

Dear Recommender,

Dr. Emilia Jarochovska,

We declare that we have considered all the comments and made almost all corrections as asked by the reviewers.

Summary of the main modifications to the manuscript:

We profoundly modified the manuscript as requested by the reviewers and you. In particular, we have deleted the “aim” concerning a test of climatic cooling as a potential influence on diversity and morphological change from the introduction and changed completely the scope of this introduction. We have also revised the taxonomy by bringing SEM observations of the same specimens observed in XPL. These observations clearly match our original interpretations and there is therefore no reason to change our taxonomy. We remain with the erection of two distinct new species in the *Microrhabdulus undosus* sensu lato lineage and we believe that there are more than enough arguments to make this suggestion. We have significantly modified the discussion of the paper.

Following the comment about the clarifications concerning preservation of the fossils by anonymous reviewer 2#, we added a new section focused on this issue (section 4.1).

Chapter 5.2 “Possible causes of morphological change in calcareous nannoplankton “ now discusses what size changes in calcareous nannoplankton generally reflect in the Recent (Quaternary), Cenozoic and Mesozoic (chapter 5.2.1. Lessons from the Meso-Cenozoic) and then discusses the problem of the Cope-Bergmann’s hypothesis (chapter 5.2.2. Are Cope-Bergmann’s rules applicable to phytoplankton?). Of particular importance to us is the fact that the Cope-Bergmann’s hypothesis has been claimed many times as a potential mechanism in plankton (see references in chapter 5.2.2.). However, following a long and fruitful discussion with David Watkins, and reading your own comments, led us to read much more on these paleontological rules and we do agree that due to their implications, it is quite controversial to apply this rule to unicellular phytoplanktonic organisms. We believe that this paper leaves us an avenue to discuss this important point and as a large part of the community of calcareous plankton specialists appears to be unaware of this controversial use, we believe that it was useful to write a chapter precisely on this point.

Chapter 5.3. “Are morphological changes in *C. ehrenbergii* and *M. undosus* lineages related to climatically-controlled episodes of speciation?” discusses the timing of the two observed episodes of rapid morphological change that we interpret as speciation events. In particular, the first episode sees the coincidence of a rapid shift in size of *C. ehrenbergii* to the first occurrence of our new species *M. zagrosensis* and the timing of these two events coincides precisely with the Late Campanian carbon isotope Event and an acceleration of cooling, a carbon cycle and climatic episode related to tectonics occurring around 76 Ma which has been recently the subject of a bunch of papers in our group (Chenot et al., 2016, 2018, Corentin et al., 2022). While we do acknowledge that our observations only come from one section, this section is particularly well dated thanks to careful previous stratigraphic work. Moreover, such morphological changes in these two lineages had never been assessed anywhere before. Although this is way beyond the scope of our study and do not want to make any claims of new personal observations, we would like to address here that a preliminary examination by both M. Razmjooei and N. Thibault of Late Campanian deposits of the English Chalk led to the observation of *M. zagrosensis* while a coincident increase in abundance and in the size of *C. ehrenbergii* has recently been spotted in the Late Campanian of Israel and is currently under evaluation by S. Marconato, PhD student of N. Thibault based at the University of Ben Gurion. It is too soon to discuss such observations in our present paper but we believe that the coincidence of these changes between two independent lineages with a clearly delineated climatic episode and perturbation of the carbon cycle are more than enough arguments to suppose a relationship between them.

Subchapter 5.3.2. discusses the timing of the emergence of the newly defined *M. sinuosus*. This timing corresponds to the interval of the so-called mid-Maastrichtian event, a ~2Myr episode characterized by numerous origination events in calcareous nannoplankton and planktic foraminifera, cephalopods and bivalves, and by the extinction of non-tegulate inoceramids. Again, we believe that the first occurrence of this new species precisely within that interval, is one out of many other first occurrences of nannofossils in that interval and therefore, it appears more than justified to elaborate on the mid-Maastrichtian event and mechanisms for diversification at that time.

We modified some of the figures and tables following reviewers' request and added a compilation carbon isotope curve for the Late Cretaceous in Figure 11, which we find relevant for several chapters of the discussion described above.

In the detailed response to reviewers below, we systematically provide reference to line numbers of our applied corrections on the version of the manuscript with tracked changes.

The reviewer comments are in black and all the answers are in green

Recommender: Emilia Jarochowska, 2020-10-28

Both reviewers agree on the importance of this research approach and the material you present, but ask for clarifications concerning a few aspects. The anonymous reviewer asked for a clarification of the aim of the paper. The taxonomic contribution is certainly achieved as the manuscript contains high-quality illustrations and new taxonomic descriptions and observations. However, the study design, the sample size, the paucity of statistical analyses, and the specificity of factors driving the size of single cell organisms limit the last of the aims, i.e. "an illustrative test for the potential link between Cretaceous cooling and the rise in diversity". Both reviewers commented on this latter aim and I second their concerns. Both Cope's and Bergmann's rules have been originally proposed for multicellular endotherms and the application of Bergmann's rule to ectotherms remains debated. In unicellular organisms, "hard" limits on the size (for any given shape) exist, imposed by the rate of intracellular transport, gas diffusion through cell surface and in the cytoplasm, and, for phytoplankton, light acquisition and penetration. A further important component is the structure of the community and the top-down control by grazers. See e.g.

Marañón, E. (2015). Cell size as a key determinant of phytoplankton metabolism and community structure. *Annual Review of Marine Science* 2015 7:1, 241-264

Cermeño, P., Marañón, E., Harbour, D., & Harris, R. P. (2006). Invariant scaling of phytoplankton abundance and cell size in contrasting marine environments. *Ecology letters*, 9(11), 1210-1215.

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., & Raven, J. A. (2010). Phytoplankton in a changing world: cell size and elemental stoichiometry. *Journal of plankton research*, 32(1), 119-137.

Peter, K. H., & Sommer, U. (2012). Phytoplankton cell size: intra-and interspecific effects of warming and grazing. *PloS one*, 7(11), e49632. and many others

These factors have been extensively documented in extant phytoplankton and, in order to assess the role of cooling in this study, they would need to be addressed with an evaluation of their plausibility, e.g. to evaluate the link between cooling and the rise in diversity, one would need to do a time-series analysis of temperature data and diversity, which is clearly beyond the scope of this, equally valuable, contribution. The study design does not allow to answer this difficult question fully - it definitely merits a discussion, but I am not sure if the data and analyses presented here warrant a definite answer.

The authors: we have now included all possible elements about size changes and their relation to diversification in calcareous nannoplankton in our discussion within the chapters cited above and we believe, that given the coincidence of our events to documented episodes of climate change, these results merit indeed discussion, though we remain cautious with our interpretation in the discussion

Both reviewers also requested that the Authors consider whether the observed changes must reflect a global trend or could they be constrained to the given ecosystem?

The authors: we answer to these concerns via previous observations of a possible distinction already made for *Cribrosphaerella* by Perch-Nielsen. Concerning *Microrhabdulus*, our taxonomic part clearly points towards our morphological changes related to the origination of new species, and therefore, it is unlikely that this is related to the specific ecosystem. Moreover, these originations occur in coincidence with known episodes of climate change. Hence we believe it is valid to raise this point.

we also agree with the anonymous reviewer that the analyses should be documented in more details. For example, the confidence intervals provided in tables and figures were calculated based on the assumption of the normality of their distributions (which is warranted, looking at the histograms), but it does not seem to be stated anywhere. What is the white dashed line in Fig. 3, which highlights the shift in length, but must be clearly a running average, because it does not

follow all small-scale shifts before and after the highlighted interval? It should be documented how it was calculated and, less importantly, individual fragments of the figure should be labeled and referred to individually in the text to make it easier for the reader to match the described results with presented data. I also struggled with the lack of labels for symbols in Fig. 10 - it is hard to assess to assess the relationship between variables without this information.

The white dashed line in figure 3 is intended to show a simplified trajectory of where the highest density is situated before and after 76 Ma, it follows areas of higher density but indeed, it is not calculated, simply drawn on the graph. We explain that in the caption and believe it is justified by the data. We can see this shift in average size pretty well in the curves of the mean length and standard deviations on the left. See modified caption of figure 3.

Figure 10 (now figure 11) shows a number of various symbols for the various tex86 data across different tropical sites. These symbols and sites have been added to the graph.

Finally, the anonymous reviewer also requested clarifications concerning preservation of the fossils.

We clarify this point as well. See lines

In my opinion, the strength of this article is the excellent documentation of an important contribution to nannofossil diversity, high-quality taxonomic data and illustrations, but the link with Cope's and Bergmann's rule warrants a bit more nuanced discussion.

We hope that the new organization and expansion of the discussion into distinct chapters now warrants a nuanced discussion on this issue.

Apart from this, this is without doubt an important and well-documented contribution. I would also like to highlight that the authors provided a complete set of data used for the study in an open access archive, which is highly commendable! I apologize again for the very long time it took to solicit reviews and look forward to the revised version.

Reviewer 1#: Andrej Spiridonov, 2020-09-02

This is very interesting morphometric stratophenetic study of an important Cretaceous algae group in the understudied Iran region. The basic size spectrum patterns are clearly detected and described. The only thing that should be improved is the ultimate explanation for the found trends, which need a conceptual improvement. My comments are below:

In the abstract it is mentioned that two species were studied, but afterwards it is explained that two more are distinguished. I think that you should list four species studied, two of which newly distinguished in this contribution.

Answer: Modified. Instead of “two calcareous nannofossil species” in the first line of the abstract, we wrote “two groups of calcareous nannofossils”

Line 45 “...morphospecies species” -> “morphospecies” since redundant.

Answer: corrected.

Figure 1. A) lacks paleogeographical legend, therefore it is difficult to interpret. What Sh means? Shahneshin section (it should be noted in the legend)? Is it site of the study? Why it is on (apparent) paleo-land (?) and not under paleo-water if I understand the map correctly? Probably paleogeography of the studied interval should be significantly different then.

Answer: a comprehensive legend was added to address all the above questions and comments

Figure 10. What those colors of data points indicate? Different data sources (studied sections)? Those should be indicated in the legend or the description of the figure.

Answer: a legend was added

The main point I see in the article is the explanation of size trends. Authors propose that the increases in sizes of nannoplankton which are associated with profound climate cooling events are caused by Cope and Bergman rules.

Contrary to the authors which see solutions here, I see a paradox here. Bergman rule which states, that in colder temperatures body size increases mostly works for endotherms such as mammals, which body size increase diminishes surface area to volume ratio, thus saving the energy and resources. In phytoplankton world rather different rules apply since radical differences in bioenergetics, life history and dominant physical forces at different size scales.

Based on the first principles of geometry, knowledge of eukaryote metabolism, modern observations of the phytoplankton, and climatology we should expect to have positive correlation of cell size increase with the average temperature. This follows from the fact that increased temperature causes higher saturation of atmosphere with water vapour and general increase in intensity of hydrological cycle and thus the flux of nutrient from continents to the oceans. Smaller cells have larger relative surface area, and relatively smaller inner metabolic volume, which allows them to thrive in nutrient poorer environments. Larger cells (all else being equal) require higher density of nutrients which could be diffusively in taken and used by disproportionately larger volume of biochemical machinery. Exactly this pattern was found by our team when studying lundgreni event in the Silurian (Spiridonov et al, 2016 - <http://www.geology.cz/bulletin/contents/art1679>) – during cooling there was sharp decrease in algae cyst sizes, and during subsequent warming there was a steady growth in their sizes.

Therefore instead of citing broad principles of questionable applicability for the given case I suggest for authors to rethink the probable causality of their excellently documented morphometric and diversity pattern. The association of cooling with increase in size (and diversity?) is against the expectation (and other empirical evidence from differing time periods) for a given group of organisms, and it is an interesting observation which could give some clues on the deeper understanding of phytoplankton ecosystem paleoecology.

My suggestions for the improvement of Discussion:

-Copes rule possibly played a role here (in a style of Steven Stanley/S.J. Gould explanation of release of a clade after extinction event). If for example other competing groups were disproportionately eliminated from the competitive pool, possibly good portion of previously unavailable nutrients were relocated to the calcareous nannoplankton which could have played a role in size increase,

-Bergman rule is too speculative here, and vaguely grounded elsewhere, and probably should be abandoned as a general source of explanation. Instead authors should think deeper what factors which are associated with this cooling episode counteracted the size decreasing effects of cooling which are expected from the first principles. Possible sources of size increase: i) cooling induced increased dust flux due to aridization from deserts to the oceans; ii) mentioned restructuring of competition/grazing networks in the ocean; iii) specifics of physiology/shape/ecology of given clade of algae; iv) other sources of nutrient enrichment and simultaneous cooling – underwater igneous activity, e.g. in Caribbean Igneous Province (???).

Answer: We agree with this long comment and strongly modified the discussion in that sense, specifically sections 5.2.1 and 5.2.2

Because there has been many claims of a unified Cope-Bergmann rule as an explanation of size changes in calcareous plankton prior to us, we believe that a point of the discussion about this was necessary but we do fully agree with the comments of the reviewers and editor as can now be read in our discussion of 5.2.2.

Reviewer 2#: anonymous, 2020-10-19

The manuscript by Razmjooei and co-authors is interesting, adding new insights in the morphometric changes of two Late Cretaceous calcareous nannofossil lineages (*Cribrosphaerella* and *Microrhabdulus*) from the Shahneshin section (Zagros Basin, Iran). Based on their relative abundances and size patterns, the authors highlight the possible first occurrence of *C. hilli* (lines 252-255) in the late Campanian of the studied site and define *Microrhabdulus* sp. nov. 1 and *Microrhabdulus* sp. nov. 2 as new species of the *Microrhabdulus* group. The comparison of the micropalaeontological data obtained here to global calcareous nannoplankton diversity and temperature reconstructions of the Albian–Maastrichtian time interval is interesting, giving a wider perspective of the interpretations following the Cope's and Bergmann's rules.

Besides, the manuscript is well written, and I think this manuscript has the potential to interest a broad scientific community, particularly when dealing with the relationships between calcareous nannofossil morphometrics and climate (temperature) changes in the past. However, the robustness of the dataset needs to be better set up, so some interpretations will be less questionable (see my comments in the section (A) below). Besides, I agree that global temperature changes might be an important forcing factor behind the morphometric changes highlighted for *Cribrosphaerella* and

Microrhabdulus groups. However, I am wondering if other (global vs local) climate parameters couldn't have played significant roles as well (see my comments in the section (B) below). At last, I propose some minor corrections in (C)

(A) *Specimen preservation*

The fact that the preservation of the calcareous nannofossil assemblage identified as moderate is only discussed lines 101-104 (chapter 3 "Material and methods"), is clearly unhelpful and I believe that a chapter devoted to the preservation of the assemblage and more particularly of the studied specimens (i.e. *Cribrosphaerella* and *Microrhabdulus*) is warranted. It is crucial when focusing on morphometrics, and particularly when interpretations are based on specimen length variations of about 1-1.5 μm . Besides, the authors refer to Razmjooei et al., (2020b) when dealing with the preservation of the calcareous nannofossil assemblages. In this previous paper, the authors highlight "moderate to poor preservation" according to criteria of Roth (1978), as well as "very low species richness", with the "absence of small coccoliths such as small *Biscutum*, *Z. erectus* and *P. stoveri*", "all indicative of a significant impact of diagenesis on the nannofossil assemblage".

Therefore, I suggest the authors to better summarize the findings of Razmjooei et al., (2020b). For example, what does "quantitative and palaeoecological studies" (line 101) mean when dealing with calcareous nannofossil preservation? I suggest also the authors to develop a paragraph dealing with the preservation of *Cribrosphaerella* and *Microrhabdulus* in particular (Actually, I totally disagree with the fact that since the studied lineage are $>3 \mu\text{m}$, they are prevented from any major influence of diagenesis on size" (line 104). Diagenesis and dissolution (or overgrowth) impact calcareous nannofossil whatever the size, and $3 \mu\text{m}$ is actually quite small.

Answer: Agree. A new section (4.1.) was added, explaining the preservation of the nanno-assemblage. In the new section, we summarized the findings of Razmjooei et al. (2020b), as you requested, and explained the preservation of *Cribrosphaerella* and *Microrhabdulus* in particular.

Also, *M. undosus* are frequently fragmented in the samples (line 200-201). Does that mean that its abundances might be biased as well? Does that reflect significant impact of dissolution? As an example, the number of foraminifera fragment is an index to highlight dissolution imprint on quaternary assemblages (higher fragments reflecting higher dissolution impact). Could it be the case here?

Answer: *Microrhabdulus* is a long rod-shaped nannolith and always prone to breakage. In many cases, even in well-preserved samples, they are often observed as fragmented, yet each fragment is counted as one. The fragmented *M. undosus* mostly show the mechanical breaks and less dissolution impact. We cannot exclude that the relative abundance of this taxon was indeed biased by enhanced dissolution producing more fragments. However, we did not observe any significant trend in preservation along the Coniacian to Maastrichtian Shahneshin section and the observed increase in % *Microrhabdulus* does not correlate with any enhanced dissolution in the upper half of the section or decrease in species richness (which often highlights increased dissolution). As a fact, the first significant increase in *Microrhabdulus* around 240 m occurs when species richness is the highest (Razmjooei et al. 2020).

Lines 204-206: "the maximum length observed in each sample still represents a valuable index as this parameter is more likely to represent the length of complete, non-fragmented specimens". Can you develop? For example, what is the actual length of specimens in literature? Is it comparable to the length obtained here? In all cases, the definition of new *Microrhabdulus* species is based on specimen widths and lengths (lines 279-281) and these parameters must clearly not be ascribed to dissolution or overgrowth overprints. SEM observations and pictures should be added to the paper to be more convincing, as well.

Answer: The definition of the two new *Microrhabdulus* species is mainly based on clear distinct morphological criteria in addition to the width (diameter) of the rod in XPL. As one can see in our text and figures, these new *Microrhabdulus* species are wider than the previous forms, not necessary longer since indeed they are fragmented. However, we believe that the maximum length, as explained in our text, still represents a valid criterion as it is likely to be close to the actual total length of non-fragmented specimens. As we do indeed observe an increase in maximum length that parallels the increase in width, we believe that this is a very serious argument to infer that *M. sinuosus* is indeed longer than other *Microrhabdulus* species. It has been noted on the excellent nannofossil database Nannotax (https://www.mikrotax.org/Nannotax3/index.php?taxon=Microrhabdulus%20undosus&module=ntax_mesozoic) that the length of *M. undosus* varies within a range of 15 to 30 microns. This range matches almost exactly the range of 14 to 27 observed in our maximum length. As for considerations on dissolution overgrowth overprints, we have amply discussed now issues concerning preservation in our chapter 4.1. SEM observations do not point to overgrowth or dissolution possibly affecting the rod diameter.

Besides, while the differences between potential morphotypes are highlighted via density plots (Matlab® script of Thibault et al., 2018) and histograms of PAST® (Hammer et al., 2001) i.e. proven tools in the field, I am still puzzled by the meaning of statistics performed on less than 50 specimens, (up to 19 for *C. ehrenbergii*; and up to 6-9 for *M. undosus* group). Can you explain what “the statistic difference between potential morphotypes is tested [...] for three distinct stratigraphic intervals that bear enough specimens for reliable statistics” mean?

Answer: We used statistical analysis via Matlab and Past software to show the differences in different morphospecies' sizes. However, as noted by the reviewer and explained in the text, counting 50 specimens for *C. ehrenbergii* and 30 specimens for *Microrhabdulus* was not always possible in all samples because these species have relatively low abundance in some intervals. This is why, in order to make a valid statistical demonstration, it was important to regroup samples of various stratigraphic intervals comprising more numerous specimens and hence more reliable statistics. Figure 5 for instance subdivides two distinct stratigraphic intervals for *C. ehrenbergii* and the total number of specimens is indicated on each graph (N=596 and N=778). For *M. undosus*, we have three intervals with N= 71, N=175 and N=90 and these three intervals quite clearly delineate the increase in width. The next step was to attempt to provide statistics as reliable as possible for the three distinguished species. Figure 6 (new figure added) shows *M. undosus sensu stricto* composed of 101 specimens identified in the interval between 164 and 243 m. *M. zagrosensis* statistics are based on 173 identified specimens from the interval 250-342 m while *M. sinuosus* statistics are based on 37 specimens identified in the interval 315-342 m. We believe that this is clear.

(B) Nannoplankton diversity and climate changes

In the introduction (lines 57-60), the comparison of *Cribrosphaerella* and *Microrhabdulus* relative abundances and sizes with global nannofossil diversity (Bown et al., 2004) and a long-term signal of TEX86 (O'Brien et al., 2017), is presented as an illustration of the relationship that might exist between global (decreasing) temperature and global (increasing) calcareous nannofossil diversity during the Cretaceous. However, it is rather presented as the main (and only?) forcing factor behind *Cribrosphaerella* and *Microrhabdulus* distributions during Campanian – Maastrichtian. Other forcing factors might exert control on them at global and local scales. Therefore, I propose the authors to adopt a clearer position regarding the relationship between *Cribrosphaerella* and *Microrhabdulus* groups and climate changes. Indeed, there are two options:

- i) the aim of the paper is to better constrain *Cribrosphaerella* and *Microrhabdulus* taxonomies and define and present new calcareous nannofossil species, testing the role of global cooling as an opening for future interpretations. In that case, I would clearly define it as the aim of the study (lines 56-60). Also, I would most clearly present chapter 5.4 as the hypothesis the authors want to test here (probably at the beginning of the discussion (5.2), not at the end (5.4)), bearing in mind that other parameters (not tested here) might play a significant role as well. I would be extremely caution when dealing with the relationship between *Cribrosphaerella* and *Microrhabdulus* behaviors and temperature (rephrase for example: “We infer here that our observations illustrate an intimate link between climatic cooling and speciation, and strongly support that the Late Cretaceous nannoplankton peak in diversity was essentially fueled by cooling», lines 378-381, and elsewhere in the manuscript.)

Answer: We agree. We changed the scope of the introduction so this aim is not presented as an aim anymore. The taxonomic improvement purpose was added to the aims of the study. We discussed all possible parameters involved in diversification and biometric changes in calcareous nannoplankton, comprising a discussion on Cope-Bergmann's rule.

- ii) the aim of the paper is to understand the relationships between *Cribrosphaerella* and *Microrhabdulus* patterns and climate changes based on their abundances and morphometrics (as exposed lines 56-60). In such a case I would suggest integrating in the discussion, local vs global climate parameters that might exert control on the studied nannofossils (local temperature and nutrient conditions, atmospheric pCO₂, sea-level), probably better integrating results and interpretations from Razmjooei et al., 2020b).

Answer: the discussion chapter for this part was improved. Also see the answer to the last comment of Andrej Spiridonov

(C) Some minor corrections:

Line 44: Do you mean morphospecies?

Modified

Line 46: I suggest you to remove “subtle”

Modified

Line 57: the ecological preferences of *Cribrosphaerella ehrenbergii* and *Microrhabdulus undosus* (particularly with temperatures) presented lines 384-396, should be presented here. Since their abundances and morphometrics are interpreted in terms of temperatures changes, it would worth mentioning it in a few words within the introduction.

Agree. Modified

Line 65: what is the environment of the studied section (neritic, hemipelagic, pelagic)?

‘Pelagic’ Modified

Line 82: Please refer to Fig. 2.

Done

Line 115: “fewer specimens were measured”. Please, give the exact number and discuss the limit of such number.

Done

Line 118: “the biometric measurements have been performed manually (?), under a light microscope...”

Corrected (The biometric measurements have been performed by using a light microscope)

Figure caption 2: the oxygen isotope signal documented here is not reported in the figure. Is there any uncertainties associated to the absolute ages?

The term oxygen was deleted. The absolute ages are based on a graphic correlation between Shahneshin and Gubbio reference section. There might be some uncertainties indeed that are difficult to evaluate.

Tables 1 and 2: please, add the units (μm) of the morphometrics in Figure captions.

Modified

What is the significance of two digits after the decimal point (for mean length and mean width of both groups) vs one digits after the decimal point (fmax length of *M. undosus*).

Unified. All the decimal point have two digits now

Line 157: relative abundance of *C. ehrenbergii* averages 5%

Modified

Line 158: then reach minima of less than 1%

Modified

Lines 166-167: reaching values as high as 17%

Modified

Line 168: from CC26a and UC20cTP to Cretaceous-Paleogene boundary

Modified

Line 178: Figure 4 should be cited before Figure 5, or Figure 4 and Figure 5 should be permuted.

We already cited figure 4 before figure 5 in section 3, line 127.

Line 186: *Microrhabdulus spp.* represents only a minor component of the calcareous assemblage. Why is that? What are his ecological preference?

Probably because of the lack or very low abundance of *M. undosus* in the Coniacian-early Campanian interval. We have no answer as to why this taxon is less abundant in this interval.

The ecological preference of *Microrhabdulus* is unclear as mentioned in the introduction.

Lines 191-192: ...upper Campanian. Above the Campanian/Maastrichtian...

Modified

Lines 193: two double peaks of abundance

Modified

Lines 220-221: The appearance of *Microrhabdulus* sp. nov. 2 (maybe linked to a temperature change?) is not associated with changes in *C. ehrenbergii*. Is there any explanation?

No explanation indeed. We do not believe that it is necessary to discuss this point. These are clearly two very distinct lineages so there is not necessarily a reason for having morphological changes in these two groups systematically coinciding. We do not think that it is necessary to comment this point in the MS.

Line 225: Do you mean longer, or wider morphotype instead of thicker? Thicker refer to the morphotype thickness, which is another parameter (not measured here).

We mean wider. Corrected throughout the manuscript.

Since *Microrhabdulus* is a rod-shaped nannolith, and the variations in the length of this nannolith are biased, we focused on the width of the rod (we use width as it is measured as such in XPL but it represents the diameter of the rod)

Lines 249-250: what is usually, the maximum size of *C. ehrenbergii* et *C. hilli*? Is it comparable to the sizes obtained here?

Based on Reinhardt (1964) the size of *C. hilli* ranges between 8 to 10 um, which is similar to our big *C. ehrenbergii* in our study. This is written in our text when mentioning *C. hilli*.

Lines 255-258 and lines 350-353: SEM observations would clearly help improving this part and therefore, the manuscript. SEM pictures were added to address this comment.

Figure 8 caption: “thick forms”. Do you mean “wide/large forms”?

Modified. We mean wide rods in *Microrhabdulus*.

Line 354: ... and the length of *C. ehrenbergii* remains very stable

Modified.

Lines 354-355: I don't totally agree. Generally, *C. ehrenbergii* appears longer after the shift compared to before. What does that imply regarding Gould and Eldredge (1977) assumption cited here?

We do not understand the disagreement here. This is exactly what we wrote. Indeed, we write that the length of *C. ehrenbergii* remains nearly constant around the same average after the shift, an observation that resembles the model of Gould and Eldredge of stasis, then rapid speciation followed by stasis again.

Lines 365-267: please, be caution when referring to a rapid shift in *C. ehrenbergii* and *M. undosus* groups in the other parts of the manuscript.

The interval of the shift can be estimated from biostratigraphy and carbon isotope stratigraphy to be less than 500 kyr. We have added this information in chapter 5.3.1

Figure 10: It would worth adding the average length of *Microrhabdulus* in the figure, as well. Could it be possible to also add the rapid temperature changes documented lines 432-435?

done

Figure 10 caption: can you mentioned the red, green, pink/ scare, circle, diamonds?

A legend was added to the figure to address this request.

Lines 442-445: If that is so, then I suggest you to change the title of the article and document climate instability instead of long-term cooling. In all cases, what do you mean by climate instability? Do you only refer to temperature instability or it could be associated to other parameters? And which ones?

Agree. We changed the title.

What we mean here is temperature instability. And we also discuss other parameters.

Line 485: ...oligotrophic areas, the global peaks in their diversity

corrected

We're looking forward to the publication of our paper in your Journal.

Best regards,

The authors.