene while the range of *N. ruttenii* extends into the late Miocene. Sharaf et al. (2005) suggest a middle Miocene range for *N. martini* and an early to late Miocene range for *N. ruttenii*. The arrangement of equatorial chambers, which is stratigraphycally significant, supports a middle Miocene age (Chaproniere 1980; Betzler and Chaproniere 1993). Since the majority of the literature supports a M9 to M11 age for

the examined *Nephrolepidina*, we will follow this line. *Cycloclypeus annulatus* ranges from the Burdigalian to the end of the Serravallian (Boudagher-Fadel and Lokier 2005; Sharaf et al. 2005; Hallock et al 2006; Renema 2015). Its presence restricts the possible age of the interval to zones M9 to M10 (Fig. 8). However, according to Renema (2015), the morphology of the examined *C. annulatus* is quite primitive and closer to those of Burdigalian and Langhian specimens. Nonetheless, planktonic foraminifera and calcareous nannofossil distributions support the M9 to M10 hypothesis. The interval from Sample 8HCC to 71X-CC should span between the Zones M9 and M11 as defined by the First Occurrence (FO) of *Fohsella fohsi* and Last Occurrence (LO) of *Paragloborotalia mayeri* (Fig. 8; Betzler et al. 2017; Spezzaferri et al. in prep.). Nannofossils distribution indicates a M5 to M12 age (Zones NN6 to NN15) for the interval 6H though 66X (Fig. 8; Betzler et al. 2017). In the second interval (Units VII and VIII; Samples 107X-CC to 110X-CC) the majority of LBF are poorly preserved and fragmented, with extensive borings and authigenic mineral fillings. Sample 108X-CC, in particular, is dominated by fragments of lepidocyclinids, probably produced by the breakage of individuals with a prominent equatorial flange (the observed fragments have equatorial chambers arranged in an intersecting curved pattern similar to that of *N*. ex. Interc. *isolepidinoides*-*sumatrensis*). The LBF assemblage is more varied and diverse than in the first interval (Tab. 1). Sample 107X-CC is characterized by *Nephrolepidina* ex. interc. *isolepidinoides*-*sumatrensis* (closer to the *N*. *sumatrensis*-type), *Heterostegina* (*Vlerkina*) *borneensis*, and *Cyclocypeus eidae* (Tab. 1; Fig. 8). This assemblage suggests a late Oligocene age, equivalent to Zone O7 (Fig. 8; Adams 1970; Van Vessem 1978; Chaproniere 1984; Boudagher-Fadel and Lord 2000; Hallock et al.

2006; Sharaf et al. 2005; Lunt and Renema 2014). In Sample 108X-CC *N*. ex. interc. *isolepidinoides-sumatrensis* is closer to the *N. isolepidinoides* type. The assemblage includes also *H.* (*V.*) *borneensis*, while *C. eidae* is no longer present (Tab. 1; Fig. 8). This association is suggestive of an older age than Sample 107X-CC, ranging from Zones O4 to O7 (Chaproniere 1984; Van Vessem 1978; Boudagher-Fadel and Lord 2000; Sharaf et al. 2005; Lunt and Renema 2014). The only biostratigraphic marker in Sample 109X-CC is *H.* (*V.*) *borneensis* (Tab. 1; Fig. 8). The specimens still present alar prolongations divided into chamberlets, pointing toward a late Oligocene age (Lunt and Renema 2014). The presence of *Heterostegina* (*V.*) sp. 1 (more primitive than *H.* (*V.*) *borneensis* because of its higher X value and lower S4+5 value) suggests this sample may be older than both 107X-CC and 108X-CC. No age-diagnostic LBF were recognized in the lowermost sample, making its placement uncertain (Tab. 1).

Planktonic foraminifera and calcareous nannofossil distributions are in agreement with the LBF stratigraphy. Sample 107X-CC can be allocated to Zone O7 due to the FO of *Paragloborotalia pseudokugleri*, while an older age is suggested for 108X-CC and 109X-CC due to the presence of *Chilogumbelina cubensis* and *Paragloborotalia opima* (Fig. 8; Spezzaferri et al. in prep.). Nannofossils indicate that Sample 107X is younger than 27.27 Ma and, therefore, younger than Zone O6 (Fig. 8; Betzler et al. 2017).

## 5.2 CT-scan and LBF biostratigraphy

By providing a large number of 3D models in short time, X-ray tomography proved to be an useful tool for LBF stratigraphy (especially in a context where samples are limited and destroying them is not an option). Approximately 12 hours for scanning

and 72 hours for processing the raw data were necessary to produce all 160 models (the measurements entailed an additional 48 hours of work). The major limitation to this approach seems to be the preservation of the specimens. Since CT-scan imaging is based on density contrast, secondary infilling of the chambers (e.g., sediment, cement or authigenic minerals), may jeopardize the results, in this instances traditional thin sections are probably more effective. Actually, due to the poor preservation of the material it was often impossible to resolve most of the chambers, especially for the nummulitids. However, exquisite results were obtained with lepidocyclinids which were well preserved. Since this group includes some of the most reliable age-diagnostic LBF, fast CT-scanning could significantly improve the knowledge on lepidocyclinids distribution, by mass-producing high-quality data and allowing non-destructive examination of the holotypes. Although our technique is fast and very good for the study of large chambers along the equatorial plane, it may not be perfect to investigate the fine structure of alar prolongations or the volume and the 3D shape of the chambers, which are potentially crucial for nummulitids evolutionary history (e.g., Cotton et al. 2015; Renema and Cotton 2015). These elements, coupled with the study of growth-invariant parameters, are key elements for improving LBF taxonomy, phylogenesis and evolution (Hohenegger 2011; Renema and Cotton 2015). Nevertheless, our fast approach produced a reliable LBF-based stratigraphy that fits well with the available information on the distribution of both planktonic foraminifera and calcareous nannofossils. More detailed analyses of the lepidocyclinids, which are by far the most useful taxa in Hole U1468A, may refine the model and provide a powerful instrument for correlations. In this framework the use of independent age

control systems, such as Strontium Isotope Stratigraphy, is crucial since planktonic foraminifera and calcareous nannofossils are rare in LBF-dominated intervals.

## 6 Conclusions

Large benthic foraminifera provided a reliable biostratigraphy for two shallow-water intervals in Hole U1468A. A late middle-Miocene age is suggested for Unit II and a late Oligocene age for Unit VII-VIII. These results are in agreement with the preliminary ages from planktonic foraminifera and calcareous nannofossils..

The evolution of the embryonic apparatus of *Nephrolepidina* appears to be an accurate biostratigraphic tool for this area. Further analyses focused on this genus will provide a powerful instrument to date these shallow-water deposits. The use of CT-scan proved to be valuable by producing non-destructive data in short time. This approach has the potential to advance biostratigraphy in shallow-water environments, opening new possibilities for paleontologists.

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**Figure Captions**

**Figure 1.** Location map of Site U1468 in the Maldivian Inner Sea (after Betzler et al. 2017).

**Figure 2.** PEEK sample holders for LBF CT-scanning. (a) PEEK rod (b) LBF mounted around the PEEK rod, in distinct intervals, with standard nail polish (c) sample holder shaft and (d) base.

**Figure 3**: biometry of LBF megalospheres. a) Schematic drawing of a nummulitids, modified from Matteucci and Schiavinotto (1980); 1 marks the chambers of the first whorl; 2 marks the chambers of the second whorl; $D_1$ = diameter of the first whorl; $D_2$ = diameter of the second whorl. b) Schematic drawing of an *Heterostegina*; X=3, S3+4=4, S4+5=6 and S10=6. c) Schematic drawing of a *Cycloclypeus*, modified from

O'Herne (1972); FL = FL chamberlet of the first annular chamber; Y=5 and SA=27. d) Schematic drawing of a *Nephrolepidina* embryo, modified from Van Vessem (1978); ACI = accessory auxiliary chambers of the protoconch. e) Arrangement patter of equatorial chambers in *Nephrolepidina*, modified from Van Vessem (1978) and Chaproniere (1980); Stellate: F=5; Wavy concentric: F=4; Polygonal concentric: F=3; Concentric rings: F=2; Intersecting curves: F=1.

**Figure 4**: *Nephrolepidina* ex. interc. *ruttenii- martini* in panels a-n, *Nephrolepidina transiens* in panel o, *Nephrolepidina* ex. interc. *isolepidinoides-sumatrensis* in panels p-x . a) External axial view of a specimen 7_1_07. b) External equatorial view of 7_1_07. c) Equatorial section of 7_1_07, a perfect *N. ruttenii* end-member of the population. d) Axial section of 7_1_07. e) External axial view of 29_3_05. f) Equatorial section of 29_3_05. g) Axial section of 29_3_05. h) Equatorial section of 29_3_02, a perfect *N. martini* end-member of the population. i) Axial section of 29_3_02. j) External equatorial view of 29_5_01. k) External axial view of 29_5_01. l) Equatorial section of 29_5_01, an intermediate form of the population. m) Detail of the embryo of 29_5_01. n) Axial section of 29_5_01. o) Equatorial section of 29_3_03. p) External equatorial view of 107_2_00. q) External axial view of 107_2_00. r) Sectioned 3D model of 107_2_00. s) Equatorial section of 107_2_00, a good example close to the *N. sumatrensis* type. t) Axial section of 107_2_00. u) Equatorial section of 108_2_09, a specimen with intermediate characteristics. v) Detail of the embryo of 108_2_09. w) Equatorial section of 108_2_10 which is closer to the *N. isolepidinoides* characteristics. x) Detail of the embryo of 108_2_10.

**Figure 5**: *Cycloclypeus annulatus* panels a-i, *Cycloclypeus eidae* panels j-n, *Heterostegina (Vlerkina) borneensis* panels o-x. a) External view of specimen 29_1_04A. b) Equatorial section of 29_1_04A. c) Axial section of 29_1_04A. d) External view of the central part of 29_4_00, a specimen whose rings were lost. e) Equatorial section of 29_4_00. f) Axial section of 29_4_00. g) External view of 29_5_04. h) Equatorial section of 29_5_04. i) Axial section of 29_5_04. j) External view of 107_1_03A. k) Equatorial section of 107_1_03A. l) Axial section of 107_1_03A. m) Equatorial section of 107_1_01. n) Detail of the embryo of 107_1_01. o) External view of 107_1_04. p) Equatorial section of 107_1_04, the specimen is clearly micro-bored. q) Axial section of 107_1_04. r) Equatorial section of 109_1_04. s) Axial section of 109_1_04. t) Equatorial section of 109_1_08. u) Axial section of 109_1_08. v) Equatorial section of 109_3_04. w) Axial section of 109_3_04. x) Equatorial section of 109_2_05.

**Figure 6**: *Heterostegina (Vlerkina)* sp. 1 panels a-g, *Operculina* cf. *heterosteginoides* panels h-k, *Operculina complanata* panels i-q, *Operculina* sp.1 panels r-x . a) External view of 109_1_02. b) Equatorial section of 109_1_02. c) Axial section of 109_1_02. d) Equatorial section of 109_1_00. e) Detail of the embryo of 109_1_00. f) Axial section of 109_1_00. g) Equatorial section of 109_1_03. h) External view of 107_2_04. i) Equatorial section of 107_2_04. j) Equatorial section of 107_2_06. k) Axial section of 107_2_06. l) External view of 29_2_04. m) Equatorial section of 29_2_04. n) External view of 109_1_07. o) Equatorial section of 109_1_07. p) Axial section of 109_1_07. q) Equatorial section of 109_2_01. r) External equatorial view of 108_2_11. s) External axial view of 108_2_11. t) Equatorial section of 108_2_11.

u) Axial section of 108_2_11. v) Equatorial section of 109_2_02 which presents clearly bend septa. w) Equatorial section of 108_1_07 which is characterized by an imperfect spiral. x) Axial section of 108_1_07.

**Figure 7**: Nummulitidae sp. 1 panels a-f, *Amphistegina lessonii* panels h-m, *Amphistegina mammilla* panels n-u, *Sphaerogypsina* sp.1 panel v, *Sphaerogypsina* sp. 2 panels w-x. a) External equatorial view of 29_3_00. b) External axial view of 29_3_00. c) Equatorial section of 29_3_00. d) Axial section of 29_3_00. e) Equatorial section of 29_4_05. f) Axial section of 29_4_05. g) Equatorial section of 7_2_00. h) External view of 22_3_00. i) Equatorial section of 22_3_00. j) Equatorial section of 22_1_06. k) Axial section of 22_1_06. l) Equatorial section of 22_1_00. m) Axial section of 22_1_00. n) External view of 107_2_03. o) Axial section of 107_2_03. p) Equatorial section of 107_2_02. q) Axial section of 107_2_02. r) External view of 108_1_06. s) Equatorial section of 108_1_06. t) Equatorial section of 107_3_02. u) Axial section of 107_3_02. v) Equatorial section of 29_5_03. w) External view of 108_1_05. x) Equatorial section of 108_1_05.

**Figure 8:** Stratigraphic range of age-diagnostic LBF, planktonic foraminifera and calcareous nannofossils biostratigraphy from IODP359 Hole U1468A. Grey shading represents samples analyzed in this study and dashed lines reflect sample boundaries whereby the exact start or end points are uncertain. Planktonic foraminifera zones are from Wade et al. (2011). Planktonic foraminifera (PF) distribution is from Betzler et al. (2017) and Spezzaferri et al. (in prep.). Calcareous nannofossils distribution is from Betzler et al. (2017).

**Table 1**: Distribution of the identified species among the samples

**Online resource** 1: Biometric values for *Nephrolepidina*. The number of analyzed specimens includes only those, which were sufficiently preserved.

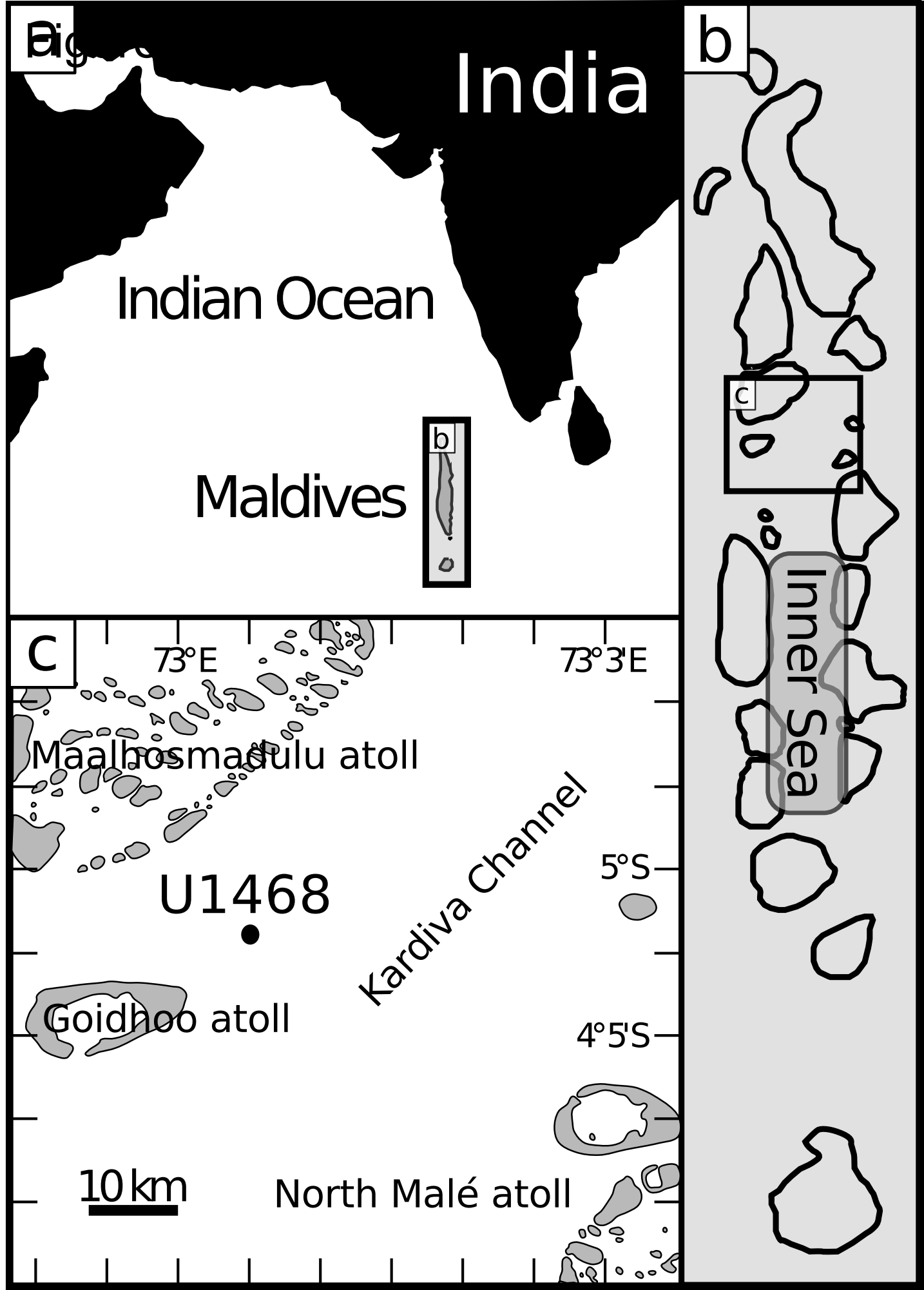
**Online resource 2**: Biometric values for *Cycloclypeus.* The number of analyzed specimens includes only those, which were sufficiently preserved.

**Online resource 3**: Biometric values for *Heterostegina*. The number of analyzed specimens includes only those, which were sufficiently preserved.

**Online resource 4**: Biometric values for nummulitids and amphisteginids. The number of analyzed specimens includes only those, which were sufficiently preserved.

**Table 1**.

| Sample | *N.* ex. interc. *rutteni-martini* | *N. transiens* | *N.* ex. interc. *isolepidinoides-samoaensis* | *C. annulatus* | *C. eidae* | *H.* (*V.*) *borneensis* | *Heterostegina* (*V.*) sp. 1 | *O.* cf. *heterosteginoides* | *O. complanata* | *Operculina* sp. 1 | Nummulitidae sp. 1 | *A. lessonii* | *A. mammilla* | *Sphaerogypsina* sp. 1 | *Sphaerogypsina* sp. 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7H-CC | x | | | x | | | | | | | x | x | | | |
| 15F-CC | x | | | x | | | | | | | x | x | | | |
| 22F-CC | x | x | | x | | | | | | | x | x | | | |
| 29F-CC | x | x | | x | | | | | x | | x | x | | x | |
| 107X-CC | | | x | | x | x | | x | | x | | | x | | |
| 108X-CC | | | x | | | x | | x | | x | | | x | | x |
| 109X-CC | | | | | | x | x | | x | x | | | x | | |
| 110X-CC | | | | | | | x | | | x | | | x | | |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Goidhoo atoll
4°5'S
10 km
North Malé atoll

Figure 2

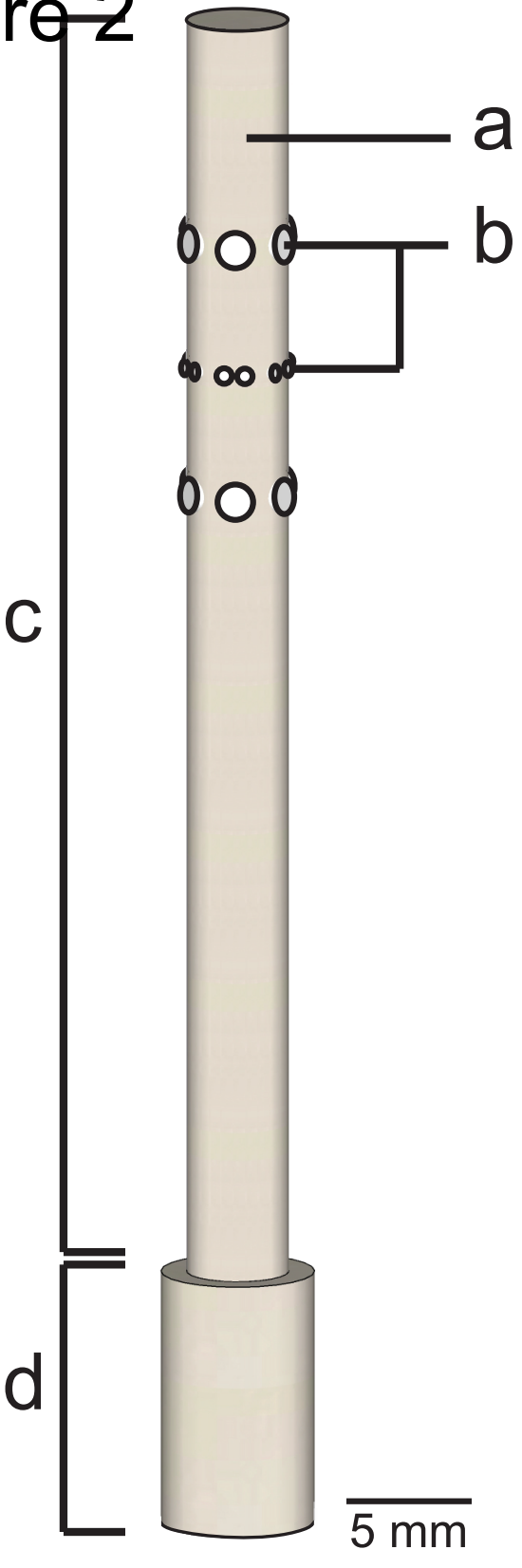
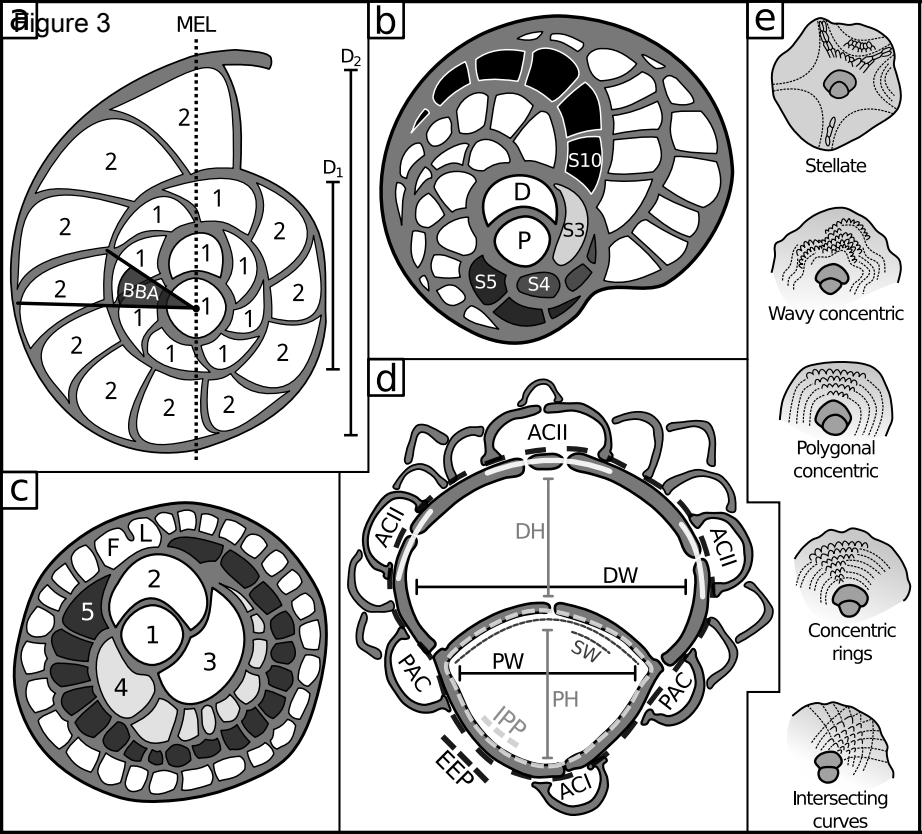


Figure 3




**PW**= width of the protoconch excluding wall thickness, measured perpendicular to the medio-embryonic line, **MEL**, the line passing through the centers of protoconch, **P**, and deuteroconch, **D**

**PH**= height of the P, measured along the MEL

**PL**= length of the P excluding wall thickness measured on an axial section and in the direction perpendicular to the equatorial plane

**PS**= P size, $\sqrt[3]{(PW \times PH \times PL)}$

**DW**= width of the D excluding wall thickness, measured perpendicular to the MEL

**DH**= height of the D excluding wall thickness, measured along the MEL

**DR**= deuteroconch ratio, DW/PW

**T/D**= ratio between the maximum thickness and maximum diameter of the test

In specimens with spiraled structure:

**$NC_X$**= number of chambers in the Xth whorl

**$D_X$**= diameter of the Xth whorl excluding the thickness of the lamina, measured along the MEL

**BBA**= backward bending angle, the angle formed between the line connecting the inner extremity of a septum to the center of the P and the line connecting the outer extremity of the same septum with the center of the P

In heterosteginids:

**X**= number of undivided chambers including P and D

**S3+4**= total number of chamberlets in the 3th and 4th chambers

**S4+5**= total number of chamberlets in the 4th and 5th chambers

**S10**= total number of chamberlets in the 10th chamber

In *Cycloclypeus*:

**PC**= number of precyclical chambers

**SA**= number of chamberlets in the first annular chamber

In lepidocyclinids:

**IPP**= internal perimeter of the P

**SW**= internal length of the shared wall between P and D

**Ai**= embracement of the P, (SW/IPP)*100.

**NACII**= number of auxiliary chambers (**ACII**)

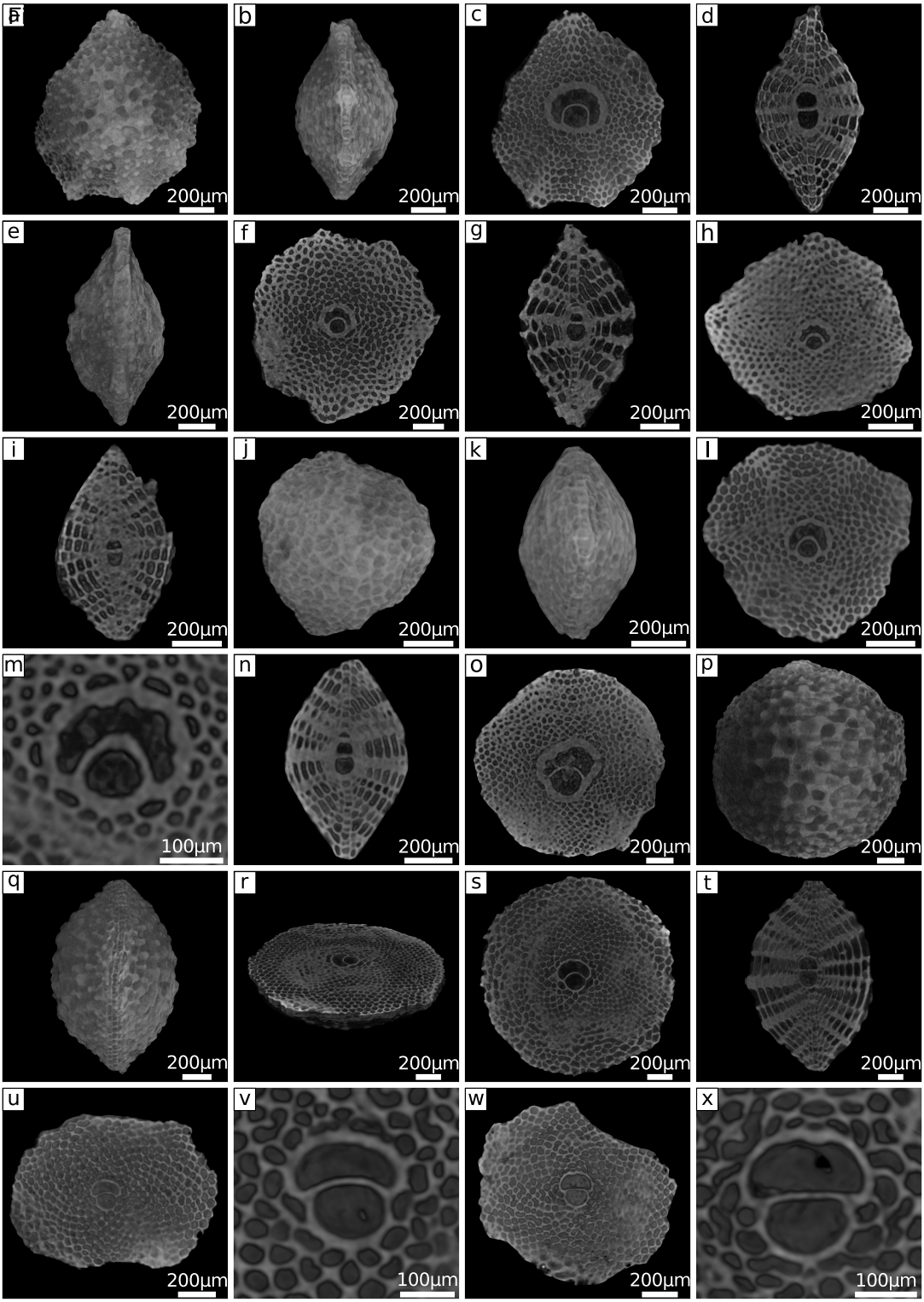
**NPAC**= number of principal auxiliary chambers (**PAC**)

**EPP**= external perimeter of the embryo

**ΣACII**= total length of the external surface of the embryo covered by **ACII**

**BΣACII**= portion of the outer perimeter of the embryo covered by ACII, (ΣACII/EPP)*100.

**F**= the arrangement pattern of the equatorial chambers; ranging from 1 to 5 following Chaproniere (1980)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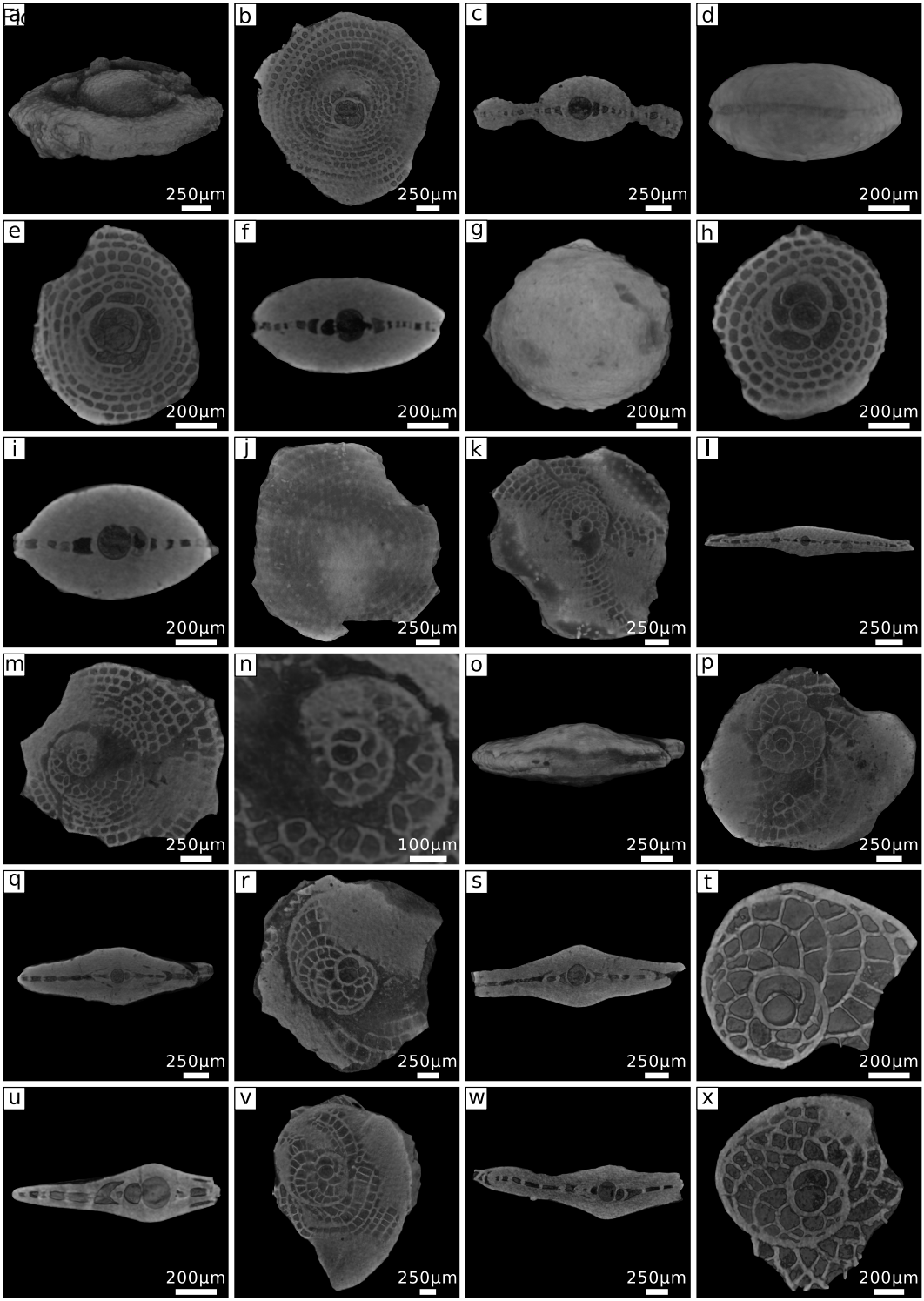
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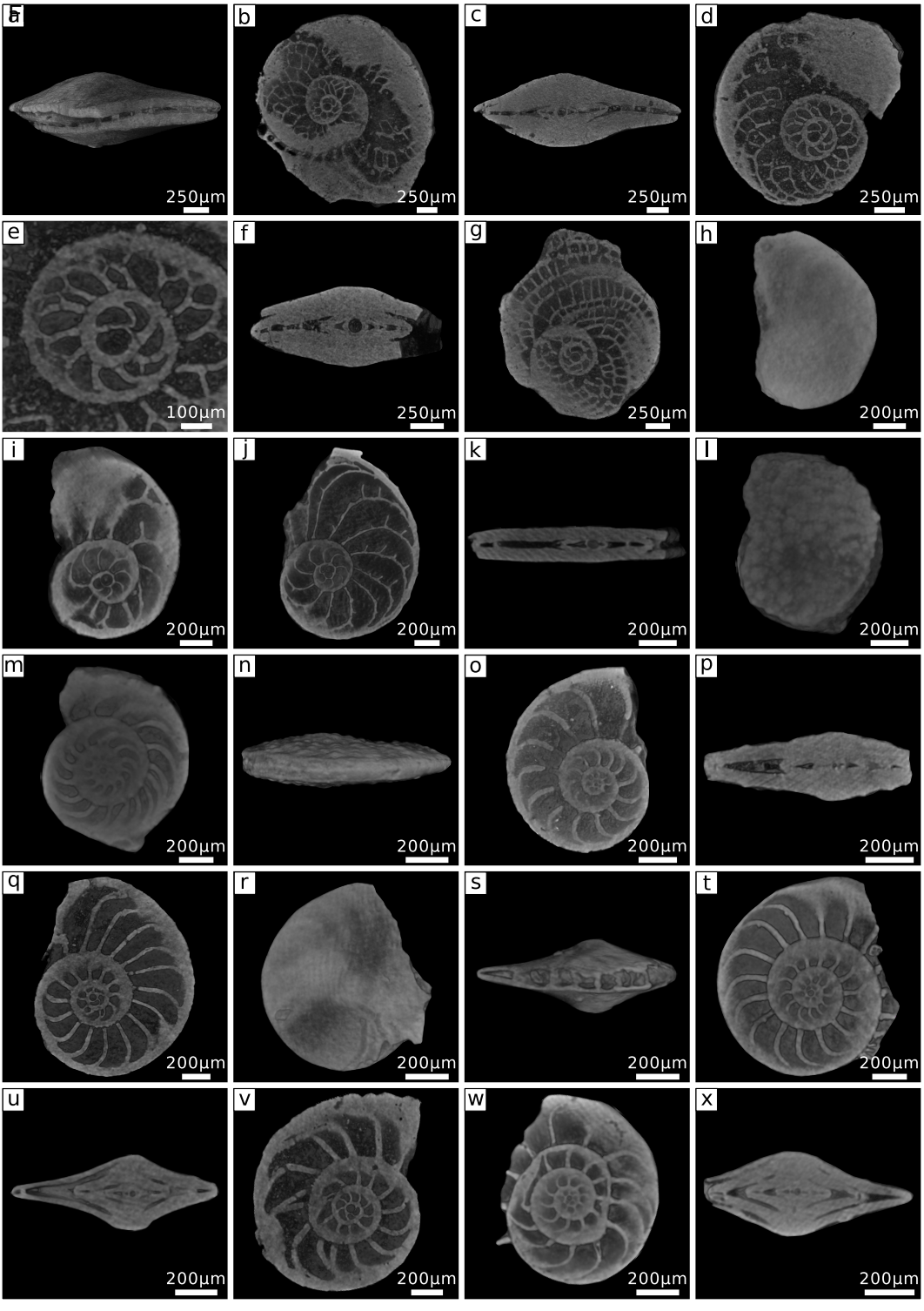
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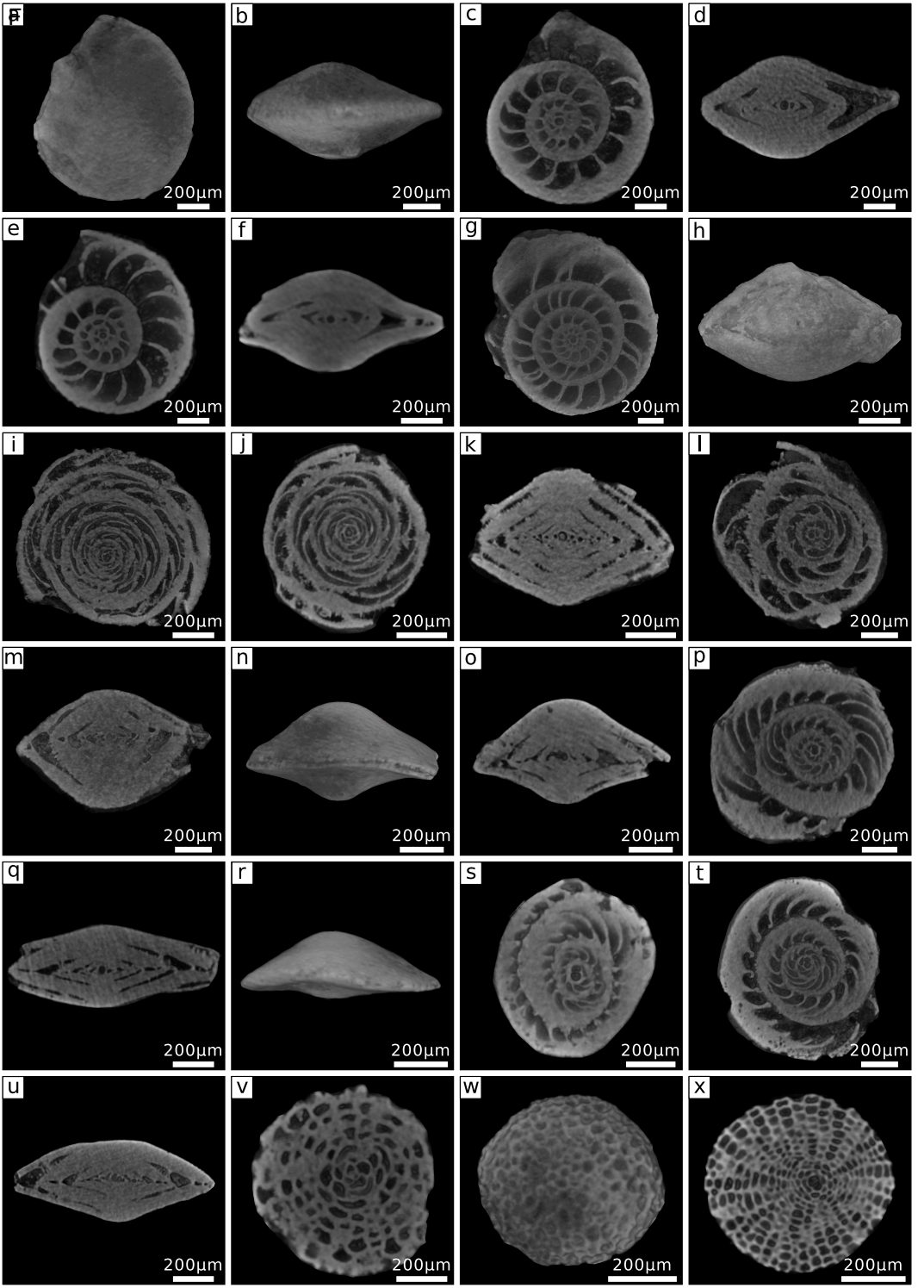
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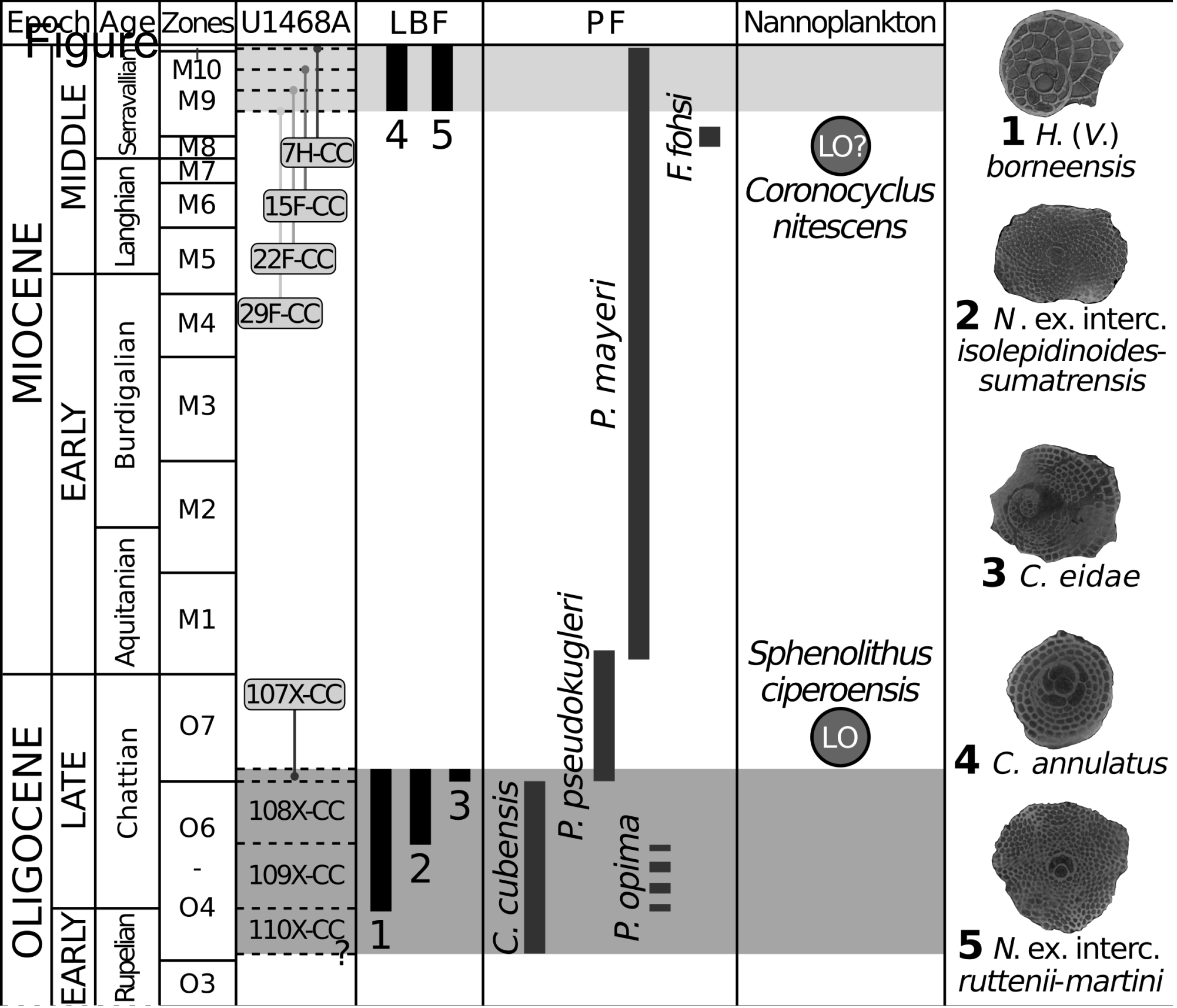
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Sphenolithus ciperoensis
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3 C. eidae
4 C. annulatus
5 N. ex. interc. ruttenii-martini

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