Peer Community In Paleontology

New insights into the palaeoecology of Miocene Eurasian rhinocerotids based on tooth analysis

Alexandra Houssaye based on peer reviews by Christophe Mallet, Antigone Uzunidis and Matthew Mihlbachler

Manon Hullot, Gildas Merceron, Pierre-Olivier Antoine (2022) Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Paleontology. https://doi.org/10.1101/2022.05.06.490903

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Rhinocerotoidea originated in the Lower Eocene and diversified well during the Cenozoic in Eurasia, North America and Africa. This taxon encompasses a great diversity of ecologies and body proportions and masses. Within this group, the family Rhinocerotidae, which is the only one with extant representatives, appeared in the Late Eocene (Prothero & Schoch, 1989). They were well diversified during the Early and Middle Miocene, whereas they began to decline in both diversity and geographical range after the Miocene, throughout the Pliocene and Pleistocene, in conjunction with the marked climatic changes (Cerdeño, 1998).

In Eurasian Early and Middle Miocene fossil localities, a variety of species are often associated. Therefore, it may be quite difficult to estimate how these large herbivores cohabited and whether competition for food resources is reflected in a diversity of ecological niches. The ecologies of these large mammals are rather poorly known and the detailed study of their teeth could bring new elements of answer. Indeed, if teeth carry a strong phylogenetic signal in mammals, they are also of great interest for ecological studies, and they have the additional advantage of being often numerous in the fossil record.

Hullot et al. (2022) analysed both dental microwear texture, as an indicator of dietary preferences, and enamel hypoplasia, to identify stress sensitivity, in a large number of rhinocerotid fossil teeth from nine Neogene (Early to Middle Miocene) localities in Europe and Pakistan. Their aim was to analyse whether fossil species diversity is associated with a diversity of ecologies, and to investigate possible ecological differences between regions and time periods in relation to climate change. Their results show clear differences in time and space between and within species, and suggest that more flexible species are less vulnerable to environmental stressors.

Very few studies focus on the palaeocology of Miocene rhinos. This study is therefore a great contribution to the understanding of the evolution of this group.

References:

Cerdeño, E. (1998). Diversity and evolutionary trends of the Family Rhinocerotidae (Perissodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology, 141, 13–34. https://doi.org/10.1016/S0031-0182(98)00003-0

Hullot, M., Merceron, G., and Antoine, P.-O. (2022). Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: Impact of climate changes. BioRxiv, 490903, ver. 4 peer-reviewed by PCI Paleo. https://doi.org/10.1101/2022.05.06.490903

Prothero, D. R., and Schoch, R. M. (1989). The evolution of perissodactyls. New York: Oxford University Press.

Reviews

Evaluation round #2

DOI or URL of the preprint: https://www.biorxiv.org/content/10.1101/2022.05.06.490903v2
Version of the preprint: 2

Authors' reply, 25 November 2022

Dear Alexandra,

We thank you very much for your thorough and constructive revision of our manuscript. We have answered all your questions, taken into account most of your suggestions and emended accordingly the concerned sections. The changes are detailed in the manuscript with track-changes (also containing the edits made after the reviewers comments).

A notable exception was the modification of the colors in some figures, which we did not do for the reasons listed thereafter, but we have tried to use dark outlines to make them clearer whenever it was possible. Our choice of colors was based on consistency with previous publications and grouping by tribs. As there are 19 species shown for some graphs, finding a better comprise seems difficult.

Independently, we have also corrected a few minor mistakes and typos. Significant edits are listed below:

- Table 6 has been modified to add taxonomic details (tribes)

We hope that this revised version will now meet the standards required for a recommendation by PCI Paleontology.

Yours sincerely,

Manon Hullot and co-authors

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Decision by Alexandra Houssaye, posted 10 November 2022, validated 10 November 2022

Dear authors,

Thank you for the changes you made and the new version of your manuscript. You have indeed taken into account most of the reviewers' comments and the manuscript is almost ready for publication. However, I have made suggestions in the attached document to further take into account some of the previous comments and to justify some parts a bit more, and I have made some small suggestions/corrections. Please take a look at this document and submit a new version of your manuscript. I have no doubt that these changes will be quick and easy for you to make.

Do not hesitate if you have any questions. I look forward to seeing the new version of your manuscript.

Best wishes,

Alexandra Houssaye **Download recommender's annotations**

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2022.05.06.490903

Authors' reply, 19 October 2022

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Decision by Alexandra Houssaye, posted 26 July 2022

Decision on preprint entitled "Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes" for recommendation by Peer Community in Paleontology (PCI Paleontology)

Dear authors,

The preprint entitled "Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes" was sent to three reviewers.

If all the reviewers underline the interest and quality of the study and of the preprint, they also suggest a moderate/major revision. Their comments (copied in full below + the 3 annotated pdfs), which should enable you to greatly improve the preprint, are attached. The comments notably address the generation of testable hypotheses at the beginning of the manuscript that will clarify the objectives of the study, the approach and the value of combining the analyses of dental microwear texture and dental hypopasias in a single study. In addition, if the statistical approach is perceived as sound and robust (although one reviewer made an interesting suggestion for a particular case), more distance from the statistical results in the interpretations and generalisations is recommended, as well as more contextualisation in the conclusion.

Thank you again for submitting your interesting work to PCI Paleo. I look forward to seeing a revised version of this manuscript. Please submit a rebuttal letter with your revision, detailing any changes you have made in response to the reviewers' comments.

Best wishes,

Alexandra Houssaye

Reviewed by Antigone Uzunidis, 25 May 2022

Hullot et al. submitted a very interesting paper entitlted "Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes" Since very few study focus on the paleocology of Miocene Rhino, this paper is a great contribution that should be published.

In general, this paper is very rich, well written with supplementary material that provide a lot of data to better understand the study.

However some points should be improve either to facilitate the understanding of the study or to moderate some affirmations :

- In the method, the authors explain which data they choose to investigate hypoplasia. However they never explain the reason behind this selection. Hypoplasia remains quite a mysterious phenomenon and I am wondering for example what information can be extrapolate from the distance between the defect and the collar of the teeth. Could the author detail more their reasoning ?

- In the discussion, ”Interactions with co-occurring herbivores” part. I find the author quite rush in their affirmation. They seem to forgot that they are studying palimpsest with a very high-resolution method. There is a discrepancy between the precision of the method and the context in which it is applied which should be taken into account and reported in the text.

These two points in particular seem to me very important to consider. Otherwise, I have pointed out in the text (see attachment) some minor errors/changes/suggestions that the authors may or may not take into account.

I hope these few comments will be helpful for the authors.

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Reviewed by Christophe Mallet, 07 June 2022

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Reviewed by Matthew Mihlbachler, 29 June 2022

Overview

This paper includes an interesting mixture of dental microwear texture analysis and documentation of dental hypopasias in Neogene Eurasian rhinos. The dental microwear analyses adopt established methods. Likewise, the distribution of hypoplasias are documented soundly. However, the results and discussion sections wander, generate unsupported paleodietary interpretations and make loose associations of the results with paleoenvironmental conditions. While the data themselves are analyzed with sound statistical methods, the authors take very large leaps from the statistical results regarding differences between the various samples to generalizations about diet and paleoecology.

The paper states that its aim is to assess ”dietary preferences using dental microwear texture analysis, and stress sensibility via the study of enamel hypoplasia”. (lines 65-67). However no hypothesis was provided, leading to an unfocused presentation. I think the authors would be better served by generating a testable hypothesis or series of hypothesis which could them be used to give the investigation purpose and focus. What ecological paleoecological questions concerning Neogene rhinos can be addresssed by these data? Answering this question may also lead to a more coherent research design. Why are dental microwear data and dental hypoplasias being presented together? Is there some hypothesis that they can both address? Presently, it seems as if microwear reveals more about diet, while hypoplasias have more to do with ecological stress. These aren’t mutually exclusive phenomena. Is there some interesting question that could be answered by examining both. If not, the authors may be better off publishing these two studies separately.

Throughout the DMT results and discussion sections and summarized in table 6, a variety of interpretations are made about diet and feeding. Most of these interpretations use the classic browser, mixed-feeder, grazer categories, but other *ad hoc* terms and special qualifications are thrown about including ”folivore, ”browser favoring leaves”, ”soft food items”, ”soft browsing”, ”browsing preferences with the inclusion of hard objects, probably fruits”.The statistical methods used to test for differences in the data give a false impression of scientific rigor. But the actual dietary interepretations have seemingly been made out of thin air. How were these interpretations made? Extant rhino microwear data are discussed in a subsequent section but it is not clear how the modern data are being used to interpret diets of extinct species. What are the confidence levels of these dieatary assignments? How are these dietary categories defined? How were the lines drawn between

browser, mixed-feeder and grazer in terms of microwear data and diet? What aspects of the microwear data lead you to make conclusions about diet? What about these other special categories, such as folivore, soft browsing, and other special exceptions (e.g. browser favoring leaves, soft browsing etc)? What elements of the data reveal these? It is already challenging enough to differentiate classic browsers, mixed feeders, and grazers using microwear data and these additional diet characterizations, I suspect, are actually beyond the powers of the available dental microwear data to differentiate.

In several areas, this paper makes strong conclusions about diet and other aspects of paleocology. For example, in the conclusion section (lines 663-665):"*Though, DMTA results suggested only browsers and mixed-feeders (no grazers nor frugivores) in the studied rhinocerotid sample, they unraveled clear niche partitioning through food resources at several diachronous localities...*" Niche partitioning is a process by which natural selection drives competing species into different patterns of resource use or different niches. Some microwear differences found in a small number of teeth do not constitute clear evidence for niche partitioning or any other complex evolutionary and ecological process. The dental microwear differences merely suggests different diets or feeding environments. It does not reveal why those diets are different. With regard to niche partitioning, it can only be concluded from this analysis that it cannot be falsified as an explaination for the differences. Perhaps it would be helpful here, and, in fact, for all the conclusions derived in this paper, to consider what is the null hypothesis regarding ecological differentiation of these species to begin with? This is one example of numerous in the manuscript where your conclusions need substantial softening.

Specific comments (see comments in manuscript for additional comments

The first two sentences of the abstract seem unecessary to me. Of course major changes are documented in most of not all geological ages. Rhinoceroses are interesting, according to who? They are abundant and diverse according to what metric?

In both the abstract and the main document, proxy data are confused with diet (or other ecological parameters of interest). For example, line 22 states, "Our results suggest a clear niche partitioning based on diet at Kumbi 4..." Replace "diet" with "DMT data". The evidence for niche partitioning is not based on diet, it is based on DMT data, which is not diet. Also see comments above about niche partitioning.

Likewise on lines 24-25, "All rhinocerotids studied were browsers or mixed feeders, and none had a grazing nor frugivore diet." Avoid such definitive conclusions. To be more precise, it would be better to write, "the DMT data are consistent with browsing and mixed feeding diets, but not grazing".

Line 27: If the prevalence of hypoplasias document the local conditions, those conditions need to be stated, otherwise omit this sentence.

Line 90: A figure of the grinding and shearing facets sampled needs to be provided. A person who is not very familiar with rhinocerotid molars will need a figure to understand this.

Line 171-172: The statement about avoiding classic thresholds is contradicted in the results tables. Table 2 appears to use P=0.1 as a threshold. Table 3 explicitly uses P=0.05 as a threshold. A keyword search for the word "significant" is needed to be sure that it is not used in ways that contradict the statements about significance in the methods (see line 666)

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