Peer Community In Paleontology

Postcrania from the Shungura and Usno Formations (Lower Omo Valley, Ethiopia) provide new insights into evolution of colobine monkeys (Primates, Cercopithecidae)

Stephen Frost *based on peer reviews by* ***Monya Anderson*** *and 1 anonymous reviewer*

Laurent Pallas, Guillaume Daver, Gildas Merceron, Jean-Renaud Boisserie (2024) Postcranial anatomy of the long bones of colobines (Mammalia, Primates) from the Plio-Pleistocene Omo Group deposits (Shungura Formation and Usno Formation, 1967-2018 field campaigns, Lower Omo Valley, Ethiopia). PaleorXiv, ver. 8, peer-reviewed and recommended by Peer Community in Paleontology.
https://doi.org/10.31233/osf.io/bwegt

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In their analysis, Pallas and colleagues identify 32 postcranial elements from the Plio-Pleistocene collections of the Lower Omo Valley, Ethiopia as colobine (Pallas et al., 2024). This is a valuable contribution towards understanding colobine evolution, Plio-Pleistocene environments of the Turkana Basin, Kenya and Ethiopia, and how the many large-bodied catarrhines, including at least three hominins, four colobines, and three papionins, all with body masses over 30 Kg shared this ecosystem.

Today, colobine monkeys have greater diversity in Asia than in Africa, where they are represented by three small to medium-sized forms: olive, red, and black and white colobus (Grubb et al., 2003; Roos and Zinner, 2022). In the Pliocene and Pleistocene, however, they were significantly more diverse, with at least four additional large-bodied genera that varied considerably in body size, and as evidenced by multiple proxies, their preferred habitats, diets, and locomotor behaviors (Frost et al., 2022 and references therein). The highly fossiliferous sediments of the Shungura and Usno Formations in the Lower Omo Valley span the period from

3.75 to 1.0 Ma (Heinzelin, 1983; McDougall et al., 2012; Kidane et al., 2014) and have contributed greatly to understanding human and mammalian evolution during the African Plio-Pleistocene (Howell and Coppens, 1974; Boisserie et al., 2008), including the enigmatic large-bodied colobines (Leakey, 1982; 1987). Despite large samples of postcranial material from the Lower Omo Valley (Eck, 1977), most of our knowledge of fossil colobine postcrania is based on a relatively few associated skeletons from other eastern African sites (Birchette, 1982; Frost and Delson, 2002; Jablonski et al., 2008; Anderson, 2021). This is because the vast majority of postcrania from the Lower Omo Valley are not directly associated with taxonomically diagnostic elements.

Based on qualitative and quantitative comparison with an extensive database of extant cercopithecoid postcrania, Pallas et al. (2024) identify 32 long bones of the fore- and hindlimbs as colobine. These range in age from approximately 3.3 to 1.1 Ma. They made their identifications using a combination of body mass estimation and comparison with associated skeletons of Plio-Pleistocene and extant taxa. In this way, they tentatively allocate some of the larger material dated to 3.3. to 2.0 Ma to taxa previously recognized from craniodental remains, especially *Rhinocolobus* cf. *turkanaensis* and *Paracolobus* cf. *mutiwa*; and the smaller ca. 1.1 Ma to cf. *Colobus*. Interestingly, they also identify several specimens, especially from Members B and C, that are unlikely to represent taxa previously described for the Lower Omo Valley and make a possible link to *Cercopithecoides meaveae*, otherwise only known from the Afar Region, Ethiopia (Frost and Delson, 2002).

Based on these identifications, Pallas et al. (2024) hypothesize that *Rhinocolobus* may have been adapted to more suspensory postures compared to *Cercopithecoides* and *Paracolobus* which are estimated to have been more terrestrial. Additionally, they suggest that the possibly semi-terrestrial *Paracolobus mutiwa* may show adaptations for vertical climbing. These are novel observations, and if they are correct give further clues as to how these primates seemingly managed to co-exist in the same area for nearly a million years (Leakey, 1982; 1987; Jablonski et al., 2008). Better understanding the locomotor and positional behaviors of these taxa will also make them more useful in reconstructions of the paleoenvironments represented by the Shungura and Usno Formations.

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Reviews

Evaluation round #3

DOI or URL of the preprint: **https://doi.org/10.31233/osf.io/bwegt**
Version of the preprint: 6

Authors' reply, 25 July 2024

Dear Editor,

I have corrected the manuscript in accordance with your suggestions. Where I have not modified the manuscript (for the mention of Eck,1977 and a mention of *Theropithecus* when commenting on the posterior femoral head encroachment), I have added comments to justify it directly in the text. I have also corrected several typos and errors/approximations (see Tracked Changes version).

Sincerely,

Laurent
Download tracked changes file

Decision by Stephen Frost, posted 16 July 2024, validated 18 July 2024

Very minor revisions for Pallas et al., 3rd revision: Postcranial anatomy of the long bones of colobines (Mammalia, Primates) from the Plio-Pleistocene Omo Group deposits (Shungura Formation and Usno Formation, 1967-2018 field campaigns, Lower Omo Valley, Ethiopia)

Dear Laurent and colleagues,

Sorry for the slow process to review this manuscript. I apreciate that you have addressed all of my larger concerns. I am ready to write a recommendation for your very interesting manuscript pending a few minor edits for clarity and typos. I've attached your latest draft with my relatively few, very minor revisions. I don't think these will take much time at all to complete, but believe they are necessary for clarity.

I look forward to writing a recommandation once these are complete. **Download recommender's annotations**

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.31233/osf.io/bwegt
Version of the preprint: 5

Authors' reply, 27 May 2024

Dear Editor,
All requested changes and comments are processed directly in the Track Changes version of the document.
Sincerely,
Laurent
Download tracked changes file

Decision by Stephen Frost, posted 25 March 2024, validated 26 March 2024

Suggested revisions for Pallas et al. "Colobine postcranials from the Plio-Pleistocene Omo Group"

I want to thank the authors for taking care to follow and implement many of the suggested revisions of the reviewers from the first submission. This manuscript is complex and long, and still requires some revisions for clarity and specificity in order to make it easier to for readers to understand and to be better able to evaluate how the decisions were made that led to the authors conclusions so that they can better decide of those conclusions follow. Below I've made some general points to this end, as well as more detailed ones after and in an attached .docx file. In summary, I believe the manuscript is close, but needs to be easier to understand what exactly was done, and exactly why each specimen was interpreted in the way it was.

General points:
1. Most importantly, this manuscript is still hard to follow. I've made some suggestions in the marked up word doc and below to this end. This is likely not enough. In the response letter you gave a justification for the order and manner in which the text is organized. Then reading the text alone this thinking does not come through. Perhaps present this logic in the introduction or at the beginning of the methods to organize the reader as to what exactly is to follow and what is in the text vs what is in the SI.

This concern also applies to many of the subsections. In the minor comments below I've made some suggestions for how to improve the clarity within some of the subsection.

2. In the materials and methods, the reasons for many of the decisions that have been made, as to why one approach is used and not another, need to be better clarified and justified. I have pointed some of these out in the detailed comments below.

3. The discussion needs further development. The discussion is also really underdeveloped and terse. It needs to better make clear why the allocations of the postcranial elements matter. Not just why each element was asinged. How do these interpretations add to those of previous work? How do they refine what we know specifically?

Also in the discussion, can you put these interesting animals better into their context. What have we learned about how they may have fit into their ecosystems? What does this mean about niche separation among the colobines? among all of the cercopithecids (including Theropithecus etc.) and indeed the hominins?

More detailed comments:

Materials and Methods

Neontological Sample

- The rationale for the taxa included needs to be better explained. Why were these taxa sampled and not others. For example, extant colobines were chosen to represent a both tribes of colobinae, or size range, locomotore diversity, etc.

Similarly, why was Papio alone chosen to represent cercopithecines? Why not other cercopithecines closer in size to colobines? Why not more arboreal cercopithecinces to better understand phylogenetic differences vs. locomotor ones. I'm not saying you need to include more taxa, but better explain your choices.

Regardless, more clearly justify which taxa were chosen.

- Data availability - the underlying data need to be accessible as a matter of scientific reproduceability. Appendix 39 (list of extant specimens) should contain individual measurement values. Alternatively, give as a .csv supplimentary data file or post them to a data archive such as Dryad.

- Page 30 (lines 475 - 493 in my document) seems out of place. Looks like a series of abbreviations in the middle of the statistical methods section. Perhaps move to abbreviations.

Body Mass Estimation

- For the dental estimations, you need to explain why you are only using mesio-distal dimensions on M1-2 and not the specific dimensions recommended by Delson et al. (2000). Delson et al. made a study of estimation accuracy found that often measurements besides M-D ones were the most accurate. What is the reason for using only mesiodistal demensions? Please justify in the text.

- Similarly, it should also be justified as to why LM3s were not used. LM3s are quite abundant in Leakey's paper and would increase the number of available estimates. Furthermore, Delson et al. found that LM3 distal M-B diameter was among the 6 most accurate estimators. What factors led to this decision?

- Is there a reason you are using measurements from casts rather than Leakey's (1987) measurements from original specimens? Please explain your rationale in the text.

- The estimates for Ce. williamsi are only based on 2 specimens. There are additional specimens avalable from Koobi Fora in Leakey (1982) and Jablonski et al., (2008). (Not to mention many from Freedman, Eisenhart and others for South Africa). I assume you would want to use the measurements for the Ce. williamsi specimen from Member F as well. At a minimum the remaining specimens from Koobi Fora should be included, and for any not included, explain why. Essentially, help the reader understand your decisions.

Results

Systematic paleontology

- Specimens referred to each taxon in the systematic paleontology (ideally listed by element/member) as well as in Table 2. Table 2 is great and really useful, and I realize this is redundant information, but it makes reading this section much clearer and easier to follow without having to constantly flip back to table 2.

- "Colobus sp. indet." is listed in the text for this section, but in table 2 it is given as "cf. Colobus sp. indet." These should be consistent, and the latter "cf." version is most consistent with the text.

- "Paracolobus cf. mutiwa" and "Rhinocolobus cf. turkanaensis" should both be changed to "cf. Paracolobus mutiwa" and "cf. Rhinocolobus turkanaensis" as the comparative samples for each genus do not allow an assessment of variation for each taxon and the generic assignments cannot be considered secure for all of the reasons listed by the authors of this paper. This is more accurately communicated by moving the "cf." to the beginning as was done for "cf. Colobus sp."

Morphological comparisons

- Each subsection of the "Qualitative and quantitative comparative anatomy" section (e.g. "Comparative anatomy of the humeral proximal epiphysis" etc.) needs to be summarized better to improve clarity for the reader. I found this section hard to follow. For example, begin the "Comparative anatomy of the humeral proximal epiphysis" subsection with a sentence such as: "There are a total of proximal humeri identified here as colobine from Omo. These include 3 larger specimens from members C, E, and upper part of G along with two smaller specimens from L."

- For each of the linear measurement tables (tables 4-20), specimens should be listed by taxon (per table 2 and Systematic paleontology)

- Many figures (e.g. 16, 19, more) list Ce. kimeui, but Ce. coronatus is used in the text.

Body mass estimates

- Why is there no estimate for the femur from Usno Fm? explain somewhere in the text. Either in the methods or results.

- Figure 23 is pretty confusing and needs more explanation. The color key in the legend led me to believe that the box plots for Mb B were for Paracolobus, those for Mb C were Colobinae indet, and those for Mb G were Rhinocolobus. Indeed, since each of the boxes and whiskers encompass multiple taxa, they are not very helpful. The range is observable from the points themselves. I would suggest removing the boxes and just making the cranial points larger. The coloring of the data by member actually adds to confusion as they overlap the colors for taxa. I spent nearly an hour trying to understand this figure.

Discussion

- For each of the functional interpretation sections, it is important to orient the reader as to what is to follow. Begin with an introductory sentence such as: "Based on our analyses, there are seven morphotypes for the humerus that can be recognized." Or something along those lines. You need to give the reader a sense of what is to come.

- Furthermore, the rationale for the order in which the different morphotypes are presented in these same sections needs to be clarified. I would recommend starting with cf. P. mutiwa
and then cf. R. turkanaensis, followed by cf. Colobus sp., and lastly those that can't be allocated to specific forms. This order needs to be the same for each section/element (obviously limited by the morphotypes that are actually represented).

- Lastly the discussion is very narrow and short after such long results section. Most of it is on the details of the individual bones and thier assignments and little effort is spent on the implications. What is the importance of your findings?What do they mean for our understanding of what each taxon was doing.

Moreover, what does this mean for our understanding of how these colobines co-existed in the lower Omo valley? How do these new pcs inform understandings of niche separation? Can they add anything to our understanding of what each member was like? What was the overall cercopithecid community like (not just

the colobines) etc. The reader is very much left with the question of why does this matter?

Supplimentary materials

- Appendix numbering in the supplimentary materials is off, especially where they continue acorss pages. Please check these.

- Appendix numbering needs to be checked in the text vs. supplimentary info. e.g. line 266 states extant specimens are in Appendix 37, but should be 39.

I've also attached a marked up .docx file.

Download recommender's annotations

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.31233/osf.io/bwegt
Version of the preprint: 3

Authors' reply, 02 February 2024

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Decision by Stephen Frost, posted 30 May 2023, validated 31 May 2023

First decision for Pallas et al. - Postcranial anatomy of colobines

My apologies for taking a relatively long time to produce this first decision. This paper is quite long and it took me several passes at reading it to really follow it, and more time to come up with a decision.

I concur with both reviewers that this manuscript represents an important contribution to our understanding of Pliocene and Pleistocene cercopithecid evolution. The African fossil record from this time period includes members of a diverse and poorly understood adaptive radiation of colobine monkeys, but relatively little is known of their postcranial skeletons except based on a relatively few partial skeletons. The contribution by Pallas et al attempts to ameliorate this situation by attributing some of the long bones from the Shungura and Usno Formations of southern Ethiopia to specific colobine taxa.

Both reviewers have provided comments, and I strongly encourage the authors to address them all. Reviewer 2 has provided particularly careful recommendations that require attention before this contribution is ready for recommendation.

I will get to the point directly. This is a solid and interesting analysis, but as currently organized it is confusing to read and hard to determine what exactly has been done. Between the main text and SI content this represents nearly 200 pages describing 32 skeletal elements. I believe careful reorganization and editing for clarity would greatly improve the readability, and therefore the scientific usefulness of this manuscript. As it is currently, this contribution reads like a thesis rather than a scientific paper.

1) Clarification of the methods section - This part of the manuscript needs the most attention as I found it hard to follow. Please edit for clarity. The most important aspects of this are hilighted by reviewer 2:

a - Include a section specifying the criteria by which each of the 32 elements were identified as colobine. This can be close to a bulleted list. It would also be useful to outline the criteria used (e.g. size, lateral epicondylar crest, etc, etc) for tentativeky allocating specific elements with particular species. These can then be checked off in systematic paleontology.

b - More clearly explain the GM and body size estimates. For the GM analysis, please list exactly which measurements were used to calculate. For the size estimates based on equations from Ruff and Delson et al.,

please exactly specify which equations (sex and subfamily specific? family only? etc. and which measurements were used). Tables may help with both of these.

2) Organization - I agree with reviewer 2 that this manuscript would be easier to follow if the descriptions of different specimens were given with each taxon in the systematic paleontology. Ideally, the sections for each species would also include a subsection checking of the diagnostic features (given in the methods section) used for allocating them to that taxon.

A further way to make this paper clearer would be to focus the morphological descriptions more on the features that are either important for taxonomic identification, functional interpretation, or of other relevance to cercopithecid evolution.

As mentioned above, by having a justification for identifying these 32 elements as colobine in the methods, the morphological descriptions can be much more specific to those important for specific ID or function and do not need to be repeated for each element.

I would also suggest given careful consideration as to what should stay in the MS and what can be moved to SI so as to make the text easier to follow

3) Taxonomy - I would recommend altering "*Paracolobus* cf. *mutiwa*" to "cf. *Paracolobus mutiwa*" as the former usage implies you are positive these postcrania represent *Paracolobus*, but just not sure which species, whereas I believe the latter better reflects the case here as it implies both genus and species are uncertain. Same for "*Rhinocolobus* cf. *turkanaensis*" to "cf. *Rhinocolobus turkanaensis*" because what other species of *Rhinocolobus* could it be?

4) The discussion would be easier to follow if the tentative taxonomic assignments (e.g. cf. *Paracolobus mutiwa*) could be used rather than listing specimen numbers which are hard for a reader who hasn't memorized the specimens in the 7 humeral, 3 femoral, ulnar, radial, and tibial morphotypes yet to keep straight. If the criteria were given in the methods were specified (see point above about organization) earlier this could be much condensed.

5) Other smaller points:

L895-1 - I didn't see any mention of this specimen in the paper (e.g. circa line 1510). It does not need to be described, but should be mentioned. Is it a colobine in your opinion? Does it better fit *P. mutiwa*, *R. turkanaensis*, *C. williamsi*, or *C. kimeui*? or none of these? Anderson's 2019 Dissertation can be cited as a reference.

A last minor note, it is odd that the Basal Member of the Shungura Fm. is not included in the figures even though it is referenced in the text.

This paper has a lot to contribute, from functional morphology, body mass estimates, colobine paleobiology, and evolution. I hope this decision and attached reviews prove useful and I really look forward to seeing this manuscript widely available and in a format that will be most useful and allow readers to access its many interesting and important ideas.

Reviewed by Monya Anderson, 29 March 2023

Overview

I have organized my comments by manuscript section with more thorough review provided for the figures. As this preprint has already gone through previous revision/review, my comments are fairly minor and I generally have no issues with any of the anatomical descriptions, functional interpretations, or taxonomic affiliations.

On a personal note, it is exciting to see a paper detailing isolated postcranial specimens for large bodied colobines as it will only improve functional interpretations of other specimens and provide a more nuanced picture of the anatomy of mixed substrate preferences. Such analyses are difficult without larger sample sizes of

relevant elements and the assemblages presented here refine previously published, functional interpretations based on much more limited sample sizes.Introduction

On line 137 to 138 the authors state that "*P. mutiwa* is currently known from only one single individual..." To stay consistent with later mention of a specific specimen number in the following sentence, I recommend providing the specimen number to which they are referring here as well.Materials/Methods

On lines 269, 271, 273, and 278 (and possibly more) the authors begin their sentences with the genus abbreviations. It is generally recommended to start a sentence with the genus name written in full even when it has been defined earlier in the manuscript. I of course defer to the editors if this is an acceptable format for this publication.Comparative Anatomy

On line 745 the authors describe a feature as being "extremely similar" I recommend removing the superlative.Discussion

In lines 1481-1482 the authors state "...KNM-WT 16827, a partial skeleton attributed to *P. mutiwa*." The fact that this specimen is attributed to *P. mutiwa* has been previously established in the paper so is redundant here. This occurs in subsequent discussion subsections as well. On lines 1483-1486 the authors use Roman numerals in their list of justifications. Unless this formatting is required by the journal, listing with numbers e.g. 1-4 would be simpler.Figures

This isn't a revision, but I wanted to compliment Figure 1 and Table 2 as they effectively convey a lot of important information very succinctly!

The functional rationales in Table 7 are a very nice touch.

The captions for Figs 2–4 seem redundant with information about the measurements already provided in Table 6. If the intention is to provided Table 6 in appendices, then they're fine, but if all are intended to be a part of the main paper, I recommend shortening the captions. Figures 10 & 18 are very busy and although the scatterplots are straightforward, but the inclusion of the density estimates below makes the whole figure difficult to read.

In Figures 11, 14, 16, 19, 22 the individual taxa shapes within the violin plots are very small and difficult to tell apart. I also recommend making the font size smaller on the fossil taxa labels so they aren't so crowded.

This could be a byproduct of uploading or the preprint viewing interface, but Table 12 has inconsistent font sizes and spacing. It's also unclear why it's split in two parts.

In footnote 3 for Table 16, "KNM-WT 1682" should be "KNM-WT 16827."

Figures 20 & 21 are very dark making details of the specimens difficult to see. I recommend adjusting the saturation.

For Fig. 23 and its mentions in the main text, "estimated body masses" may be more accurate than "inferred body masses." I also assume that the color coding on the individual points within the boxplot is based on taxon so a legend should be added for clarity.

Download the review

Reviewed by anonymous reviewer 1, 19 April 2023

Review of Postcranial anatomy of colobines (Mammalia, Primates) from the Plio-Pleistocene Omo Group deposits (Shungura Formation and Usno Formation, 1967-2018 field campaigns, Lower Omo Valley, Ethiopia)

First, let me commend the authors for all of the work that went into this MS....this is a lot of information and data and the basic descriptions and analyses all seem well done. All of the figures, plots, and data are very nice and useful to have. It is very nice to see this new monkey material be described and published, and I will look forward to its final publication. My more detailed comments are provided in the annotated PDF, but I will summarize my main thoughts/suggestions here :

1) My biggest criticism /concern with the current MS has to do with the organization. As I mentioned above, the content is generally great, but the current organization is really hard to follow in a MS of this size. To me, I think you need to describe all of the bones and interpret them within each taxonomic category rather than by anatomical element. It is really hard to keep everything straight when you are discussing 5 different morphotypes element by element. Instead, it would be much easier for the reader and much clearer if you describe everything within the Sys Paleo section. For example, under the Pa. mutiwa heading, describe all of the elements you are assigning to this taxon, explain why you are assigning them to Pa. mutiwa, and provide a brief functional interpretation for this taxon. Then move on to the next taxon. Etc. Right now, all of this information is in the MS to be sure, but it's really difficult to put it all together because it's spread out across all of the anatomical subheadings and then you start to put it together in the discussion. This should all be synthesized in the Sys Paleo section and then the Discussion can focus more on the evolutionary implications and other things that you discuss on pages 96 onward.

2) Somewhere up front, in the Introduction or Materials and Methods, you need some sort of discussion or justification as to how you came to decide that the specimens in this paper are all colobines rather than cercopithecines. Because some of these colobines are large and overlap the size and morphological features of extant and fossil cercopithecines, the reader needs to know why these specimens are likely to be Pa. mutiwa rather than Soromandrillus or T. brumpti, for instance. Or why the arboreal looking specimens must be colobine rather than Lophocebus cf. albigena. What morphological criteria did you use to decide they are all colobines? This needs to be addressed early in the paper.

3) Along similar lines, I think there also needs to be some additional justifications in the Materials and Methods as to why the measurements were chosen and why the comparative sample was chosen. The measurements chosen are fine (and are a nice set of indices), but why were these chosen? Have they been used in past studies to assess various aspects of locomotor behavior? In Table 7, it would be helpful to provide references to studies that have used these indices before to infer locomotor behavior. It might also be worthwhile to look back at classic references like Fleagle (1976) and Harrison (1989) for additional features that have been definitively linked to differences in locomotor behavior in colobines and Old World monkeys more broadly. Many of the indices you have chosen have been used before and correlated to behaviors by studies in the field. Where possible, you should cite these references rather than just make assumptions about the functional rationale for each of these measurements. For any new index you are using, you could perhaps collect basic behavioral data from the literature and run correlations between these indices and the frequency of behaviors of interest to conclusively document the connection between these indices and certain behaviors. See Arenson et al. (2020) paper for a recent example on extant monkeys and %terrestriality. They were able to clearly demonstrate which indices were most highly correlated with %terrestriality data collected from field studies.

The comparative sample of extant colobines seems reasonable….but why only Papio for comparison? Is it because it is a large terrestrial monkey? Is it because it is a large cercopithecine? Or both? And why not sample a more arboreal cercopithecine for comparison as well? Throughout the plots, the sample is compared with extant colobines and Papio, which is fine, but in some cases you are possibly conflating taxonomic distinctions (colobines vs. Papio/cercopithecines) and locomotor distinctions (arboreal vs. terrestrial).

Also, captive specimens are obviously not ideal for a study like this, but I understand that sometimes that's the best you can do. Can you at least confirm that they are non-pathological ? Some comment on the criteria for inclusion in the study for the captive specimens is needed.

And finally, there needs to be some comment on the adult/subadult status of the included specimens. Are

these all adults? How was adult status determined (i.e., all epiphyses fused, all epiphyses fused with no lines, some epiphyses fused, M3/m3 eruption, ???). If it is a mixed subadult/adult sample, this needs to be stated and identified in Table 3 with an additional column listing numbers of adult/subadult specimens or perhaps in an appendix somewhere.

4) Body mass estimation, GM, and sexual dimorphism- The section discussing body mass estimation and geometric means on pages 23-25 is unclear...I do not understand what is being calculated here. Please clarify in greater detail.

It would appear that a number of different Geometric means are being calculated for different anatomical elemetns from the data available, which is fine. But each of the GMs needs to be calculated for as many of the extant taxa as possible as well so you can have some idea of how well they track dimorphism in extant taxa. If these GM values lead to sexual dimorphism ratios similar to that seen from actual body mass data, then that's great and they can assumed to be accurate, but this needs to be empirically demonstrated first. A Male GM/Female GM for the humerus, femur, ulna, etc. cannot be assumed to track actual body size dimorphism well without comparing these GM dimorphism values to extant body mass dimorphism values through a regression. This needs to be provided for all GM dimorphism indices. There seems to be some attempt at this using Nasalis at the top of page 24 (again, it's not entirely clear what was done), but for the comparison to be meaningful, the exact GMs that are used for the fossil taxa need to be applied to extant taxa, and not just Nasalis, but as many colobines as you have in your sample and definitely need to be done for some African colobines in addition to Nasalis.

Similarly, in Fig. 24, I have no idea what is going on, in part because I don't think these ratios are well explained in the Materials and Methods. What is meant by a 'male baseline' in this Fig. 24? What is being calculated as a GM ratio ? It is unclear what is going on here. I would think that a GM Sex dimophism ratio in any monkey should be greater than 1 if dividing male GM by female GM. Please clarify what is going on in this plot and explain it up front in the Materials and Methods.

5) In some of the Figures (e.g., Fig. 10), regression statistics are provided between the variables being examined. However, there seems to be some inconsistency as to what numbers are being reported. What are the p-values of the regressions ? In some cases, r-squared values are so low, that I have to wonder if they are even worth reporting if the relationship is really weak. In any case, p-values should be provided.

6) The variable used for ulnar olecranon process height (e.g., see Fig. 14) seems to be capturing more of what I would argue is actually the relative LENGTH of the olecranon, not the HEIGHT, which is usually described in relation to its proximal extension. You would expect colobines (and arboreal quadrupeds more generally) to have a more proximally extended or TALLER olecranon process above the sigmoid notch, even if Papio has a relatively long olecranon because it is retroflexed posteriorly. So I would just change the terms here and it might be nice to add in a measure capturing the proximal extension of the olecranon above the sigmoid notch, i.e., olecranon HEIGHT. The angulation measure is somewhat capturing this, but maybe a height linear measure in the proximal direction would be helpful as well ?

7) Page 68 and onward, discussion of the extension of the articular surface onto the femoral neck- Some caution in the broad taxonomic and functional utilityof this feature is warranted and should be noted or cautioned in the text here. It's not unusual for many cercopithecines to have a bit of an extension onto the femoral neck, so I don't know if this is a very good taxonomic indicator in terms of colobines vs. cercopithecines. I would be very wary of assigning proximal femora to colobines on the basis of this feature. For instance,

Theropithecus often displays an extension of the articular surface onto the femoral neck. Are the colobine specimens described here significantly smaller than T. brumpti and/or T. oswaldi of this time period ? And/or to they display other distinctive features? More broadly, this is why we need to have some additional justification as to why these specimens were determined to be colobines in the first place, as I have indicated in point #2 above.

8) Discussion page 97- In the discussion regarding the interpretation of Pa. mutiwa's locomotor adaptation, a number of features are noted as being suggestive of a more mixed climbing/arboreal component to this species' repertoire than previously suggested. Some of these features, such as a well-defined/deep sigmoid notch, have been associated with terrestrial quadrupedalism in that past. Here, you are suggeting they indicate more climbing/arboreal behaviors instead. Can you provide refernce to support this interpretation an provide an example of an extant species exhibiting these features that is more of a climber than a terrestrial quadruped? Mandrills have many of these features and are quite terrestrial, for instance, so while it seems reasonable to point out that there might have been more climbing in the repertoire of Pa. mutiwa than previously appreciated, many of these features seem associated with more terrestrial behaviors. If you have a reference for the deep sigmoid notch being indicative of climbing, please provide it. But it has been noted previously to be associated with a stable elbow and terrestrial quadrupedalism. And since Soromandrillus is also found in the Omo, can we be certain that these specimens belong to Pa. mutiwa rather than Soromandrillus? Some comment on why they are likely to be mutiwa rather than Soromandrillus is needed somewhere in here. Can T. brumpti be ruled out as well? This is why it needs to be established why these specimens must be large colobines rather than large cercopithecines somewhere at the beginning of this paper. The evolutionary interpretations depend heavily on making the correct assignments to subfamily and genus, so they need to be well-justified from the beginning. To be clear, I'm not saying the assignments in this paper are unlikely to be correct, only that they need to be better justified from the beginning of the paper so we can be confident that they are all colobines.

9) Finally a few taxonomic notes- Cercopithecoides kimeui has been recently synonomized with C. coronatus (see Frost et al., 2022 colobine book chapter). If you don't agree, that is fine but you must state reasons why or I would suggest using the more currrent taxonomic arrangement. Similarly, in the same book chapter, Frost et al. (2022) point out that the colobine at Laetoli is better referred to cf. Kuseracolobus rather than cf. Rhinocolobus based on the presence of a maxillary sinus, among other features, shared with Kuseracolobus and not found in Rhinocolobus. This taxonomy should also be followed here, unless the authors want to argue more specifically otherwise.

10) Appendices- During the re-organization of the paper, it seems to me that much of the descriptions in Appendix 1 should be moved to the main text in the Sys Paleo section.

The Appendix 2 figure should incorporate the taxonomic changes I noted above in point #9.

Additional information regarding the sex and ontogenetic stage (adult, subadult, etc.) of each extant specimen and the numbers of males and females in each mixed sex samle should be given in the appendices.

Other than that, my more detailed comments and suggested edits are in the attached annotated Word .docs. I look forward to seeing the revised paper published sometime soon...

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