




Peer Community In Paleontology

A Rhino from Lake Baikal

Faysal Bibi  based on peer reviews by **Jérémy Tissier**, **Tao Deng** and **Panagiotis Kampouridis**

Alexander Sizov, Alexey Klementiev, Pierre-Olivier Antoine (2024) An Early Miocene skeleton of *Brachydiceratherium* Lavocat, 1951 (Mammalia, Perissodactyla) from the Baikal area, Russia, and a revised phylogeny of Eurasian teleoceratines. bioRxiv, ver. 6, peer-reviewed and recommended by Peer Community in Paleontology.

<https://doi.org/10.1101/2022.07.06.498987>

Submitted: 07 July 2022, Recommended: 07 March 2024

Cite this recommendation as:

Bibi, F. (2024) A Rhino from Lake Baikal. *Peer Community in Paleontology*, 100182. [10.24072/pci.paleo.100182](https://doi.org/10.24072/pci.paleo.100182)

Published: 07 March 2024

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As for many groups, such as equids or elephants, the number of living rhinoceros species is just a fraction of their past diversity as revealed by the fossil record. Besides being far more widespread and taxonomically diverse, rhinos also came in a greater variety of shapes and sizes. Some of these – teleoceratines, or so-called ‘hippo-like’ rhinos – had short limbs, barrel-shaped bodies, were often hornless, and might have been semi-aquatic (Prothero et al., 1989; Antoine, 2002). Teleoceratines existed from the Oligocene to the Pliocene, and have been recorded from Eurasia, Africa, and North and Central America. Despite this large temporal and spatial presence, large gaps remain in our knowledge of this group, particularly when it comes to their phylogeny and their relationships to other parts of the rhino tree (Antoine, 2002; Lu et al., 2021). Here, Sizov et al. (2024) describe an almost complete skeleton of a teleoceratine found in 2008 on an island in Lake Baikal in eastern Russia. Dating to the Early Miocene, this wonderfully preserved specimen includes the skull and limb bones, which are described and figured in detail, and which indicate assignment to *Brachydiceratherium shanwangense*, a species otherwise known only from Shandong in eastern China, some 2000 km to the southeast (Wang, 1965; Lu et al., 2021).

The study goes on to present a new phylogenetic analysis of the teleoceratines, the results of which have important implications for the taxonomy of fossil rhinos. Besides confirming the monophyly of Teleoceratina, the phylogeny supports the reassignment of most species previously assigned to *Diaceratherium* to *Brachydiceratherium* instead.

In a field that is increasingly dominated by analyses of metadata, Sizov et al. (2024) provide a reminder of the importance of fieldwork for the discovery of fossil remains that, sometimes by virtue of a single specimen, can significantly augment our understanding of the evolution and paleobiogeography of extinct species.

References:

Antoine, P.-O. (2002). Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum National d'Histoire Naturelle, 188, 1–359.

Lu, X., Cerdeño, E., Zheng, X., Wang, S., & Deng, T. (2021). The first Asian skeleton of *Diaceratherium* from the early Miocene Shanwang Basin (Shandong, China), and implications for its migration route. *Journal of Asian Earth Sciences*: X, 6, 100074. <https://doi.org/10.1016/j.jaesx.2021.100074>

Prothero, D. R., Guérin, C., and Manning, E. (1989). The History of the Rhinocerotidae. In D. R. Prothero and R. M. Schoch (Eds.), *The Evolution of Perissodactyls* (pp. 322–340). Oxford University Press.

Sizov, A., Klementiev, A., & Antoine, P.-O. (2024). An Early Miocene skeleton of *Brachydiceratherium* Lavocat, 1951 (Mammalia, Perissodactyla) from the Baikal area, Russia, and a revised phylogeny of Eurasian teleoceratines. *bioRxiv*, 498987, ver. 6 peer-reviewed by PCI Paleo. <https://doi.org/10.1101/2022.07.06.498987>

Wang, B. Y. (1965). A new Miocene aceratheriine rhinoceros of Shanwang, Shandong. *Vertebrata Palasiatica*, 9, 109–112.

Reviews

Evaluation round #3

DOI or URL of the preprint: <https://doi.org/10.1101/2022.07.06.498987>

Version of the preprint: 4

Authors' reply, 31 January 2024

Dear Editor,

We are really sorry for the delay between your former decision and the making of this updated version, mainly due to non-scientific reasons.

We have now addressed the corresponding issues (see our point-by-point response below).

Query: The latest version of the main text appears to address all previous comments. However it seems that the Supplementary Material uploaded with the latest version of the manuscript is incomplete. Please make sure that all supplementary files (S1 to S5) are associated with the latest version of the preprint, and that they are clearly labelled as such.

Response: We have now upgraded the preprint, be it for the main text or other items, such as supplementary material files (five items: <https://www.biorxiv.org/content/10.1101/2022.07.06.498987v5.supplementary-material>).

Query: Additionally please note my suggestions regarding the last version of S5: In S5, please also provide the measurement number descriptions for the skull and mandible (note spelling of skull). Do not just refer to Guerin 1980 as many readers may have difficulty finding this publication. Additionally, presenting the actual measurements in a graphic table format is not so useful. I suggest you provide these in spreadsheet (e.g. excel, csv) format so the data can more easily be reused.

Response: We have transferred all the measurements within an Excel sheet, for facilitating copying-pasting of any tables. Nevertheless, we experienced problems in uploading an xlsx/xls/csv sheet to BiorXiv and finally had to convert it into pdf, and the upload was successful, after a dozen of aborted tries with a spreadsheet format...

Query: An additional note: you previously mentioned in a response to reviewers that the phylogenetic matrix was uploaded to Morphobank. However it seems that the manuscript still does not indicate this anywhere.

Please clarify what the status is here – if you are using Morphobank, then you should provide a link to the dataset in the manuscript.

Response: The matrices corresponding to S1 (preliminary analysis, with 32 taxa) and S3 (final analysis, with 31 taxa) are embedded in a Morphobank project, as duly mentioned in the manuscript (see lines 1342-1344), and accessible through the permalink <http://morphobank.org/permalink/?P5029>

We hope that the manuscript now meets the standards of PCI Paleontology and thank you once again for your deep involvement and tremendous patience while editing our manuscript.

Best wishes,

Alexander Sizov, Alexei Klementiev, and Pierre-Olivier Antoine

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Decision by **Faysal Bibi** , posted 21 July 2023, validated 02 August 2023

Revision – Please ensure Supplementary Materials are complete

The latest version of the main text appears to address all previous comments. However it seems that the Supplementary Material uploaded with the latest version of the manuscript is incomplete.

<https://www.biorxiv.org/content/10.1101/2022.07.06.498987v4.supplementary-material>

Please make sure that all supplementary files (S1 to S5) are associated with the latest version of the preprint, and that they are clearly labelled as such.

Additionally please note my suggestions regarding the last version of S5: In S5, please also provide the measurement number descriptions for the skull and mandible (note spelling of skull). Do not just refer to Guerin 1980 as many readers may have difficulty finding this publication. Additionally, presenting the actual measurements in a graphic table format is not so useful. I suggest you provide these in spreadsheet (e.g. excel, csv) format so the data can more easily be reused.

An additional note: you previously mentioned in a response to reviewers that the phylogenetic matrix was uploaded to Morphobank. However it seems that the manuscript still does not indicate this anywhere. Please clarify what the status is here – if you are using Morphobank, then you should provide a link to the dataset in the manuscript.

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2022.07.06.498987>

Version of the preprint: 3

Authors' reply, 13 July 2023

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Decision by **Faysal Bibi** , posted 05 June 2023, validated 06 June 2023

Minor Review Required

The revised manuscript was examined by all three original reviewers as well as myself. One reviewer was fully satisfied with the revision. Two of the reviewers provided annotated versions with suggestions for minor corrections. I also made suggestions for improvement in the attached pdf (best viewed in Acrobat).

Please revise your manuscript, addressing the comments made by myself and the two reviewers. Since these are mainly changes to the text, this should be minor address. [Download recommender's annotations](#)

Reviewed by [Jérémy Tissier](#), 14 May 2023

I am very grateful to the authors for taking all my comments and suggestions in consideration. The manuscript is very good, and I was very happy to review it. I think that it is a very useful paper and the work has been done very seriously and is quite exemplary. All data are now available, and very detailed.

I only have very minor comments, that I have reported on an annotated pdf. I repeat some of them here, that are perhaps a bit more important:

- L. 174-185 is a very long sentence, which could be broken in several parts.
- L. 716: the organization of the whole comparison section is slightly confusing, and would be perhaps easier to read if it was reorganized by including all anatomical parts together, instead of separating this section by skull/mandible/teeth/postcranial. But I leave the choice to decide to the authors, this is very minor.
- L.738-741: the mandible of *D. shanwangense* is not compared at all with the material from Tagay, I think this is quite missing. Perhaps they are actually identical.
- L. 943-946: The authors say that *D. asphaltense* and *D. lemanense* have a “low number of morpho-anatomical discrepancies” and thus that “they could be considered as intraspecific variants within *D. lemanense*”, but Jame et al. (2019) have provided a differential diagnosis of *D. lemanense*, which highlights a number of morphological differences with *D. aginense* and *D. asphaltense*, among others. However, most of these characters are not included in any character’s matrices, and could potentially be intraspecifically variable characters. I think that this study should at least be mentioned or discussed.
- Fig. 4G has not been corrected I think, and the mesostyle and paracone fold are incorrect. Also, “valley posterieure” should be corrected in postfossette.
- Fig. 7: it seems that fig. 7A, H and I are upside down, with the distal side facing upward, contrary to other parts of the figure.

Otherwise, this is truly a very detailed and thorough work, and I will be very pleased to read the final version of this manuscript once it accepted.

[Download the review](#)

Reviewed by [Panagiotis Kampouridis](#), 05 May 2023

In this revised version, Sizov et al. improved their already well-written manuscript. They completed the figure captions, added some additional figures, and added a more detailed comparison to other relevant taxa. They also corrected most issues raised by the reviewers. I have only few more comments to make: 1. In the added comparison, the genus name *Diaceratherium* is used for species that otherwise are regarded as members of *Brachydiceratherium* in the study. So, this should be amended. 2. Because the manuscript is an extensive study and revision of this group I would suggest adding a short part in the comparison where you explain why the material from Tagay belongs to the genus *Brachydiceratherium* and not any other teleoceratine, before comparing it with the other species within the genus *Brachydiceratherium*. This part does not have to be long; it could be only a couple of sentences long.

Some additional minor changes are also noted (in red colour) in the attached .pdf file of the revised manuscript.

It is an excellent contribution to the study of fossil rhinos and I am truly looking forward to seeing the manuscript in its final form.

Panagiotis Kampouridis

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Reviewed by [Tao Deng](#), 25 April 2023

I agree to accept this revised manuscript for publication.

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2022.07.06.498987>

Authors' reply, 14 April 2023

Dear Recommender,

We thank you warmly for being given the opportunity to revise our manuscript. First of all, we deeply apologize for such a delay in submitting the revised version, as a collateral damage of the dramatic events started in February 2022.

We have taken into account most issues listed by the three reviewers and we are providing detailed responses to your suggestions and theirs here below (denoted by "R: ").

The revised manuscript shows edits and new elements, highlighted either in yellow (following Deng Tao's suggestions), green (following J r my Tissier's recommendations), or blue (our own changes).

We hope that this new version will fulfill the standards of PCI Paleontology and look forward to get your feedback on it.

Best regards,

Alexander Sizov on behalf of coauthors

Moderate revision

This manuscript was seen by three reviewers as well as myself. All provided detailed comments on the manuscript including pdfs with commentary. Overall, the manuscript appears to be a welcome addition to the paleontological literature, with the detailed description of a skeleton from Tagay and a phylogenetic analysis and revision of teleoceratines that the reviewers find convincing.

R: Thank you very much for this general comment.

I recommend moderate revision, as the changes to be made are largely in the text, though these are quite substantial. In particular the Comparison section is quite lacking, and it is not clear that so much description of the phylogenetic results is needed (we can see the relationships in the tree).

R: We do think that the thorough description of the tree is of interest (notably for readers who are interested in these aspects, such as the reviewer #1) and we have therefore left this part as it was in the original manuscript. On the other hand, we have considerably enhanced the comparison section.

One reviewer proposes that more taxa should be added to the dataset, and also suggests considering other morphological datasets.

R: Not agreed. In our opinion, these requests fall beyond the scope of the current paper.

Two reviewers would like images of the carpals and tarsals.

R: OK. This was a pretty relevant request! Done.

The figure captions are also all in need of improvement.

R: OK. Sorry for that. Done.

Measurements of the cranium and teeth are missing from the supplementary dataset S3, in which also almost all cells are blank. Please provide measurements for all listed taxa, or remove these rows.

R: We are sorry. This was a wrong (provisional) version of the table, not intended for submission or publication. We have replaced it by more convenient ones (with more measurements/without the blank rows).

Further details are needed on which specimens were used to score taxa in the analysis.

R: In the original submission, these details were already provided as notes related to every terminal taxon in the PAUP matrix itself (e.g., *Hyrachyus eximius* was "scored after Bin Bai et al. (2017) and personal observation (AMNH material) by POA"; *Brachydiceratherium lemanense* was "scored after Boada Sa a (2007, 2008), Boada Sa a et al. (2008), Becker et al. (2009), Jame et al. (2019), and personal observation by POA (notably Gannat material: Rhinopolis, FSL, MNHN; MHNT)"). We admit that they were not immediately available and therefore we have added a sentence in the text, in order to guide the readers toward this part of the document. Please

note that this information is accessible through any free word-processing software (e.g., Wordpad, Notepad or TextEdit), notably for readers who do not use PAUP or .nex matrices in general.

Additionally, I suggest you upload the morphological matrix to a repository such as Morphobank which will make it more visible and easier to use for later workers.

R: Thank you for your suggestion. We have uploaded the final matrix to Morphobank accordingly.

Also please add page numbers to the next version.

R: Sorry for that. Our mistake! We have added the page and line numbers in the current version (R1). Also, a circus is

Reviews

Reviewed by Jérémy Tissier, 27 Jul 2022 21:16

This is an excellent and very-well written manuscript on new rhinocerotid remains from the Early Miocene of Russia. It presents the first phylogenetic analysis of a major Rhinocerotid group, the Teleoceratina, which was greatly needed. The results are extremely interesting, and have profound taxonomical implications (monospecific Diaceratherium, “resurrection” of Brachydiceratherium), as well as palaeobiogeographical, which are all clearly justified by the phylogeny. As such, the title and abstract are totally appropriate for this manuscript.

R: Thank you very much for your kind comments.

All the necessary data are provided to replicate the phylogenetic analyses, with a lot of details, which is very helpful and appreciated.

I ran the phylogenetic analyses and obtained the exact same results as presented here, with the same parameters. The discussion on the phylogenetic results is very detailed and very useful.

R: Thank you.

However, I wasn't sure if the new specimen had been coded on its own as a terminal in a prior analysis, before being merged with *B. shanwangense*, or not? If that is the case, it should be mentioned, as that would greatly support the identification of the new specimen.

Indeed, it is mentioned in the Conclusion that “the numerous associated features documented and scored in the Tagay rhinocerotid skeleton have allowed for assigning it to the same teleoceratine species (*Brachydiceratherium shanwangense*) as in Shanwang, eastern China.” But I could not find that in the rest of the text.

R: We are grateful to the reviewer for this remark. We had indeed scored the Tagay individual and *B. shanwangense* as two distinct terminals in a prior analysis (not included in the previous version) and we have now integrated the corresponding matrix, with 32 terminal taxa, and the resulting PAUP buffer. In that analysis, the Tagay skeleton and the previous hypodigm of *B. shanwangense* were differing in a single and only feature (char. 36: occipital crest concave in the former).

However, if that is not the case (i.e. the specimen was merged with *Brachydiceratherium shanwangense* prior to the analysis), then I would say that the “Comparison” section should be improved, and should justify the attribution of this specimen to the species *B. shanwangense*. Currently, there only seems to be one character (mentioned in this section) that supports it: the absence of p1/d1s. However, the d/p1 is also absent in some (or maybe all) specimens of *B. aginense* (Répelin 1917) and some of *B. lemanense* (e.g. from Wischberg, Jame et al. 2019). Although I fully agree with the identification, I think it should be further justified. In addition, very few *Brachydiceratherium* species (or even Teleoceratina) are mentioned in this comparison.

R: We have now included the prior analysis (with 32 taxa and Tagay/Shanwang skeletons scored separately; see above). Unfortunately, the comparison section provided with the original submission was not the last – updated – version but a drafted one. We are really deeply sorry for that. The comparison provided here.

I would also suggest mentioning, if possible, which specimens, or localities or even references have been used to score the taxa in this matrix. I think that is important for *Brachydiceratherium* in particular, due to its quite complicated taxonomic history, which led to confusions (see Boada et al. 2007 or Jame et al. 2019 for

example).

R: In fact, this information was already available in the original submission (as notes related to every terminal taxon in the PAUP matrix itself. We have added a sentence in the text, in order to guide the readers toward this part of the document (see response to the Recommender for further details).

Otherwise, the text is is very clear, and the descriptions are very well made. The figures are also of very high quality, although I have a few suggestions:

- Fig. 1: I thought that a small map, locating the Tagay locality in a larger scale (e.g. Russia) would be useful

R: OK. Done.

- Fig. 3: the caption for fig. D is missing.

R: OK. Done.

- Fig. 4: there is a confusion with the position of the mesostyle and paracone fold. Also, change "Valley posterieure" to "posterior valley"

R: OK. Done.

- Fig. 5: Please mention the different views shown (ventral, anterior etc.)

R: OK. Done.

I would add however, that figures of the carpal and tarsal bones would be extremely useful. Although the descriptions are very good, a figure is almost always better than words. If necessary, they could be added in supplementary material instead of the paper.

R: OK. We do agree that these figures facilitate understanding the corresponding descriptions. We have added them in the new version, with classic views.

I have also noted a few minor corrections in the annotated pdf that should be addressed/corrected. I found one reference in the legend for fig. 13 that was not cited in the reference list (Jame et al. 2019), and the reference for Heissig 1972 should mention a or b, as there seem to be two.

R: OK. Thanks a lot. We have added Jame et al.'s work in the reference list and distinguished both monographs by Heissig (1972) in the text and in the reference list. Most issues detailed in the annotated pdf originate from shared documents with successive versions and edits.

Overall, I think my main suggestions would be to improve the comparison section, by detailing which characters (in addition to the d/p1 absence) support the identification of the new specimen to *Brachydiceratherium shanwangense* OR to mention whether this specimen was added as a separate terminal; to mention (even shortly) the material on which the scoring of some terminals has been made; and to provide figures for some of the unillustrated carpal and tarsal bones. This remains nonetheless an excellent manuscript, and I am looking forward to reading the final paper!

R: No further comments (see above for detailed responses) except that we thank you again for the depth of your review and the relevance of your suggestions.

Reviewed by Panagiotis Kampouridis, 15 Jul 2022 16:49

The manuscript of Sizov et al. entitled "An early Miocene skeleton of *Brachydiceratherium Lavocat, 1951* (Mammalia, Perissodactyla) from the Baikal area, Russia, and a revised phylogeny of Eurasian teleoceratines" represents a very detailed description of a partial skeleton of *Brachydiceratherium shanwangense* from the early Miocene locality of Tagay and an overview of the Eurasian teleoceratines. I believe that it is a very nice example of how such well-preserved material should be treated with detailed descriptions and many detailed photographs of every bone. Especially the figures of the cranial, mandibular and dental material are very well made with very nice drawings of the specimens, which make it much easier for the reader to understand the morphology.

This kind of comprehensive study of all available material, including almost all of the postcranium of the skeleton, is definitely extremely helpful for future studies of teleoceratines and fossil rhinos in general. The results of this study have an important impact on the phylogeny and biogeography of Eurasian teleoceratines.

The manuscript is well structured and well written. The methods the authors use to study the material is adequate. The phylogenetic analysis performed by the authors is sound and appropriate for the group.

R: We really appreciate your general comments.

I only have few comments to make on the manuscript. The most important one concerns the Comparison of the material (p. 27-28). It is rather short and very limited concerning the taxa with which the material from Tagay is compared to. Especially since the description is so comprehensive, it would be great to also have a more comprehensive comparison including also a bit more information about postcranial features (where possible).

R: OK. As mentioned in our response to the Recommender and Reviewer #1 (see above), we have expanded the comparison in providing details on features of interspecific / intergeneric interest.

I would suggest to split the comparison in two. The first part would concern the comparison of the material across the Eurasian teleoceratine genera (Prosantorhinus, Brachypotherium, Diaceratherium and Brachydiceratherium) and demonstrating that the material belongs to the genus Brachydiceratherium. In the second part the material from Tagay can be compared within the genus Brachydiceratherium with the most important species to show that it belongs to *Bd. shanwangense*.

R: We deeply acknowledge you for this suggestion. As mentioned above, the comparison as provided in the original submission was not the up-to-date version, but a draft. We apologize for that. In fact, the comparison is organized by anatomic region (skull, mandible, forelimb, and hindlimb). We hope that this section would nevertheless read well as it stands.

Otherwise, first the taxonomy of the Tagay material could be established and then in the second part it can be compared more widely to other Eurasian teleoceratines.

R: See our response to the previous comment.

On the other hand, the phylogenetic analysis is discussed in very much detail. I think that it could be somewhat shortened, leaving out information about some not so relevant taxa. Although it's not necessary.

R: Not fully agreed. Some readers may focus on a classic comparison (post-description), whereas others may prefer reading a node-by-node depiction of sequenced synapomorphies, at inter-tribal, intergeneric and interspecific levels in the phylogenetic section. We do think that both deserve to appear in the paper, especially as it is online only and there might be no strong constraints on length.

My last comment concerns the figure captions of the photographs. The figures themselves are very nicely done, however, the respective figure captions are too short, not giving any information about the views in which the specimens are seen. I would suggest to change all figure captions of the photographs of the material and mention in every one of them the taxon (*Brachydiceratherium shanwangense*) and the views in which each specimen is portrayed, to compliment the very detailed figures.

R: OK indeed. Sorry for having provided incomplete captions in the original version.

Some minor changes are also noted in the attached .pdf file of the manuscript.

R: Thank you. We have taken into account these complementary suggestions.

Thank you for considering me as a reviewer and I would like to congratulate the authors on this well written manuscript. I am looking forward to seeing it in its final form!

R: We are very grateful for your comments and suggestions. We have also modified typos and most stylistic suggestions you had provided in the annotated pdf.

Panagiotis Kampouridis

Reviewed by Tao Deng, 25 Jul 2022 10:18

Because the manuscript has no line numbers, I upload the annotated original MS with my comments.

R: We deeply apologize for having uploaded the original MS without line numbers and we warmly acknowledge your constructive comments and suggestions, even if some of your remarks may appear tactless (e.g., "ridiculous", "not reliable"). We have addressed most of them (i.e., added references, contextualized the study,

improved the comparison, added figures for carpal and tarsal elements, and provided synthetic measurements). Nevertheless, here below you will find detailed rebuttals to the ones we are not agreeing on:

-We have chosen to use the current matrix, originally intended for Elasmotheriinae and a broad sample of non-Elasmotheriinae (Antoine, 2002, 2003). It has long proven to provide also consistent results on stem Rhinocerotinae (Antoine et al., 2003, 2010; Boada Saña, 2008) and stem Rhinocerotidae (e.g., Becker et al., 2013). Note that slightly reworked versions have also been used more recently for Rhinocerotina within Rhinocerotinae (Pandolfi et al., 2021; Antoine et al 2022) or other taxa among Rhinocerotidae (works by Geraads, Tissier, Sanisidro and colleagues). The fact that we “could not get reliable results” based on this very matrix or that it “is not reliable and acceptable” without more elasmotheriines is quite harsh as a statement – and, to our mind, unsupported.

-We acknowledge your suggestion to add more elasmotheriines and more rhinocerotid taxa, but we prefer to maintain our original taxonomic sample, as it was thoughtfully elaborated to address the question (phylogenetic affinities of Tagay rhinoceros; systematic arrangement of Eurasian teleoceratines).

-We do not agree either about Rhinocerotidae comprising Rhinocerotinae, Elasmotheriinae, and Aceratheriinae (with Aceratheriini and Teleoceratini) as being “universally accepted”, as it is at odds with phylogenetic results published by Antoine and other workers (e.g., Becker, Geraads, Sanisidro, Pandolfi, or Tissier, among others), depicting instead Aceratheriini as being subordinate to Rhinocerotinae. This is the classification favored in the “Database of Fossil Rhinoceros Species: Neogene and Quaternary Old World Localities” edited by Geraads et al. (2021), with most World specialists of rhinocerotids, including yourself, as coauthors. We have therefore maintained the arrangement, as is further coincides with phylogenetic results obtained in the current work.

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Decision by [Faysal Bibi](#) , posted 29 July 2022

Moderate revision

This manuscript was seen by three reviewers as well as myself. All provided detailed comments on the manuscript including pdfs with commentary. Overall the manuscript appears to be a welcome addition to the paleontological literature, with the detailed description of a skeleton from Tagay and a phylogenetic analysis and revision of teleoceratines that the reviewers find convincing.

I recommend moderate revision, as the changes to be made are largely in the text, though these are quite substantial. In particular the Comparison section is quite lacking, and it is not clear that so much description of the phylogenetic results is needed (we can see the relationships in the tree). One reviewer proposes that more taxa should be added to the dataset, and also suggests considering other morphological datasets. Two reviewers would like images of the carpals and tarsals. The figure captions are also all in need of improvement. Measurements of the cranium and teeth are missing from the supplementary dataset S3, in which also almost all cells are blank. Please provide measurements for all listed taxa, or remove these rows. Further details are needed on which specimens were used to score taxa in the analysis. Additionally, I suggest you upload the morphological matrix to a repository such as Morphobank which will make it more visible and easier to use for later workers. Also please add page numbers to the next version. [Download recommender's annotations](#)

Reviewed by [Jérémy Tissier](#), 27 July 2022

This is an excellent and very-well written manuscript on new rhinocerotid remains from the Early Miocene of Russia. It presents the first phylogenetic analysis of a major Rhinocerotid group, the Teleoceratina, which was greatly needed. The results are extremely interesting, and have profound taxonomical implications (monospecific *Diaceratherium*, “resurrection” of *Brachydiceratherium*), as well as palaeobiogeographical, which are all clearly justified by the phylogeny. As such, the title and abstract are totally appropriate for this manuscript.

All the necessary data are provided to replicate the phylogenetic analyses, with a lot of details, which is very helpful and appreciated.

I ran the phylogenetic analyses and obtained the exact same results as presented here, with the same parameters. The discussion on the phylogenetic results is very detailed and very useful. However, I wasn't sure if the new specimen had been coded on its own as a terminal in a prior analyses, before being merged with *B. shanwangense*, or not? If that is the case, it should be mentioned, as that would greatly support the identification of the new specimen. Indeed, it is mentioned in the Conclusion that "the numerous associated features documented and scored in the Tagay rhinocerotid skeleton have allowed for assigning it to the same teleoceratine species (*Brachydiceratherium shanwangense*) as in Shanwang, eastern China." But I could not find that in the rest of the text.

However, if that is not the case (i.e. the specimen was merged with *Brachydiceratherium shanwangense* prior to the analysis), then I would say that the "Comparison" section should be improved, and should justify the attribution of this specimen to the species *B. shanwangense*. Currently, there only seems to be one character (mentioned in this section) that supports it: the absence of p1/d1s. However, the d/p1 is also absent in some (or maybe all) specimens of *B. aginense* (Répelin 1917) and some of *B. lemanense* (e.g. from Wischberg, Jame et al. 2019). Although I fully agree with the identification, I think it should be further justified. In addition, very few *Brachydiceratherium* species (or even Teleoceratina) are mentioned in this comparison.

I would also suggest mentioning, if possible, which specimens, or localities or even references have been used to score the taxa in this matrix. I think that is important for *Brachydiceratherium* in particular, due to its quite complicated taxonomic history, which led to confusions (see Boada et al. 2007 or Jame et al. 2019 for example).

Otherwise, the text is very clear, and the descriptions are very well made. The figures are also of very high quality, although I have a few suggestions:

- Fig. 1: I thought that a small map, locating the Tagay locality in a larger scale (e.g. Russia) would be useful
- Fig. 3: the caption for fig. D is missing.
- Fig. 4: there is a confusion with the position of the mesosyle and paracone fold. Also, change "Valley posterieure" to "posterior valley"
- Fig. 5: Please mention the different views shown (ventral, anterior etc.)

I would add however, that figures of the carpal and tarsal bones would be extremely useful. Although the descriptions are very good, a figure is almost always better than words. If necessary, they could be added in supplementary material instead of the paper.

I have also noted a few minor corrections in the annotated pdf that should be addressed/corrected. I found one reference in the legend for fig. 13 that was not cited in the reference list (Jame et al. 2019), and the reference for Heissig 1972 should mention a or b, as there seem to be two.

Overall, I think my main suggestions would be to improve the comparison section, by detailing which characters (in addition to the d/p1 absence) support the identification of the new specimen to *Brachydiceratherium shanwangense* OR to mention whether this specimen was added as a separate terminal; to mention (even shortly) the material on which the scoring of some terminals has been made; and to provide figures for some of the unillustrated carpal and tarsal bones. This remains nonetheless an excellent manuscript, and I am looking forward to reading the final paper!

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Reviewed by [Panagiotis Kampouridis](#), 15 July 2022

The manuscript of Sizov et al. entitled "An early Miocene skeleton of *Brachydiceratherium* Lavocat, 1951 (Mammalia, Perissodactyla) from the Baikal area, Russia, and a revised phylogeny of Eurasian teleoceratines" represents a very detailed description of a partial skeleton of *Brachydiceratherium shanwangense* from the early Miocene locality of Tagay and an overview of the Eurasian teleoceratines. I believe that it is a very nice example of how such well-preserved material should be treated with detailed descriptions and many detailed photographs of every bone. Especially the figures of the cranial, mandibular and dental material are very well

made with very nice drawings of the specimens, which make it much easier for the reader to understand the morphology.

This kind of comprehensive study of all available material, including almost all of the postcranium of the skeleton, is definitely extremely helpful for future studies of teleoceratines and fossil rhinos in general. The results of this study have an important impact on the phylogeny and biogeography of Eurasian teleoceratines.

The manuscript is well structured and well written. The methods the authors use to study the material is adequate. The phylogenetic analysis performed by the authors is sound and appropriate for the group. I only have few comments to make on the manuscript. The most important one concerns the Comparison of the material (p. 27-28). It is rather short and very limited concerning the taxa with which the material from Tagay in compared to. Especially since the description is so comprehensive, it would be great to also have a more comprehensive comparison including also a bit more information about postcranial features (where possible). I would suggest to split the comparison in two. The first part would concern the comparison of the material across the Eurasian teleoceratine genera (*Prosantorhinus*, *Brachypotherium*, *Diaceratherium* and *Brachydiceratherium*) and demonstrating that the material belongs to the genus *Brachydiceratherium*. In the second part the material from Tagay can be compared within the genus *Brachydiceratherium* with the most important species to show that it belongs to *Bd. shanwangense*. Otherwise, first the taxonomy of the Tagay material could be established and then in the second part it can be compared more widely to other Eurasian teleoceratines.

On the other hand, the phylogenetic analysis is discussed in very much detail. I think that it could be somewhat shortened, leaving out information about some not so relevant taxa. Although it's not necessary.

My last comment concerns the figure captions of the photographs. The figures themselves are very nicely done, however, the respective figure captions are too short, not giving any information about the views in which the specimens are seen. I would suggest to change all figure captions of the photographs of the material and mention in every one of them the taxon (*Brachydiceratherium shanwangense*) and the views in which each specimen is portrayed, to compliment the very detailed figures.

Some minor changes are also noted in the attached .pdf file of the manuscript.

Thank you for considering me as a reviewer and I would like to congratulate the authors on this well written manuscript. I am looking forward to seeing it in its final form!

Panagiotis Kampouridis

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Reviewed by **Tao Deng**, 25 July 2022

Because the manuscript has no line numbers, I upload the annotated original MS with my comments.

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