PALEVOPRIM
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Paléoécosystèmes Paléoprimatologie
UMR 7262 - CNRS INEE - Université de Poitiers UFR SFA

BEDANE Tomas Getachew

29 November 2024

Dear Dr. Vera Weisbecker,

We are pleased to resubmit the revised version of our manuscript *"New Data on Morphological Evolution and Dietary Adaptations of Elephas recki from the Plio-Pleistocene Shungura Formation (Lower Omo Valley, Ethiopia)"* to *PCIPaleo*. We have addressed the reviewers' comments and made the necessary revisions, as detailed in the attached response document (with our replies highlighted in gray). Thank you for your time and consideration. Please feel free to contact me at **tomas.getachew.bedane@univ-poitiers.fr** with any questions.

Sincerely,

Tomas Getachew Bedane

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ANSWERS TO REVIEWERS

Revision round #1

Decision for round #1 : *Revision needed*
First of all, let me apologise again for the extensive time this review has taken. We had 16 reviewer invitations, with one agreeing to review and then declining after 6 weeks of waiting. Both reviewers find the study interesting and worth publishing, and I agree that the results are beautifully presented and include an excellent range of data. However, both raise some important issues that need to be addressed.
Both reviewers agree that the taxonomic context of the Elephas recki species (or complex) which requires more careful contextualisation, and hopefully their extensive comments will be helpful to address this issue.
Reviewer 1 also raises an issue about the interpretation of the results and suggests that incorporation of more recent literature might provide a clearer explanation of the pattern shift that the manuscript observes. In this context, Reviewer 2's suggestiong might be useful that a more differentiated view of the data by adding some analyses, which are not hard to implement (multivariate clustering/basic descriptives).

by [Vera Weisbecker](#), 01 Oct 2024 23:37
Manuscript: https://osf.io/preprints/paleorxiv/qexuf
version: 3

We would like to deeply thank you for your explanations and for the work done managing this paper and the dearth of reviewers.
We also would like to express our gratitude to both reviewers who agreed to review this manuscript and for their comments that significantly help to improve our manuscript. We have read these carefully and below we addressed in detail the questions they raised.

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Review by anonymous reviewer 1, 29 May 2024 12:46

General comments

I find the subject of this study worth exploring and the results interesting and promising. However, it seems to me that some key concepts have been slightly misunderstood by the authors and that's why I must recommend a major revision to the text. My main concern is that the authors use the apparent lack of correlation between dietary signal (mesowear) and the patterns of change in the dental traits (hypsodonty and enamel thickness) as their main argument for stating that there is a lag between ecological change and the evolutionary patterns that would call for alternative explanations. However, as has been recently shown (Saarinen and Lister 2023), dental evolutionary patterns in proboscideans are in fact associated with major climatic changes (aridification pulses), although not being driven by a shift to grazing diet (at least not at this late evolutionary change when elephants were already largely grazers and had a rather derived tooth morphology to begin with). The authors consider this mysterious and point at need for alternative explanations, but in fact all that is

needed is a careful re-evaluation of results that already exist, and correction of some misconceptions.

We did not consider any mystery here, but a clear difference with what literature has been proposing for decades. In this we agreed with Saarinen & Lister (2023) but cannot limit our discussion to a comparison with this single work. The dental evolution of *Elephas* (notably HI and ET) has been interpreted abundantly and for a long time as a response to dietary changes. We simply discussed our results against previous works in a rather chronological framework, of course including the recent work by Saarinen & Lister, but also paleoenvironmental data relevant to the Shungura Formation within this discussion. Please also note that even recent studies demonstrate that the debate is not over on the factors of dental wear (e.g., Sanson et al. 2017 Biosurface and Biotribology).

For example, more grazing mesowear signal does not have to mean more arid and open environment (grazing resources are most prominent in intermediate precipitation range). Mesowear is above all a signal of grazing (grass consumption), not aridity, openness or grit consumption (see Saarinen and Lister 2023, and references therein). Thus, a pattern emerges where the steps in dental trait evolution (similar in the Shungura formation based on the new data presented in this manuscript and for elsewehere in East Africa (Saarinen and Lister 2023)) are associated above all with peaks of aridification (that may involve factors such as shift to more drought-adapted plant diets and exogenous grit (dust)), but not shift to grazing (because at this point the elephants were already largely grazers).

We provide answers to particular remarks below, but we would like to summarize the debate related to mesowear interpretation here.

1) Various authors acknowledged that mesowear may be the result of diet AND of exogenous grit.

Mihlbachler et al. (2023 Front. Ecol. Evol.): "The most widely recognized confounding variable when relating mesowear to diet is the relative impact of extrinsic geological material (e.g., dust, silt, sand) that is ingested along with food (Schulz et al., 2013; Wronski and Schulz-Kornas, 2015) and this additional source of abrasion may be responsible for some degree of dietary misclassification."

Sanson et al. (2017 – cited by Saarinen & Lister 2023): "Other findings emphasize the complexity of the issue. For example, Schultz et al. [21] showed that mesowear in the browser/grazers and gazelle (Gazella marica) at different times of the year, when the proportions of grass and browse changed, was not reflected in measurable tooth wear. They suggested that this might be because levels of abrasives in the desert environment may have been high across seasons and food types, masking any dietary abrasive signal."

This latter work concluded that interactions between grit (potentially larger particles) and plant silica could be required to actually explain dental wear.

2) The hypothesis of a uniform action of exogenous grit (small particle size) on mesowear, resulting in no change in mesowear scoring that strictly indicates diet, was notably proposed by Kaiser et al. (2013 Mammal Review). This study was based on a large dataset mainly including ruminant taxa. It was however suggested that because of the food residence in the rumen, exogenous particles ingested by

Another major issue in this manuscript (apart from the need to revise the interpretation of results) is the treatment of "*Elephas recki*" as a coherent taxonomic entity, despite recent evidence suggesting that it consists of more than one species (and likely more than one genus). The authors are clearly aware of this, but decide not to address this other than saying that the purpose of this study is not to revise taxonomy. However, the taxonomic uncertainty is a critical issue for interpreting whether the observed patterns of dental trait evolution represent changes within an evolutionary lineage or differences between taxa. For this reason, at minimum I think it should be more clearly acknowledged throughout the text that "*Elephas recki* compex" is an informal and uncertain taxonomic group. Thus, I suggest at the very minimum to add quotation marks to "*Elephas recki*" throughout the text. In summary, the results and their presentation seem fine, but the interpretation of the results needs revision. See more detailed comments in the annotated manuscript file.

Detailed Comments

Please note that some minor edits directly suggested by Reviewer 1 in track changes were incorporated. We thank the Reviewer for this help!
Lines refer to the original ms

Line 47: this is fine, but I suggest: "grass-dominated"

We have accepted 'grass-dominated' and added herbaceous monocot (such as grass and sedges).

Line 79: extant Earth vs. extant land animals

Suggestion accepted.

Lines 100-101: This was not quite what Saarinen and Lister (2023) noted: Rather they noted a stepwise increase in loph count and hypsodonty that followed peaks of particularly harsh (arid) climatic phases. It is true, however, that shift to grazing diet alone appears to have a milder effect on the evolution of dental traits than the climate fluctuations.

We have modified this sentence to read: "Lister (2013) demonstrated a decoupling between these morphological trends and paleoecological signals at a regional scale (e.g., eastern Africa), suggesting a significant delay between environmental changes, dietary behaviors, and morphological responses. However, Saarinen and Lister (2023) recently observed a stepwise increase in crown height (hypsodonty) in true elephants happened rapidly but in distinct stage after 5 Ma, specifically corresponding to peaks in arid climatic phases."

Lines 110-112: The remains species representing the "Elephas recki lineage" vs. Elephas recki lineage, which has been considered a coherent evolutionary lineage, but may comprise species in genera Elephas and Palaeoloxodon (see e.g. Sanders 2023)

Thank you for this suggestion. We have made some edits to this section but keep the species unchanged or without quotation marks (see detailed comments to Reviewer 2). We have added the citation (Sanders 2024). Actually *Palaeloxodon* is not universally considered as a genus, but is also seen as a subgenus.

Line 157: isn't this 2023? I think this book was published in last year's autumn.

Indeed the book was out online in 2023, but the copyright page indicates 2024 and "first edition published 2024", so we will keep 2024.

Lines 160-161: There are distinct difference in dental morphometrics and skull morphology between these taxa (as discussed by both Zhang 2020 and Sanders 2024), which are not arbitrary and rather suggest that these are separate species rather than subspecies. I think the wording needs to be changed here. I think it starts to be clear that the question is not whether

the "subspecies" of "E. recki" are separated taxa (they clearly are), but rather which genera of elephants they should be assigned to. Even if the authors state that the purpose of this study is not to test taxonomic hypotheses, I strongly suggest to do at least the following:
-acknowledge that "Elephas recki" probably represents more than one species, which have formerly been called subspecies, and thus, if the name "Elephas recki" is used in this manuscript all the former "subspecies", I strongly recommend to spell it with the quotation marks ("Elephas recki") across the manuscript.

Beden (1980) also intended to describe subspecies as separate taxa, but the taxonomic level of attribution is a matter of appreciation based on individual experiences. In this case, quotation marks added to *Elephas recki* imply a taxonomic view that we do not necessarily support. Regarding differences in subspecies vs. differences in genera, the question has different levels – e.g., our morphometrical data shows little or no differences between *shungurensis* and *atavus*, it would be awkward to propose even specific distinctions without further analyses. And again there are definitely not the purpose of this paper and needs to be addressed properly on its own, not as a marginal topic. Despite recent and welcome efforts by Zhang (2020), subspecies of *Elephas recki* are not so readily attributable to different genera, and the taxonomic debate is far from being over (Sanders 2024 made this quite clear). We provided a more detailed answer about this for Reviewer #2. To sum it up, we think that this material can indeed form a real lineage as it was previously interpreted, and that splitting a single anagenetic lineage into several genera is a greater risk for the stability of taxonomy than keeping subspecies within *Elephas recki*.

Line 166

We have added the citation (Saarinen & Lister 2024).

Lines 209-212: references needed here (for example: Janis and Fortelius 1988; Fortelius et al., 2002; Damuth and Janis, 2011)

We have added the citations (Janis & Fortelius 1988; Damuth & Janis 2011).

Lines 239-240: the meaning of this is unclear to me. Do you mean the differences to other mesowear measurements form more complete specimens was not significant?

This is not about the completeness of the specimens. Results were compared on a series of same specimens for three measurements and two measurements, and no differences were found between the two samples.

Line 274: What do you mean by members? I assume the stratigraphic members of the Shungura Formation? Check if they should be written with capital letter (in case they are formal stratigraphic units)

Indeed, these are the stratigraphic members. We precised "Shungura stratigraphic members" but retain the plural 'members' lowercase when listing several named units. A capital letter is required when providing the formal name of a given member, e.g., Member B, but not when

discussing "members A to C" or just "members." Same applies to the Shungura Formation (upper case), which is a geological formation (lower case).

Lines 275-276: this may be partly because the group likely consisting of several species rather than a continuous evolutionary lineage (or species) (although e. g. Saarinen et al. 2023 also noted similar stepwise hypsodonty increase in other elephant lineages)

We fully agree with the Reviewer that such changes in evolutionary rate can be observed within a single lineage, and do not necessarily demonstrate the presence of several lineages within this material. Our data does not provide decisive support to the several species.

Line 421: The threshold values between "mixed" and "purely grazing" values have been received (see Saarinen and Lister 2023), and they should not in any case be considered fixed. Thus, I would avoid very precise numeric categorizations such as "4.3 % have fully grazing signal"

Thank you very much for your comment. We indeed overlooked the change introduced by Saarinen & Lister. We have revised our text as follow:

"a third of individuals (N = 24 out of 68) exhibiting a grazing signal. This is at odd with our findings, where a clear majority of individuals (N = 63 out of 80) fall in the grazing range, […]"

We also adapted our result part and Figure 1 accordingly to the revised thresholds from Saarinen & Lister (2023).

Line 421: This is not categorically true, but rather depends on the population and species observed. For example, for many populations of Palaeoloxodon recki recki (of "E. recki recki") the mesowear value of Saarinen and Lister 2023 indicate grazing dietary composition (also note that the threshold values were updated in Saarinen and Lister (2023)). There is now also microwear data (unpublished) that suggests more mixed-feeding dietary signal for many of the Kenyan "E. recki" than has been thought before.

Saarinen & Lister (2023) observed that some specimens had a mixed dietary composition, unlike *E. recki recki* from the Omo for which all specimens are grazing. Discrepancies are particularly marked for earlier subspecies, mostly in the mixed range (106°-117°), when they fall mostly in the grazing range in the Omo (above 117°). The difference of a more grazing diet at Shungura is correct for each subspecies. We provided below a figure illustrating this (in blue, our data, in orange, Saarinen & Lister's data). We therefore prefer to keep the general figure as it reflects also the subspecific cases.
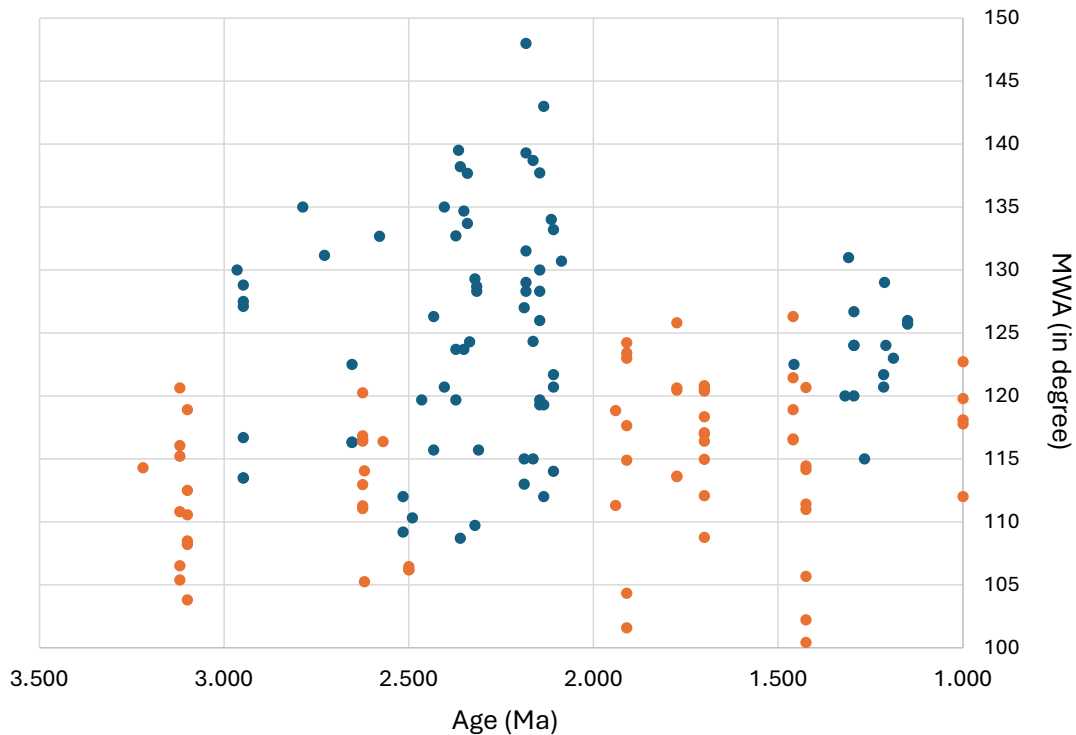
Line 423: This reasoning is not necessarily correct. Note that more arid and open environment does not automatically indicate more grass recourses. Grass cover is at its most extensive under intermediate precipitation conditions, and in extremely arid environments (sub-deserts rather than grasslands), browse resources can be proportionately higher than in grassland. Thus, you can't argue that more arid climate should automatically be equal to a more grazing dietary signal in proboscideans

We have retained the original wording to highlight the importance of local-scale (small-scale) habitat heterogeneity, as demonstrated by Barr (2015, JHE) through his ecomorphological analysis of bovid astragali. Barr showed that the Lower Omo Valley in Ethiopia had wetter, more vegetated habitats near the Omo River, while the Nachukui and Koobi Fora Formations in Kenya had drier, more open habitats. This is also congruent with interpretations from paleosol carbonates obtained by Cerling et al. (2011, Nature) that Shungura had systematically more tree cover than Nachukui and Koobi Fora. Bobe et al. (2007, in Hominin Environments in the East African Pliocene) and Bibi & Kiessling (2015, PNAS), among others, reported significant differences in grazing taxa among bovids (Alcelaphini, Antilopini, and Hippotragini) being consistently more abundant in Nachukui and Koobi Fora than at Shungura, advocating for Shungura reflecting more wooded and moist environment whereas the rest of Turkana Depression was more likely dominated by the presence of grasslands.

Do Nachukui and Koobi Fora were "extremely arid environments (sub-deserts rather than grasslands)" displaying more browse vegetation than grasslands during the Plio-Pleistocene? The general faunal pattern is not in favor of this interpretation and recent literature on environmental reconstructions do not depict subdeserts in which grasses are not so abundant, but instead environments wetter than today in which wooded grasslands and open grasslands are important components (see among others Bobe et al. 2022 in African Paleoecology and Human Evolution).

Although we agree that proboscideans could feed on grass despite a relatively lower abundance of these plants, we nevertheless find counterintuitive that the same taxa in the Turkana would eat more grass in more wooded environments (Shungura) and had a more mixed diet in more grassy ones (Nachukui, Koobi Fora). This is particularly astonishing given that Saarinen & Lister (2016) indicated that: "despite the underlying differences in dietary preferences and adaptations, proboscideans tend to be flexible feeders that are able to consume relatively more grasses in open, grass-dominated environments and more browse in wooded environments. This is also seen today in the African savanna elephant (*Loxodonta africana*), which has essentially purely browsing diets in forested areas and mixed-feeding diets in more open savannas with grassy vegetation (Cerling et al., 1999)."

So, if indeed the view that more arid climate should automatically be equal to more grazing is definitely too simplistic, we maintain that in the particular case of the Turkana Depression, *Elephas recki* displays a pattern that is opposite to what one would normally expect, and that the reasons for this should be investigated.

Lines 423-426: This is possible, but unlikely. In general, there is a lot of variation in the measurements (also seen in your data), and in fact a difference of ca. 10 degrees is not very much towards the grazing end of the spectrum.

A difference of 11° is also what is observed between the limits of the whole "mixed diet" category, hence separating grazers and browsers. We strongly believe that this hypothesis needs to be tested, especially when the Reviewer thinks it could be a possibility. This would actually be quite easily done and, proven wrong, would allow looking for other explanations. Therefore we prefer to keep our suggestion.

Lines 432-433: true, but it should be noted that mesowear only captures a signal of grazing and not other kinds of dietary changes (for example shift to consuming tougher or more dry-adapted vegetation). Saarinen and Lister (2023) noted that major steps in proboscidean dental evolution coincide with major peaks of aridification, thus arguing that aridification in general was a major driving force of the evolution of dental adaptations in Proboscidea, and changes in plant resources may have been part of the factors associated with the aridification (although grazing specifically does not seem to be the main driver)

We modified the wording 'However, Saarinen and Lister (2023) observed that, over long timescales, major proboscidean dental adaptations align with periods of aridification, suggesting that increasing aridity and not just grazing was a key driver of these evolutionary changes due to shifts toward tougher, dry-adapted vegetation.'

Line 439-440: although some widening of the range of mesowear values towards grazing can also be seen in your data (even if the mean does not differ significantly)

We modified the paragraph as following.
"Isotopic results obtained by Negash et al. (2020) for elephantids from the Shungura Formation are not fully congruent with this view. As for our MWA results, they were interpreted as a graze-dominated mixed diet to strictly grazing diet, with values similar to those observed for bovids and suids from the same formation (Bibi et al. 2013), but also

display significant differences between Member B and Member C values (matching an increase in our MWA results between these two members, although non-significant) and an increase in C_4 plants between the lower and the upper part of the sequence. These results could be more in line with the stepwise morphological changes we observed. Yet, these isotopic contents at family level cannot be attributed with certainty to *Elephas recki* and may include different dental positions, and as such are not fully comparable with the dataset used in the present study. In addition, the interpretation of a shift toward a more C_4 signal may not necessarily reflect a significant change of dietary category (see discussion by Blondel et al. 2018). Future work on Shungura isotopic ecology will be required to test these results specifically for *E. recki*."

Line 450-452: However, again, note that it has been shown that there was a strong connection between climate changes and proboscidean dental evolution (Saarinen and Lister 2023). So, even if there is no clear association between grazing and dental trait evolution (although there probably was in enamel folding at least in the big picture), it doesn't mean that other factors related to climatic aridification could not have played a role.

We discussed first the influence of dietary adaptation on dental trait evolution as proposed in older literature, and then we discussed the other possible factors such as dust or grits below below in paragraph starting at line 461.

Line 455: Not necessarily! See the association between aridification and dental trait evolution (decoupled from shift to grazing) (Saarinen and Lister 2023)

We did not say this is necessary but prefer to keep a comprehensive discussion that mentions different relevant hypotheses. By the way, these two possibilities are not incompatible.

Line 461-464: Ok, yes, here it is, and this may be one mechanism to explain why Saarinen and Lister (2023) noted the association of proboscidean dental evolution with climatic aridification

We understand that Reviewer 1 was expecting that from the beginning, but it was quite important to us to discuss other hypotheses existing in literature. We believe the readers will benefit from a comprehensive discussion instead of a partial and one-sided one.

Line 471-472: This is an important part of what Saarinen and Lister (2023) did, and found there to be a relationship between these (although the dust accumulation was measured from marine sediments, thus reflecting general aridification and increased dustiness in East Africa)

We incorporated further details on Saarinen & Lister's work in this paragraph.
"Saarinen & Lister (2023) reached this conclusion after observing tight correlations between changes in dental feature changes (including HI and ET) and picks periods of increasedof aridity (based on dust in marine sediments as a proxy of general aridification and dustiness in eastern Africa)."

Line 483-484: There is no discrepancy here, because it has been shown that while grit increases overall tooth wear rates, it does not have a major effect on mesowear signal (which is driven by grass consumption) (again: read Saarinen and Lister (2023), and the references therein carefully). Thus, it is very important to keep these matters separate in this discussion: aridification and increased dustiness seem to have been the major drivers of proboscidean dental evolution, while the amount of grass in diet had a more subtle (but possibly complementing) role in that process

Again, we simply would like to reflect the complexity of this topic in our paper, and while this Reviewer believes grit and diet factors need to be totally separated, many authors have discussed them together in an extensive literature for the last ten years. We modified this sentence to make our intention clearer, and to develop our views on it.

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Review by Steven Zhang, 01 Oct 2024 12:41

General comments

Getachew et al. conducted dental morphometric and mesowear analysis on the classic sequence of elephantid fossils from Ethiopia's Shungura Formation, ascribed to the "*Elephas recki*" complex. As the authors duly noted in their manuscript (MS hereafter) with appropriate citations, there has been recent research progress which convincingly argued on the basis of cranial morphology, that "*Elephas recki*" from the Shungura Formation is likely to represent a number of time-successive species lineages, as opposed to a single anagenetic lineage whose dental evolutionary pattern resembles that of a ring species rolled out in time; notwithstanding that the authors' own data reject the simple linear anagenetic scenario. Therefore, I recommend for the authors to acknowledge, in revising the MS, that they made an entirely valid and pertinent study of community-level ecomorphological shift in Shungura elephantids within the timespan of the stratigraphic sequence they investigated (3.75–1.09 Ma), but their data should not be conflated with investigation of morphological trends within a single species or genus. Therefore, to avoid confusion I recommend the authors use lexicons such as "*Elephas recki*" complex (ERC hereafter), or "*recki*" instead of *Elephas recki* to delineate the taxonomic group they are investigating, and I believe this to be consistent with the authors' intension to state their positional neutrality on the taxonomic and phylogenetic context of the ERC. This does not detract the value of this contribution to the discipline in the slightest.

We thank the reviewer for his thoughtful taxonomic comment. We indeed clearly cited the nomenclature he suggested, i.e. "*Elephas recki* complex", and in our revision we propose to add it to the abstract to make this clear as early as possible. Yet, we believe that the use of *Elephas recki* is appropriate. Regarding attributions to different genera, in his extensive review Sanders (2024) disagreed with placing *Elephas recki brumpti* within *Phanagoroloxodon*. The fact that *brumpti* does not display all the derived features of later taxa does not necessarily mean it should be placed into a different genus, and in addition our own observations remain congruent with the possibility that in the Omo Valley, *E. r. brumpti*

could really be the primitive stock from which later *Elephas recki* emerged. Placing it within *Phanagoroloxodon* would not be really helpful in that regard.

The attribution of *E. r. ileretensis* and *E. recki recki* to *Palaeloxodon* seems convincing to most authors, however there is a debate about the rank of this taxon, either a genus or a subgenus of *Elephas*. In addition, recent paleogenetic analyses (Meyer et al. 2017 and Palkopoulou et al. 2018) nested *Palaeloxodon* within *Loxodonta*, not with *Elephas*, which is contradicting the morphological evidence and calls for caution. But in any case this does not disprove that the "*Elephas recki* complex" represents a lineage displaying anagetic evolution. We are not convinced that using everywhere "*Elephas recki* complex" is really simplifying the taxonomic discussion or the understanding of readers. Until it can be clearly demonstrated that these specimens belong to multiple lineages, that anagenetic evolution within a single lineage can be totally excluded, that *Palaeoloxodon* should be a genus on its own, and that the apparent contradiction between molecular and morphological data is solved, we prefer to follow the principles of the International Code for Zoological Nomenclature mentioned in its preamble: 1) the promotion of taxonomic stability, 2) the freedom of taxonomic thought and action. For these reasons, we prefer to keep using *Elephas recki* that remains widely present in literature, and to remain cautious for the use of the subgenus, or genus, *Palaeloxodon*. We however acknowledge that further analyses may demonstrate that *Elephas recki brumpti* is a chronospecies of this lineage (i.e. *Elephas brumpti*), and possibly that it could be the same for *E. r. ileretensis* and/or *E. r. recki*.

In all of this, we opt for the same solution as Sanders 2024, who is using "*Elephas recki* complex" to refer to the taxonomic conundrum, but in practice uses *Elephas recki*. Regarding the Reviewer's remark on our data rejecting the "simple linear anagenetic scenario," we would like to note that our data could well be explained with differential evolutionary rates in some features within a single anagenetic lineage (mosaic evolution), or could be also the result of the existence of multiple lineages. However, our data do not unambiguously support lineage diversity or cladogenetic events. For the time being, the first interpretation seems most parsimonious to us, and within the framework of this work, as suggested by the Reviewer, it will not alter the value of our conclusion.

We propose to further clarify the on-going discussion on taxonomy of the "Elephas recki Complex" and modify its depiction as following.

"There is an on-going debate about these systematic biology of the "*Elephas recki* complex" (Todd 2005; Zhang 2020; Sanders 2024). The disagreement is specifically about whether the earliest and youngest subspecies should be placed within the genus *Elephas* or, instead, within *Phanagoroloxodon* and *Palaeoloxodon*, respectively. Based on cranial morphopology, Saegusa & Gilbert (2008) and Zhang (2020) advocated for relating *E. recki ileretensis* and *E. recki recki* within *Palaeoloxodon*. However, the implications of this result remains discussed in the literature (Sanders 2024). First, the inclusion of *Elephas recki brumpti* within *Phanagoroloxodon* is not universally approved (Sanders 2024). Second, *Palaeoloxodon* is considered as a subgenus of *Elephas* by various authors (e.g., Saegusa & Gilbert 2008) instead of a genus on its own as proposed by Zhang (2020). Third, recent paleogenetic work (Meyer et al. 2017; Palkopoulou et al. 2018) suggested that recent Eurasian specimens of *Palaeoloxodon* are nested within *Loxodonta*, which conflicts with phylogenetic results based on morphology (Zhang 2020). Consequently, for this paper, not intending to test conflicting taxonomic hypotheses, we choose to retain the classical use of subspecific division within *Elephas recki* because it was not demonstrated that the vast majority of this material cannot be interpreted as forming a single anagenetic lineage, and its subspecific subdivision retains a practical dimension. We note however that subspecies is a term more relevant to geographic

variations within a species than to evolutionary stages, and that the subspecies of *E. recki* are more adequately viewed either as arbitrary, practical temporal stages displaying marked overlaps, or as substitutes for chronospecies (see Sanders 2024 for a more thorough discussion). Although we believe that further examinations of the Shungura record may eventually lead to the definition of chronospecies, this paper that does not consider all relevant data to perform a proper taxonomic revision is not the right place to take such decisions."

In addition, we added one paragraph to the discussion about the interpretation of our data regarding the alternative hypotheses.

"One way to interpret these results is that they would correspond to the lumping of multiple lineages within the "*Elephas recki* Complex" (see Zhang 2020). However, similar stepwise changes in evolutionary rates can be observed in single lineages (Saarinen & Lister 2023) and should not necessarily seen as evidence for taxonomic comingling. As indicated above, the debate on the taxonomic status of *Elephas recki* has still not reached a conclusion (e.g., Sanders 2024). We considered here that the studied material is more parsimoniously interpreted as belonging to a single lineage (following Beden 1980 among many others). We acknowledge that subspecies were used as a practical rank for chronological stages, and that alternatively at least some of them could be reconsidered as chronospecies, notably *Elephas recki brumpti* in agreement with Sanders (2024). Yet we are convinced that further work is required for finalizing the taxonomic revision of the Shungura material attributed to *Elephas recki*."

We believe that following these explanations, readers will not be confused by the use of *Elephas recki*, or by the fact that we are – for the time being – not fully convinced by the multiple lineage hypothesis.

Lister (2013) and Saarinen & Lister (2023) all used community-level dental trait and foraging ecology approach. I recommend the publication of this MS, contingent on suitable revisions being carried out concerning the feedbacks addressed here.

In the 4th paragraph of their Materials and Methods section, the authors acknowledge the problem I alluded to in the previous paragraph. Without intending to dismiss the authors' understanding of this issue, my impression is that their wording has slightly misrepresented the debate. There can now be little doubt on the basis of craniodental morphology that the comparatively 'advanced', nominotypical *recki* from late Early Pleistocene East Africa represents a progenitor to subsequent species of *Palaeoloxodon* (Saegusa & Gilbert 2008; Larramendi et al. 2020; Zhang 2020; Sanders 2024).

We would like to thank the Reviewer's concerns about our understanding of taxonomic questions. We propose to further clarify our position: we do not have issues with the emergence of derived features of *Palaeoloxodon* within *Elephas recki*, but it is also necessary to take into account that paleogenetic results establish a link between *Palaeoloxodon* and *Loxodonta*, complicating the debate, and that the rank of *Palaeoloxodon* is, depending on the authors, viewed as subgeneric or generic. Our own observations of the Shungura material are not necessarily in agreement with multiple lineages included within *Elephas recki*. For practical reasons, and for the sake of nomenclatural stability, we again choose retaining *Elephas recki* for this paper, and we are totally convinced that an in-depth revision/discussion of taxonomic questions will require more time and space for insuring its quality.

The central problem is whether earlier materials attributed to the ERC all represent progenitor populations that lead up to nominotypical *recki*, a proposition not supported by Zhang (2020) on the basis of his comparative studies of the referred skulls of "*Elephas recki brumpti*" and "*E. r. atavus*" from the Omo-Turkana Basin. By the nature of the East African fossil record, the earlier materials attributed to the ERC is very likely to contain the ancestor of nominotypical *Palaeoloxodon recki*; and Zhang's (2020) core argument was simply that materials representing other elephantid lineages were lumped within the "*recki*" complex by earlier authors such as Arambourg (1948) and Beden (1980; 1983; 1987). By measuring first-hand 140 Shungura elephant molars covering much of the entire stratigraphic span of the ERC, the authors have in fact contributed outstandingly valuable data concerning debate. I thereby encourage the authors to add simple descriptive statistics and multivariate clustering analysis (e.g. linear discriminant or principal component analysis) for molar morphological variance across each stratigraphic bin they have analysed, as a basic means of discerning the number of dental morphotypes present in each stratigraphic bin. Given the authors collated good sample sizes for elephantid dental mesowear at different Shungura horizons, this can potentially detect 'niche partition' between different morphotype-groups. If discernible dental morphotype-groups are identified, I would recommend the authors refrain from ascribing taxonomic identities to different morphotypes, beyond descriptions of principal morphologies that characterise each morphotype-group (cf. Todd 2005).

Descriptive statistics for molar features for each taxonomic bin are already provided within the paper for HI and ET (Table 1, see also supplementary data). We have run a LDA as proposed by Reviewer 2 based on width, height, laminar frequency, HI, and ET (length is unfortunately too often incomplete). The results (see below, 97 % of variability explained by axes 1 and 2, axis 1 largely dominated by HI) do not clearly demonstrate the presence of different morphotypes within a given time bin. Instead, the results (see below) are in line what is already presented in our paper, compatible with the idea of a lineage displaying alternations between phases of morphological changes (from B to C, from G to L) and stasis (from C to G).
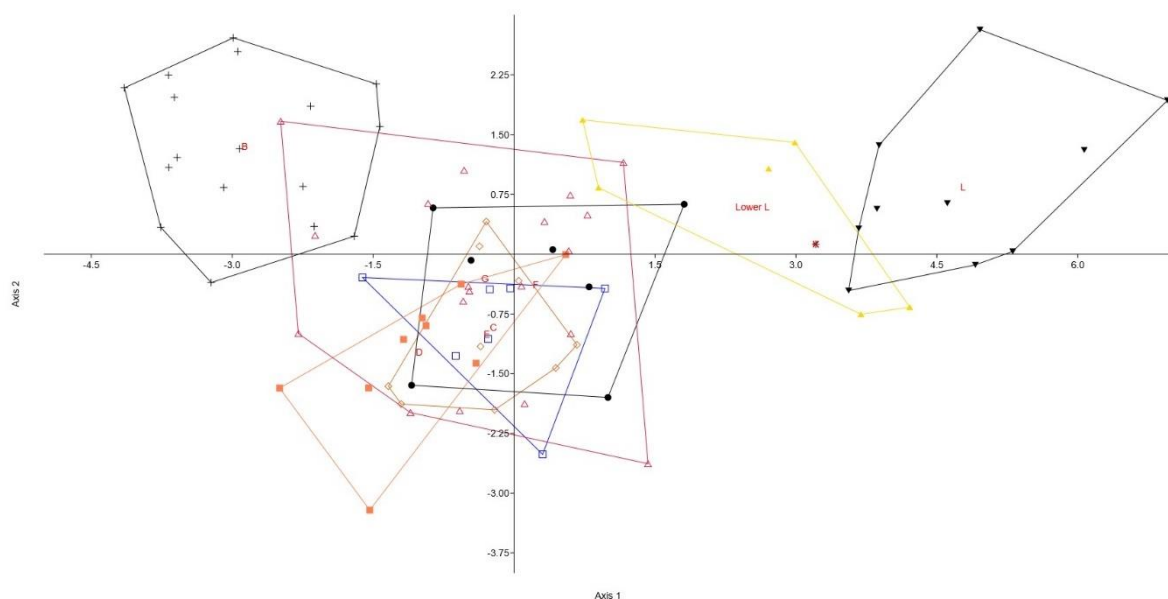
Concerning one statement from the opening paragraph, although it is indeed true that elephantids underwent precipitate net decline within the last two million years, it should not be overlooked that major phylogenetic events within the clade that led to the highly successful modern and Late Pleistocene species took place within this interval. The successful occupation of Northern Eurasia by *Mammuthus* and *Palaeoloxodon* during their Pleistocene radiation, amid intense glacial-interglacial cycles, also vastly expanded the ecological envelope of this lineage. Admittedly I am falling short of finding a suitable way to integrate some nuance into the statement about their steep recent decline in a pithy fashion, I would suggest this to be a worthwhile exercise during revision.

We fully agree. We tried to propose a phrasing taking into account the remark.

I was personally intrigued that the authors cited Arambourg (1938) as the authority for the currently conventional procedure of measuring hypsodonty in proboscideans. Osborn, Gregory and Matthew have all noted in their earlier works trends of hypsodonty increase in herbivorous mammal lineages including proboscideans, although in the time of completing this review I had been unable to find examples of a comparable hypsodonty index employed in their works. I encourage the authors to briefly demonstrate their literature factchecking in revision.

We simply cited Maglio's monograph (1973) on this. For the time being we were unfortunately not able to find the original paper by Arambourg, and a quick search did not find other mentions of an hypsodonty index prior to the 1950s. We placed the reference to Maglio (1973) at the beginning of the sentence to make it more clear.

The authors duly highlighted Maglio's (1973) hypothesis of the craniomandibular apparatus evolving as a suite to explain the apparent discordance between direct dietary signal represented by mesowear and signals of dental morphological adaptation. Yet in their wording they slightly misrepresented the relevance of Zhang (2020) here. Zhang (2020) examined cranial osteology in fossil elephantids (including those from the Turkana Depression) primarily for the purpose of inferring taxonomy and phylogeny, rather than from the perspectives of function, modularity and developmental constraints. I agree with the authors that constraints brought about by the gross evolutionary morphology of the craniomandibular apparatus could have been a factor that impeded elephantid dental evolution in the studied region from showing trajectory that aligns 'perfectly' with mesowear-based dietary signal, and in my knowledge Zhang (2020) said nothing to explicitly contradict such postulation. This would serve a riveting subject for future research!

We agree that Zhang (2020) was not focusing on function in his study of craniomandibular characters. But since Zhang (2020) is a major source of morphological data on cranial evolution in elephantids, we looked at character changes documented in Zhang (2020) and try to see if any conspicuous changes could have had an impact on dental evolution. We did not find anything relevant – not meaning of course that these do not exist, but indeed that future

work in that direction is needed. We could either delete this paragraph or modify its wording. We proposed the latter solution.

Detailed Comments

Please note that some minor edits directly suggested by Reviewer 2 in track changes were incorporated. We thank the Reviewer for this help!
Lines refer to the original ms.

Line 38: Proboscideans are neither abundant nor diverse today, but they comprise a appreciable and palaeoenvironmentally significant component of the Cenozoic mammalian fossil record!

Modified as following: The proboscideans, abundant and diverse throughout the Cenozoic, are essential terrestrial megaherbivores for studying morphological adaptations and reconstructing paleoenvironments in Africa.

Line 79: Order

A rank does not need to start with an upper case letter, unlike taxa.

Line 81: Cantalapiedra et al. (2021) would also be appropriate citation here.

Added.

Line 82: Common mistake that I occasionally made also - dispersals are longer-term shifts in the distribution of organisms (appropriate here); whereas migrations occur on a periodic basis on the scale of an individual animal's lifespan, often in conjunction with seasonal or life history events

We totally agree. This was corrected.

Line 121: Zhang (2020) would be a suitable citation here

Added.

Line 226: What about width?

We are not certain of what Reviewer 2 asked for here. HI as a ratio is of course also dependent on crown width. Similarly, absolute width is also submitted to interindividual differences in size, and the HI ratio appears more relevant to comparisons given it is a relative proxy of the molar shape.

Line 247: Not sure title capital spelling is merited here. Saarinen et al. (2015) didn't use capital letters when introducing this part of the procedure

Corrected.

Line 353: Damuth & Janis (2011) would also be an appropriate citation here

Added.

Lines 516-518: Possibly!

Indeed, and we hope somebody will be able to test these hypotheses in a near future.

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