Peer Community In Paleontology

Of elephant teeth and plants: mesowear and dental adaptations do not track in Plio-Pleistocene elephants of the Shungura formation (Omo Valley, Ethiopia)

Vera Weisbecker *based on peer reviews by* ***Steven Zhang*** *and 1 anonymous reviewer*

Tomas Getachew Bedane, Hassane Taïsso Mackaye, Jean-Renaud Boisserie (2024) New data on morphological evolution and dietary adaptations of *Elephas recki* from the Plio-Pleistocene Shungura Formation (Lower Omo Valley, Ethiopia). PaleorXiv, ver. 4, peer-reviewed and recommended by Peer Community in Paleontology.
https://osf.io/preprints/paleorxiv/qexuf

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Bedane et al. (2024) provide a beautifully illustrated demonstration of the difficulties in using dental adaptation as proxies for the diets of elephants, which are in turn often used to determine the vegetation in an area. This study set out to assess mesowear, which is the relief on the teeth that forms due to abrasion by food, and therefore a good proxy of dietary composition in herbivores. The team was interested in testing whether this mesowear relates to morphological adaptations of hypsodonty (high-crownedness) and enamel thickness over a period of ~3.4–~1.1 million years in an elephant species (*Elephas recki*) commonly found in the Plio/Pleistocene of the Shungura formation (Omo Valley, Ethiopia). To answer this question, the team scored these metrics in 140 molars between ~3.4 and ~1.1 million years of age, separated into time bins. Their results show surprisingly low levels of variation in mesowear, indicating relatively low variation in diet that was overall mostly composed of graze (as opposed to mixed or browsing diets, which are softer). Hypsodonty and enamel thickness were correlated, but changed erratically rather than suggesting a trend towards a particular dietary adaptation. The exciting conclusion is that dental morphologies that we often consider to be adaptive to certain conditions are very slow to evolve, and that a wide variety of morphologies can support the survival of a species despite little variation in diet. For me as a functional evolutionary morphologist, this clear case of many-to-one-mapping is

a timely reminder that evolution does not work either quickly or just on the one character complex I might be considering. And in terms of using elephant teeth as ecological proxies – this job clearly just got a little harder.

References:

Bedane, T. G., Mackaye, H. T., and Boisserie, J.-R. (2025). New data on morphological evolution and dietary adaptations of *Elephas recki* from the Plio-Pleistocene Shungura Formation (Lower Omo Valley, Ethiopia). PaleorXiv, qexuf, ver. 4, peer-reviewed by PCI Paleo.
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Reviews

Evaluation round #2

DOI or URL of the preprint: https://osf.io/preprints/paleorxiv/qexuf
Version of the preprint: 3

Authors' reply, 02 January 2025

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Decision by Vera Weisbecker, posted 11 December 2024, validated 12 December 2024

Thank you for your exhaustive explanations and responses - I am completely happy with these and have my recommendation text already written up. The only thing I would like changed is just a formality - could you please add the analyses and figures of the linear regressions (Fig. 6) into Materials and Methods and Results? You might also want to have a last quick look through some of the grammare (e.g. "is at odds" is spelled without an "s" in line 452).

Evaluation round #1

DOI or URL of the preprint: https://osf.io/preprints/paleorxiv/qexuf
Version of the preprint: 3

Authors' reply, 29 November 2024

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Decision by Vera Weisbecker, posted 01 October 2024, validated 02 October 2024

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).

Reviewed by anonymous reviewer 1, 29 May 2024

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. 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). 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.

Title and abstract

- Does the title clearly reflect the content of the article? – Yes
- Does the abstract present the main findings of the study? – Yes (but see my comments on how the interpretation of the results needs to be revised)

Introduction

- Are the research questions/hypotheses/predictions clearly presented? – Mostly yes, but see my comments, especially on the taxonomic position of the "Elephas recki complex"
- Does the introduction build on relevant research in the field? – Yes

Materials and methods

- Are the methods and analyses sufficiently detailed to allow replication by other researchers? – Yes, as far as I can tell
- Are the methods and statistical analyses appropriate and well described? – Yes, as far as I can tell

Results

- In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? – Maybe not applicable in this case
- Are the results described and interpreted correctly – Mostly yes (but see detailed comments)

Discussion

- Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? – Mostly yes.
- Are the conclusions adequately supported by the results (without overstating the implications of the findings)? – No (More discussion is needed and concepts need to be clarified. Now there is too much confusion and misunderstandings which make the results look more confusing in relation to other studies. See detailed comments in the text on my suggestions of what should be done to improve this)

Download the review

Reviewed by Steven Zhang, 01 October 2024

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. 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). 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 *Palaeloxodon 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).

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.

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.

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!

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Steven Zhang

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