

Dear Editor,

You will find in this letter a detailed response to all required changes and clarifications. We accepted most of the requested changes and modified the manuscript accordingly.

Specifically, we have taken great care to properly edit the Materials and Methods section as requested by you and Reviewer #1. We performed a new analysis regarding the comparison of geometric means between fossil colobines and *Nasalis larvatus*. This new analysis notably required the measurement of additional *Nasalis larvatus* specimens. A qualitative size comparison was also undertaken to reinforce our previous results. We have added a table summarizing the anatomical hallmarks of colobines in the Materials and Methods section to justify our taxonomic assignment. In terms of taxonomy, we added qualitative comparisons with arboreal papionines (*Lophocebus*) to justify the attribution of small specimens to *Colobus*. In addition, we added a new morphometric analysis to demonstrate that the large colobines described here are indeed not *T. brumpti* but *P. mutiwa* and *R. turkanaensis*. Finally, we have considered all minor revisions reported by Dr. M. Anderson and Reviewer #2.

However, we have not reorganized the manuscript and you will find a precise justification in this letter, along with other unaddressed points raised by Reviewer #2.

As a minor modification, please note that we changed the title to “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)”

Comments to the Editor

"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."

We have added a table (Table 8) referencing features considered diagnostic of colobine monkeys. However, we point out to the editor that several characteristics of the shoulder, elbow, hip and knee of *Ce. williamsi*, *Pa. mutiwa*, and *Pa. chemeroni* can be seen in large terrestrial cercopithecines. We have mentioned such exceptions in Table 8 and in the paragraph I. 392 (*Anatomical rationale for taxonomic attribution*).

The new table adds to the previous tables already present in the MS (Table 10,11,14,16,18, and 20) which demonstrate the specificity of the colobine postcranium compared to that of *Papio*.

"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."

The BM equation used to obtain body mass in Figure 23 is now clearly stated in the text (see l.359 and l.365) and it can be reproduced using data presented in our morphometric dataset of fossil colobines.

However, we removed GM computation from the Appendix because it conveys no new information and introduces confusion with Figure 24. Similarly, we dropped the GM comparison with *Colobus* for similar reasons.

We have also removed the GM of the ulna and radius from the Appendix 38 as it is not relevant to mix GM and BM in the same table. Furthermore, this information is already conveyed in Figure 24 for the ulna.

We also changed the calculation of BM on the distal humerus because we incorrectly used the formula stated by Ruff (2003). Indeed, instead of using $[(2,107 * (\ln(\text{HDML})) - 4.063)]$ we used $[(2,107 * (\ln(\text{HDML})) - 4.106)]$. Although this error resulted in a < 4.4% difference in body mass estimates and does not change our conclusion and results, we have corrected the graphs accordingly and edited them so that accession numbers of the fossil postcranial specimens appear for clarity. We have also specified in the text that we used the colobine regression parameters from Ruff (2003:28).

However, all the information necessary for dental data is already present in Appendix 38 (accession numbers of the fossil specimens used) and in the paragraph dedicated to this in the Materials and Methods section. We have only added the fact that we used the colobine regression parameters for body mass estimation of teeth in the text (see l.365).

"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 [...] As it is currently, this contribution reads like a thesis rather than a scientific paper."

Our taxonomic rationale is based on our comparative and functional interpretation of postcranial specimens. Such a view has already been developed and published several times in high-profile (paleo-)primatological studies.

For instance, in classic references (Rose, 1984, 1992, 1988; Harrison, 1989), sections are organized by bone and functional interpretations take precedence over taxonomic interpretations. Indeed, it is the results of our functional interpretations that confirm or infirm the attribution of a long bone to any fossil taxon. While such an approach can lead to lengthy manuscripts, it also provides the most recent and comprehensive study of the postcranial anatomy of fossil colobines from the Plio-Pleistocene of Africa. Since the aim of the PCI organization is to promote the publication of scientific articles in open access for free, we believe that our effort should be considered as a positive point even if we are aware that it also represents an additional effort for the recommenders and the reviewers.

"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?"

Paracolobus cf. mutiwa means we are confident it is *Paracolobus*, but we remain cautious about species affinities (although there is plenty of information confirming the affinity of the specimens with WT 16927). See Sigovini et al. (2016:1219) for use of open nomenclature and our choice of using *P. cf. mutiwa* instead of *cf. P. mutiwa*. As for *Rhinocolobus*, it could represent another species but given the assessment only of isolated postcranial specimens, we prefer to remain cautious with the taxonomy and refer to *R. turkanaensis*.

"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."

We agree with this and have corrected this in the discussion, thereby dropping specimen accession n° when we were not making direct reference to a specific specimen.

"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."

We are currently carrying out its study. As it stands, we are not able to share non-peer reviewed results.

"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."

Indeed, so we have added the Basal Mb. in the new version of the manuscript.

Comments to Dr. M. Anderson

"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."

We have corrected it.

"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."

We have corrected it.

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

We have corrected it.

"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."

We have corrected it and removed Roman numerals.

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

We have corrected it.

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

We have adjusted saturation as requested.

"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."

We have modified the figures accordingly.

"The captions for Figs 2–4 seem redundant with information about the measurements already provided in Table 6."

We agree with this, but there are editorial issues behind this (the paper will be submitted to CRAS PalEvol) and we need to indicate the meaning of all abbreviations in the figure captions.

Comments to Reviewer #2

"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."

See our comment to the Editor for more details. Taxonomic attribution is the direct byproduct of our functional and descriptive analysis and the presentation of the manuscript around morphotype identification has the advantage of reflecting this logic. Precisely, our hypothesis is postulated in this way: we are expecting *Rhinocolobus*, *Paracolobus*, *Cercopithecoides* and *Colobus* based on craniodental data, and our functional analysis gave several morphotypes for each long bone. The distinct morphotypes, once identified, are then compared to the anatomy of known fossil colobines.

"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."

We have added a table (Table 8, as requested by the editor) to support this suggestion. But see also our comments below regarding *T. brumpti* and *Soromandrillus*.

"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."

A functional rationale is now provided in Table 7 and we have added references as requested. We cited the work of J. Arenson. We also cited Harrison (1989) and J. Fleagle (among others).

We completely agree with Reviewer #2's suggestion to correlate % of substrate use to skeletal traits. However, this comment seems to neglect the equifinality in the interpretation of the postcranium. Stereotypical behaviors such as leaping and running, which require significant stabilization of the hip, knee and ankle in the parasagittal plane could potentially bias these results, notwithstanding examples drawn from squatting and climbing (see Pallas et al., 2023 but also Gebo & Sargis, 1994 for other behaviors). Moreover, it also raises

questions regarding the impact of high frequency vs. punctual behavior on shaping the skeletal anatomy of primates.

In any case, the objective of this article is not to provide a novel functional analysis of the cercopithecoid postcranium but to better understand the locomotion of fossil colobines using current knowledge (see Table 7).

"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.

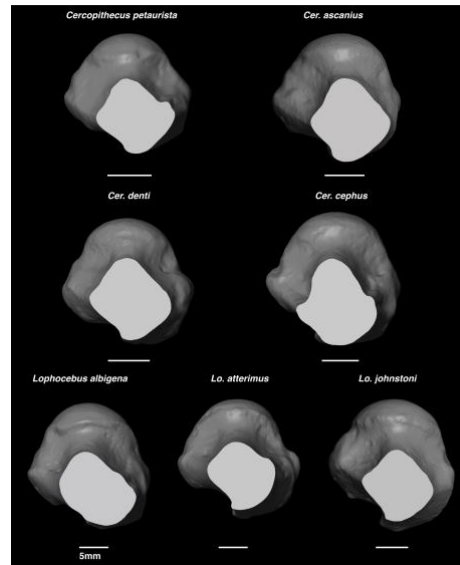
And finally, there needs to be some comment on the adult/subadult status of the included specimens. Are these all adults? How was adult status determined (i.e., all epiphyses fused, all epiphyses fused with no lines, some epiphyses fused, M3/m3 eruption, ???). If it is a mixed subadult/adult sample, 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."

Indeed, *Papio* was chosen because it is a cercopithecine of similar size to most of the colobines described here, thus controlling for the substantial potential effect of allometry. Baboon locomotion is also much more stereotypical than that of most guenons and other forest-dwelling cercopithecines, making functional comparisons straightforward and easier. In the absence of large arboreal cercopithecines, we decided to provide a summary paragraph (see l.253) summarizing substrate preferences and our rationale for a deeper comparison with *Colobus*, *Nasalis*, and *Semnopithecus* (all relatively large colobines). Such comparisons made it possible to identify postural and locomotor adaptations in addition to making taxonomic inferences.

Certainly, parallelism within cercopithecids is a misleading effect and that, for example, anatomical traits related to climbing and squatting in large monkeys could potentially lead to anatomical parallelism and blurring functional inferences in fossil cercopithecids (Pallas et al., 2023). But, throughout our manuscript, we place varying levels of confidence in our taxonomic hypotheses depending on the degree of confidence we can place in our functional hypotheses using multiple sources of anatomical evidence. Future studies should tackle these hypotheses, notably those on aff. and cf. Colobinae specimens, which are, as suggested in cf. and aff., in open nomenclature.

However, to account that small specimen from Mb. L could be guenons and/or *Lophocebus* based on the shape of the surgical neck, we have provided additional comparative data in the Supplementary (see Figure inserted below), qualitatively comparing the Mb. L specimens with three species of *Lophocebus* and four species of *Cercopithecus*.

We also added all the requested information regarding ontogenic status and pathologies in the text (see l.252).



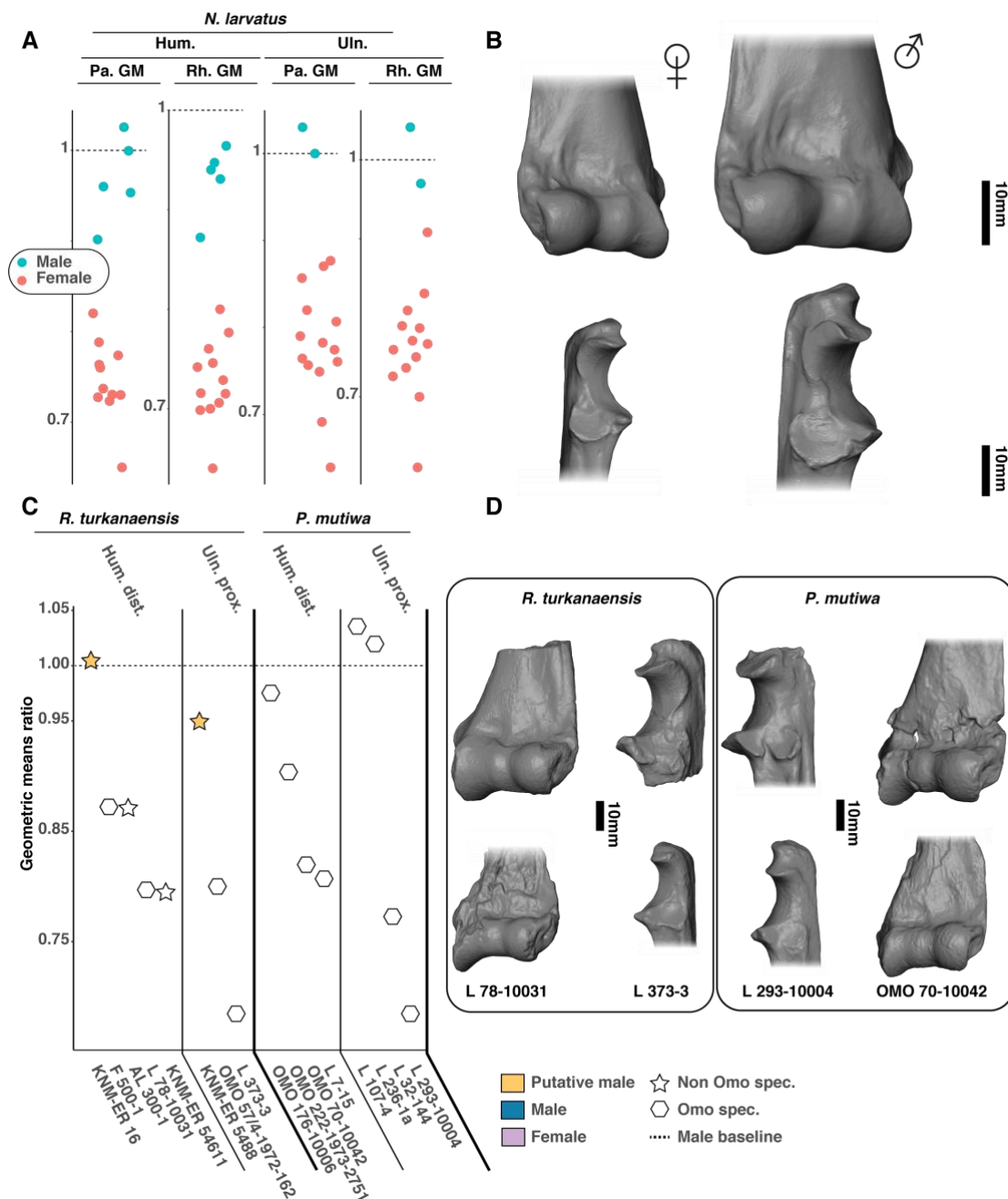
"Body mass estimation, GM, and sexual dimorphism- The section discussing body mass estimation and geometric means on pages 23-25 is unclear...I do not understand what is being calculated here. Please clarify in greater detail.

It would appear that a number of different Geometric means are being calculated for different anatomical elements 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 be 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 dimorphism 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."

We have rewritten this section, provided new data, and modified the protocol according to #Reviewer 2's suggestions (see graph directly below).

As for the example of *Nasalis larvatus*, we want to clarify things. We used this taxon because it is a large and highly dimorphic colobines (see also the main text of the manuscript), a general condition expected to approximate that of *R. turkanaensis* and *P. mutiwa*. Such a comparative framework has also been endorsed by Plavcan and Cope (2001). As a result, we consider that comparing low-dimorphic *Presbytis* of ca. 4kg with *P. mutiwa* and *R. turkanaensis* is not relevant. However, we agree that we are lacking data on *S. entellus* and large *Rhinopithecus*, and that any additional data on these taxa would be of valuable interest. In the meantime, we think that our comparative framework is sufficient to guarantee reliable results, which demonstrate that 1) there is high sexual dimorphism in size between male and female specimens of *P. mutiwa* and *R. turkanaensis*, and that 2) the specimen included here in *P. mutiwa* and *R. turkanaensis* does not exceed the magnitude of size difference between male and female *N. larvatus*. To make this even clearer, we have added photos of female *N. larvatus* specimens in comparison, at the same scale, with male *N. larvatus*. We did the same thing with fossil colobines. Conclusively, this demonstrates the marked sexual dimorphism of the large colobines from Shungura on quantitative and qualitative grounds.



"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."

That is true. We removed the regression statistics because they do not provide interesting information.

"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?"

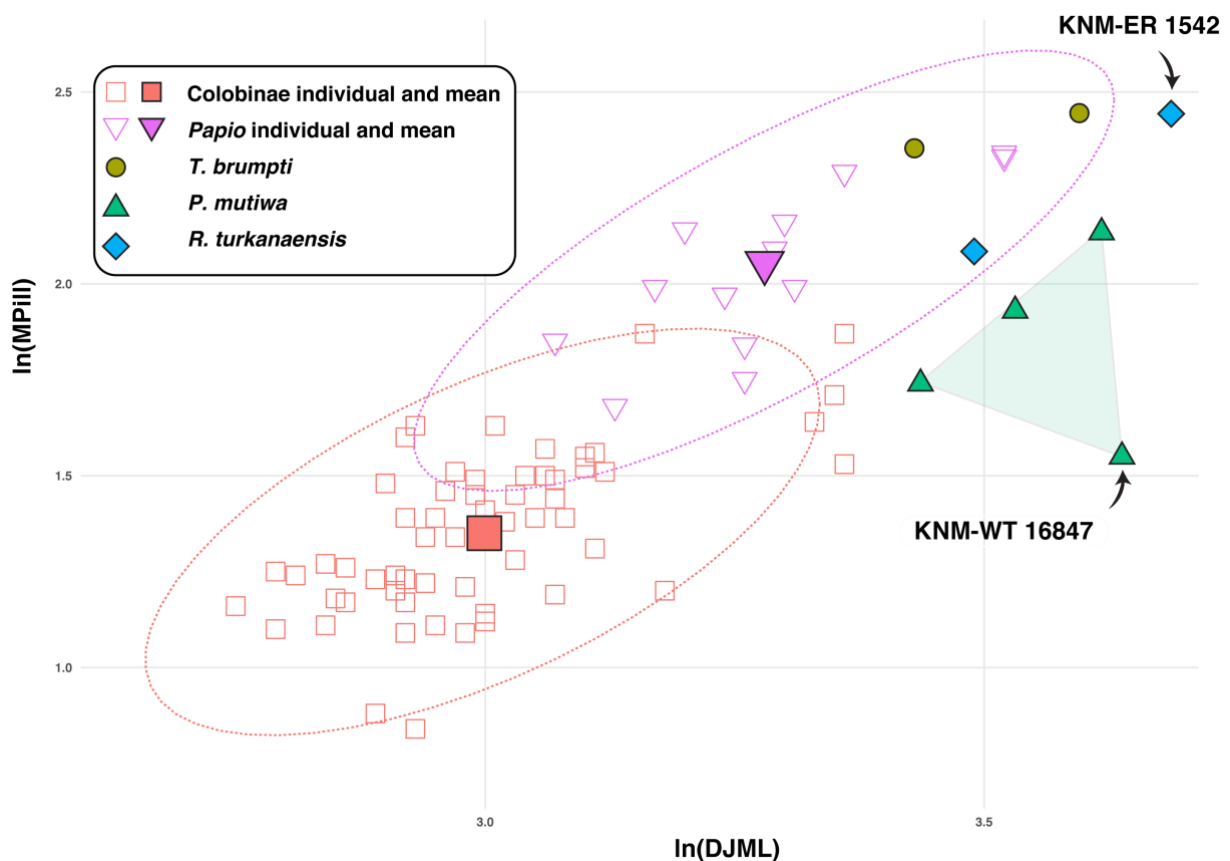
It is true that length is a better word than height. We modified it throughout the manuscript. Reviewer #2's comment is interesting and calls for further thought. However, olecranon height, as #R2 suggests, is probably not a good biomechanical proxy because it will underestimate the lever arm of the triceps brachii (see Nishimura et al. (2022), among others). A combination of indices evaluating the length of the olecranon and its orientation, as is the case in our manuscript, is to be preferred, because they are both reliable biomechanical proxies (but see also M. Drapeau's works).

"Page 68 and onward, discussion of the extension of the articular surface onto the femoral neck- Some caution in the broad taxonomic and functional utility of 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 do 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."

First, there are no published isolated or associated postcranial specimens of Soromandrillus yet, and this taxon hypodigm is based only on cranial, dental and mandibular remains. Should we expect to see Mandrillus-like or Papio-like traits in Soromandrillus? This issue is currently being addressed by our research team in another article but given the amount of data already presented in this article, it will be difficult to address them all in one article dealing primarily with fossil colobines.

Furthermore, we have presented compelling evidence in our manuscript that it is highly unlikely that the material assigned here to *Paracolobus mutiwa* and *Rhinocolobus turkanaensis* is that from a large papionin (e.g., breadth of the medial pillar or shallow medial trochlear keel). To make this point clearer, we added a biplot of the width of the natural logarithm of the distal humeral articular surface to the natural logarithm of the width of the medial pillar, demonstrating that apart from the diagnostic enlarged medial pillar of *R. turkanaensis* KNM-ER 1542 and F 500-1 (discussed in the text and see graph included below), all *P. mutiwa* specimens fall outside the range of variation of the humerus of *T. brumpti* (L 865-1 and KNM-WT 39368) but within that of extant colobines. Conclusively, the new analysis excludes an attribution to *T. brumpti*.

We are also not sure whether we can use the Poirier's-like facet on the femoral neck to identify colobine taxa. In fact, there is no mention in the manuscript of a taxonomic assignment based on this trait, and we only comment on its functional value. It is also not surprising to note convergences between a climbing primate and a squatter in this aspect. In both cases we are expecting flexion and abduction of the hip (see Pallas et al., 2023 for more details on this aspect).

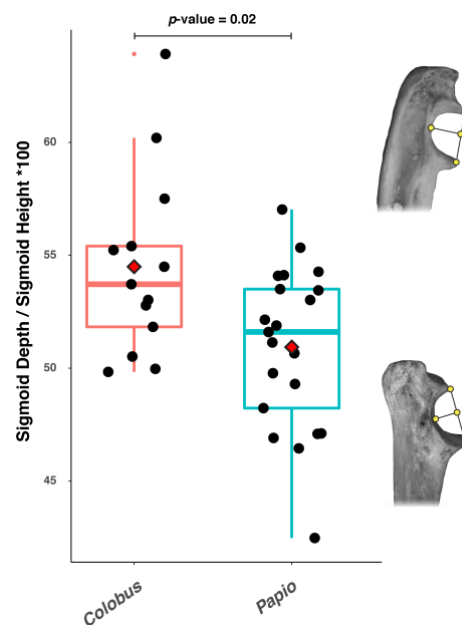


"Discussion page 97- In the discussion regarding the interpretation of *Pa. mutiwa*'s locomotor adaptation, a number of features are noted as being suggestive of a more mixed

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 suggesting they indicate more climbing/arboreal behaviors instead. Can you provide reference to support this interpretation and 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."

Deep sigmoid notches are also observed, among others, in chimpanzees and orangutans (Nakatsukasa et al., 1996; Drapeau, 2008; Alba et al., 2012), which are adept climbers. Deep and keeled notches permit to resist transverse loadings of the joint generated by the contraction of wrist and finger flexors (highly recruited during climbing) in hominoids. A brief assessment of the depth of the sigmoid notch, as quantified according to our protocol, demonstrates that the notch of *Colobus* is significantly shorter and deeper (index closer to 1) than that of *Papio* (index deviating from 1). These preliminary data on cercopithecids highlight the fact that a deep sigmoid notch may not directly be linked to substrate preferences but rather to joint stability in various behavioral contexts. Here again, the convergences between distinct behaviors used on different substrates should not be neglected. It is reasonable to expect a large arboreal and climbing quadrupeds such as *P. mutiwa* to have a deep and stabilized sigmoid notch.

We have added Nakatsukasa et al. (1996), Alba et al. (2012) and Drapeau (2008) to the main text.



#Reviewer 2 is also suggesting that *Mandrillus* is a largely terrestrial monkey and that its postcranium should be interpreted in the light of its presumed stereotypical substrate preferences. That is not exactly true, and we are lacking data on the locomotion of *Mandrillus* (see references in Table S2 in Pallas et al., 2023 for more details). See also Fleagle and McGraw for traits related to substrate preferences and climbing behaviors (2002:272; 'Both *Mandrillus* and *Cercocebus* have been reported to regularly engage in vertical climbing up tree trunks as they ascend from the forest floor in search of arboreal foods (as noted by a reviewer, this is evident in the Nature television program "Mask of the Mandrill"). See previous comments regarding the absence of *Soromandrillus* from the analysis.

"Finally a few taxonomic notes- Cercopithecoides kimeui has been recently synonymized 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 current 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."

We have cited in the main text the taxonomic hypothesis of Frost et al. 2022 in addition to the original taxonomy (providing the reader with the information that the taxonomy of certain taxa is evolving and not consensual). We are open to discussion of the monophyly of Cercopithecoides and we consider Frost et al. 2022 hypothesis regarding the identification of Kuseracolobus at Laetoli (mentioned in Table 1).

"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."

This will considerably lengthen the manuscript without providing new data. We believe it is best to retain the functional and taxonomic interpretations for the main text to make it more readable.

We have corrected all grammatical errors according to the .pdf provided by Reviewer #2.

Minor comments regarding the .pdf annotations of Reviewer #2

"Why only these 4 taxa ? There are data for some of the other taxa you have sampled...for Presbytis/Trachypithecus going back to Fleagle and Piliocolobus/Procolobus I believe McGraw and colleagues have multiple papers looking at locomotor behavior and anatomical correlates. It seems like you should make greater use of the information out there in the literature. I don't understand why only these 4 taxa with no justification."

First, there is justification in the text (see paragraph l.256 and this letter). Also, we do not think it is wise to undertake extensive comparisons between >20kg fossil primates with <7kg extant

primates (e.g., *Presbytis* and *Procolobus*) as we suspect that they do not use arboreal substrates in the same way (especially terminal branches). To address this topic, we have added a few words to clarify the issue and stating that *Co. guereza*, *Se. entellus*, *N. larvatus* and *P. hamadryas* are roughly similar in size to *Rhinocolobus* and *Paracolobus*.

"Really? The greater tuberosity looks above the humeral head in Figure 5"

We have added pictures of the 3D model of F 501-1 to Appendix 4 for more information on the anatomy of the specimen. We have also replaced the sentence to "[...] does not extend significantly" to improve the wording. For clarity, the exact phrase in the original text was "a greater tuberosity that does not extend extensively above the proximal articular surface", emphasis added. Illustration was improved compared to the previous version of the manuscript and if you look at 3D model images in Appendix 4, you will notice that the GT is about the same height as the articular surface of the humeral head (also taking into consideration that orientation of the proximal humerus in fragmentary specimens is not fully adequate).

"Are they outside the size and morphological range of fossil *Lophocebus cf. albigena* from Koobi Fora?"

Unfortunately, we did not have access to KNM-ER 30299 and there are no quantitative data in Jablonski et al. (2008) which would allow a comparison.

When referring to Table 1: "Add specimens from Andalee (Frost, 2001) and new MA specimens from Brasil et al. (2023)?".

Table 1 refers only to specimens from which we had access to. Unfortunately, we did not have access to the Andalee and MA collections. However, and as requested, we have added references to these collections/studies in the Introduction (which is more general in terms of overview than Table 1).

Sincerely,

Laurent Pallas

