**Responses to reviewer comments**

**Overview:**

**Both reviewers found the manuscript of value, but both raised similar concerns regarding the analyses, rationale, and context with the broader literature. We have incorporated these concerns by re-writing the manuscript and giving the analyses a complete overhaul. We have rewritten the introduction and discussion extensively to ensure the rationale and context are better described, with more literature (20 new references) to back up our choices of analysis and hypotheses; added analyses of evolutionary mode, module-by-module allometry, integration, and modularity among modules; and improved the figures to also present real specimens. The new results do not change the conclusions of the study, but provide substantially more depth and context.**

**Please note that the previous corresponding author (first author A. Marcy) was unable to complete the very extensive revisions due to professional time limitations. The code, interpretation/ integration of new results, manuscript re-write, and this response thus needed to be taken over by V. Weisbecker, previously the last author. It was therefore agreed to change the designation of corresponding author from A. Marcy to V. Weisbecker.**

**Our point-by-point responses are below (with our comments in bold).**

**Reviewer 1**

I’ve reviewed the manuscript titled ‘Beyond CREA: evolutionary patterns of non-allometric shape variation and divergence in a highly allometric clade of murine rodents.’ This is an incredibly relevant and timely study given the recent work published on mammalian cranial allometry, and this paper offers a much necessary perspective. The authors present an enticing story: if CREA arises from biomechanical effects of cranial scaling, then deviations from CREA should have deviant biomechanical functions.

**Thank you for this overall positive appraisal!**

This story, however, gets lost in methodological weeds. I think that this is a very important study that would be a significant contribution to the literature, but there are a number of methodological concerns that need to be addressed prior to publication. Specifically, a deeper discussion of the biology of the deviant taxa (Mastacomys, Hydromys, and Xeromys, etc) and how their biomechanical functions result in their straying from CREA, instead of the ‘will integration be reduced if we remove allometry’ discussion, is necessary.

**Agreed! We have now included a lot more of the wider literature (20 more references) – observational and experimental – into the introduction and discussion, which has made the paper far more relevant to the biomechanics of living animals.**

In the paragraph on lines 98-116, the authors state that it is a key question whether or not there are trends of cranial evolution away from the main allometric line, and then state that it is conceivable because allometry explains 36% of variation in their dataset. The authors have already answered this question however – about two-thirds of the cranial variation in the dataset is not related to size.

**We have re-written this section entirely, but it is worth pointing out that cranial evolution away from the main allometric line does not mean that these deviations follow a pattern or trend. They could also just be noise or non-directional, e.g. through vicariance or founder effects. It is common for GMM datasets to have large amounts of residual variation that is not explained after accounting for size (and other variables). It is therefore legitimate to ask if the residual variation follows a pattern or not.**

The degree to which this non-allometric variation is related to function, I believe, is a very interesting and important question, one that the authors should focus on, but instead the authors ask how the removal of allometric variation will affect patterns of integration and modularity in their dataset.

**We agree that this is an interesting question, and have placed more emphasis on the how well the deviations from the common allometric line are consistent with existing hypotheses about rodent biomechanics. However, a statistical approach to how the non-allometric variation is related to function is difficult beyond this moderate expansion because (as we now raise in the discussion) we do not have the sample sizes for comparative analysis of shape ~ diet/locomotion.**

Once allometric variation is removed, the amount of integration will necessarily decrease because you’re removing a shape axis that describes covariation among landmarks – you’re removing covariation. This is the case for the removal of any axis of shape variation, there will be less covariation if you remove some of the covariation. This effect will be very large if allometry is aligned with one of the first PC axes (in your case PC1, line 169 & 282).

**This is correct and we had described this effect (both that it removes most of PC1 and will reduce integration). A drop in integration was also expected but the extent of this drop (and whether it relates to an increase in modularity) is relevant information for the question of whether size is the only – or main – integrating factor. That said, we agree our earlier lack of module-by-module analysis made this information very superficial and deprived it of useful context. This is now hopefully rectified.**

On lines 324-327 the authors even state that the decreased integration in the residual dataset means that ‘size variation relates to an integrated response of modules across the whole cranium’, but to measure allometry they regressed size onto all of their shape variables, necessitating an ‘integrated’ response.

**This is correct, we essentially said the same thing twice (allometry is measured as the as the co-variation of all shape variables with size, which of course automatically means that there is an integrated response of shape to size). We made it clearer that we were interested in understanding whether there is significant integration left after size is removed. As per the above, we have extensively expanded this section to include a more in-depth analysis of integration significance and relative strength.**

Modularity will probably also increase because you’re removing among-module covariation, but the most-supported pattern of modularity might be different and this difference might be related to function (e.g., are the rostrum and molar landmark partitions found to be a single module when allometry is included, but found to be separate modules when allometry is removed? And is this related to the supposed stabilizing selection for gnawing?). The manuscript in its current form can’t accommodate this question though because there’s no analyses to find the most supported pattern of modularity either before or after the removal of allometry, only a comparison of the CR coefficient of the same modularity pattern in the allometry-included and -free datasets.

**We had reported the degree of correlation between each pair of modules before and after allometric correction in Table 1 and discussed them. As reviewer 2 pointed out, however, these analyses were not standard and we could go into a lot more detail, which we have done by adding a stronger emphasis on the integration tests (the overall conclusions remain the same, however). We also agree that our discussion missed the opportunity to discuss the functional implications of these results, which we have hopefully now addressed.**

These analyses could easily be substituted in, however. The authors on lines 98-100 state that allometry should be stronger in certain parts of the skull, which I agree with. Testing for allometry within each module, asking how much % variation it explains in different parts of the cranium, would be a highly relevant analysis for your questions.

**Agreed! And implemented now, with extensive contextualisation of allometry, integration, and modularity. This has made the manuscript must stronger, thank you for the suggestion!**

The authors seem to be unsure whether or not their removal of allometry is removing allometry, for example on line 172: ‘… to confirm that the allometry-free dataset lacks allometric information’. And on line 122: ‘if the allometry-free shape variation relates to the capacity of the cranium to diverge independently of allometry, we would expect…’ – what else would an allometry-free morphospace capture? If you’re unsure that the residuals of a linear model defining the shape-size axis is ‘allometry free’ then the rest of your analyses crumble because what, then, does the removal of allometry actually remove and therefore what can your subsequent analyses tell you about CREA? If the authors think that there’s additional allometry that’s not recovered in the linear model, then they should state that. The authors do state that there’s still ‘CREA-like shape variation’ in the allometry-free PCA, but this does not necessarily mean that your allometry removal didn’t remove all of the allometry, or that the initial allometry analysis didn’t capture all of the allometry, it just means that there’s additional face-length variation that’s not related to size. CREA states that proportional face length increases with size between species, not that all interspecific face-length variation is the result of size-related variation.

**It was indeed unnecessary to run these tests, they should not have gone into the published code or the manuscript and are now removed.**

On lines 111-112, the authors state, ‘high integration between modules (i.e., all modules co-varying strongly, also known as global integration’ and cite Bookstein 2015. Bookstein’s global integration analysis doesn’t consider covariation between landmarks, that was actually the motivation behind it, to measure ‘integration’ by leveraging the spatial structure of the data, not landmark covariances. The utilization of the global integration, specifically why this method to quantify integration is used over others (i.e., eigenvalue variances), isn’t discussed as much as necessary. This isn’t the most commonly used method, so it would be good to explain in more detail how it differs from other more conventional methods and why, given your questions, it’s the best choice. I would say that it makes sense to use it given that integration measured from landmark covariances will necessarily decrease once you remove allometry. Also, you should use species means for this analysis, not all of the specimens (line 237). Different sample sizes within species will lead to a miscalculation of the mean shape, whish is a crucial step to the global integration analysis.

**Thank you for this useful advice! The sample size figure was an error, the analyses were always done using the species mean. However, with the re-focussing of the manuscript on the more widely-used analyses of integration and modularity, we did not see much benefit in keeping this analysis in the manuscript and opted to remove it.**   
  
The authors state that they would expect to see Ornstein-Uhlenbeck type shape trends through time if diversification of the rodent crania is under functional allometric constraints (lines 119-120), but don’t perform any evolutionary model fitting. I agree that an OU analysis would be relevant (for the PC scores and size), so I was surprised that it wasn’t included in your analyses.

**We have added an extensive set of analyses that fits models of OU *versus* BM (and Early Burst, which is commonly co-analysed as a variant of OU), confirming our impression that shape evolves according to OU (details and potential caveats on P. 9., lines 169-176)**

Line 113-116: I’m confused with the wording of this sentence. What do the authors mean by ‘an underlying ability to change relative to the common allometry’? By this do you just mean morphological divergence in directions not aligned with the common allometric trajectory recovered by Marcy et al 2020? Or do you mean that allometry is evolutionarily labile?

**Apologies for the unclear wording – we have re-written the introduction extensively to clarify what we mean. The sentence that is probably closest to correcting the sentence in question is on P. 6, l. 113:**

**“***Further, if non-allometric variation is also under stabilising selection due to other biomechanical selection acting in parallel to allometry-generating selection, similar bounded divergence over time should arise in the residual cranial variation*.**”**

Lines 155-158: It would be interesting to see how the allometric axis differs when performing a phylogenetically-uninformed linear model. I say this because Mitchell, Sherratt, and Weisbecker 2023 astutely point out that when there’s a phylogenetic signal to body size (e.g., Cope’s rule), relevant size information will be removed when accounting for phylogenetic relatedness. Not necessarily in the main text, but it would be informative nonetheless.

**We have now added a supplementary figure showing that there is very little difference in PC1/PC2 space and shape variation based on residuals of a phylogenetically uniformed linear model.**

Lines 222-229: This is a peculiar way to measure phenotypic modularity. Why not use rPLS values from 2B-PLS analyses? It’s also unclear whether or not the authors re-ordinated the shape data per module before performing this analysis. Also, the panels D and E in figure 5 are the averaged rPLS value after each between-module 2B-PLS analysis, right? I don’t think this is mentioned in the text.

**We have re-designed both our analyses of modularity (using CR coefficient comparisons to accompany the similar results of the previous modularity analyses) and integration using r-PLS as suggested. Apologies for not noting that the values presented in Fig. 3 are averaged, this is now fixed.**

Figure 3: Make aspect ratios 1 for the PCA plots.

**Done – thank you for picking this up!**  
  
Line 486 and elsewhere: The authors never cite Cardini & Polly 2013, the original ‘CREA’ paper.

**Thank you for picking this up, this should not have been omitted. There was a lot of literature missing in this manuscript, which R2 also commented on and which we have hopefully addressed.**

**Reviewer 2**

Comments to the Author (see also attached annotated manuscript pdf)  
I revieved the manuscript entitled "Beyond CREA: evolutionary patterns of non-allometric shape variation and divergence in a highly allometric clade of murine rodents" that aims to compare patterns of allometric and allometry-free shape patterns of evolution in murine rodents.  
  
The present manuscript has (at least) a few aspects that positively impressed me like the presence of a Discussion section with almost no overstatements (except for the last paragraph) and the general aim to compare allometric and non-allometric shape variations (that is not so common topic in GMM and particularly interesting). Although in its current state the manuscipt is focused almost only on murine biology, these aspects clearly suggest that the manuscript has a good scientific potential.

**Thank you very much for this positive appraisal!**

However, there a few aspects that worry me in this ms. First of all, there is a severe lack of literature references (I explicitly mentioned it for the Introduction in the attached .pdf, but also Materials & Methods are impacted as I indirectly highlighted in other comments).

**We definitely needed to add more references reflecting the work of the major innovators in this area and have done so. We have added much of the literature recommended in the PDF comments and a few others related to rodent cranial function. However, we are reluctant to review some of the deeper history of CREA because this would be a very large addition to the manuscript and also has just been done exhaustively in a review we recently published, which we reference throughout.**

Following this line of reasoning, many procedures used in this research are not adequately motivated in the text (e.g., no references provided, no explanations for unusual procedures in GMM like removing PC1 in a morphological PCA to perform a matrix comparison, etc). Finally, the hypothesis of study concerning the presence of an evolutionary optimum not related to allometry appears to me to be described in a poor way and, more importantly, I suspect that the procedure adopted to (indirectly) validate such an hp is incorrect (and very dissimilar to the common application of multivariate phylogenetic comparative methods required to test for the occurrence of Ornstein–Uhlenbeck evolution and any other common evolutionary scenario that can be validated in shape data).

**Thank you for this advice, which mirrors the comments from Reviewer 1. We have now extensively modified the analyses to be more in line with general use, and removed analyses that did not contribute relevant information on the effects of size removal (including the mantel test comparisons between PCAs criticised above). The changes are all summarised at the top of this response.**

I attach a .pdf version including all my comments in detail, hoping these suggestions/criticisms might help the authors to improve the manuscript and increase the scientific impact of this research.   
  
For all these reasons, I suggest a (severe) "Major revision" outcome for the present manuscript.

**Thank you for going through the PDF so thoroughly – below are responses to most comments (not the small typo ones, they were just fixed).**

**Comment 1- Pg 5, line 47-50, sentence starting “The most widely discussed of these…”**

The description of this evolutionary pattern (i.e., CREA) in recent times was first included in Cardini and Polly 2013. However, several previous works pointed out such a relationship of braincase: facial scaling (see as an example some of the Radinsky's works I listed below concerning the mammalian order Carnivora).

Cardini, A. & Polly, P. D. Larger mammals have longer faces because of size-related constraints on skull form. Nat. Commun. 4, 2458 (2013).

Radinsky, L. B. 1981. Evolution of skull shape in carnivores. 1. Representative modern carnivores. Biological Journal of the Linnean Society 15:369-388.

Radinsky, L. B. 1982. Evolution of skull shape in carnivores. 3. The origin and early radiation of the modern carnivoran families. Paleobiology 8:177-195.

Radinsky, L. B. 1984. Basicrainial axis length vs skull length in analysis of carnivore skull shape. Biological Journal of the Linnean Society 22:31-41.

**We only added one of the Radinsky publications because a detailed discussion of these is already contained in a recent review two of us (VW and DRM) published recently. Adding these would necessitate to additionally add the same level of detail on the biomechanics-related aspects of CREA, which is beyond the scope of this manuscript (see comments below that we need to reduce references to not make the ms another review).**

**Comment 2- Pg 5, line 54 “(in Press)”**

Now you can replace it and add the citation: I saw this paper a few days ago published on Biological Reviews! :)

**Indeed 😊!**

**Comment 3- Pg 5, line 55-57 “closely related species tend to have similar diets and are thus…”**

N.B. This is not always true, just think about really famous case studies in evolutionary biology (e.g., cichlid fishes, Anolis lizards, Darwin's finches, etc) in which closely related species are very divergent in terms of dietary adaptations. Even without considering such extreme cases, resource partitioning as a way to reduce interspecific compatition is something that can be very common in nature (e.g., Stewart and Levin 1973; Pacala and Roughgarden 1982; Jenkins and Wright 1988, etc)

Partitioning of Resources and the Outcome of Interspecific Competition: A Model and Some General Considerations

Frank M. Stewart and Bruce R. Levin

The American Naturalist 1973 107:954, 171-198

Stephen Pacala, Jonathan Roughgarden, Resource Partitioning and Interspecific Competition in Two Two-Species Insular Anolis Lizard Communities. Science 217,444-446(1982).

Jenkins, K. J., and R. G. Wright. “Resource Partitioning and Competition Among Cervids in the Northern Rocky Mountains.” Journal of Applied Ecology 25, no. 1 (1988): 11–24. https://doi.org/10.2307/2403606.

DOI:10.1126/science.217.4558.444

**Ha! Exactly! The review you mentioned that has just come out (co-authored by VW and DRM) argues that CREA is often “broken” where the phylogenetic niche conservatism we refer to in this line is not upheld. The issues with adding more literature to this paragraph is that the literature suggested here only scratches the surface of this very broad topic, and the sentence in question explicitly starts with “Briefly…” as a means of ensuring that no expansive review is undertaken here. We therefore prefer to keep just the reference to our review, but the paragraph is now changed to more clearly reflect that we are referring specifically to Mitchell et al. (2024)’s argument.**

**Comment 4- Pg 5, entire paragraph line 54-65**

N.B. Throughout this entire paragraph, you only used one/two citation(s) (that was/were not published when you submitted the manusctpt). Please add some references for the assumptions you are making. I am not saying that they are not reasonable, but that is a good standard for general readers.

**This paragraph summarizes our very large review which just came out. To expand on it more than as a “setting the scene” paragraph seems excessive because, as you say, it contains a large amount of literature that is simply too sprawling to be digested here.**

**Comment 5- Pg 7, line 98-100 “shape variation independent of evolutionary allometry is expected…”**

N.B. For a non-expert of rodents as me, this part of the sentence does not seem so obvious. Can you please explain the reason behind it (maybe implementing some references)?

**This section was re-written – the most relevant sentence now is on p. 6, line 117:**

“*In addition, the biomechanical processes leading to CREA should be reflected in high allometry and high levels of co-variation in cranial areas that are expected to vary most under CREA as described above – the rostrum, cranial vault, and potentially orbital region….”*

**Comment 6- Pg 8, line 118-126, entire paragraph starting with “If diversification of rodent crania is bounded…”**

N.B. I disagree with this paragraph. For example, you might be in presence of a pattern of shape variation dominated by allometry (that seems likely to be your case, even considering Marcy et al. 2020 results) that, after removing the allometric shape component, is still dominated by a (different) evolutionary optimum, produced by another (but non-allometric) functional constraint, which is blurred by the dominant impact of allometry on the morphospace/disparity through time plot. If such a weaker optimum is related to some aspects of ecological specialisation, then you will be in presence of a contraddiction with your sentence "By contrast, if the allometry-free shape variation relates to the capacity of the cranium to diverge independently of allometry, we would expect to see the highest morphological distances between species that have ecological specializations with divergent functional requirements, compared to those whose shapes follow the expected pattern of hyperallometric gracility." because you will be in presence of OU conditions of evolution in the allometry-free context produced by ecological specialisation.

Even in this paragraph, despite the presence of complex assumptions concerning the application of phylogenetic comparative methods and the interpretation of its biological meaning, no references at all are included in the text.

**These points are correct and we were trying to argue exactly this (that there could – in fact should – be a “weaker” optimum hidden behind the strong impact of allometry). We clearly did not articulate this well and have therefore re-written the introduction with view to clarifying this point, which we fully agree on with the author. We are also now more strongly emphasizing the importance of this “hidden” selection in the discussion. More references to explain the OU pattern of diversification are now also added (and a separate OU analysis is now added as well, see below).**

**Comment 7- Pg 8, line 130 “size from the dataset completely removes variation due to CREA”**

N.B. Sorry but I do not get it: can you please rephrase? I do not understand the practical (and also the theoretical) meaning of this part of the text.

**This was also picked up by Reviewer 1 and should not have been in the manuscript – of course removing allometry removes variation due to CREA. Corrected now.**

**Comment 8- Pg 9, line 133-135 “between distantly-related species and/or species…”**

N.B. This comment is referred to the previous paragraph, this sentence, and the following parts of Mat&Met, Results and Discussion that are related to the same topic. I wrote it as the last comment at the end of my revision process.

For me, this hypothesis of study is extremely confusing and it is not described in a very clear way throughout the manuscript. In any case, if I understood well the authors are trying to validate the presence/absence of an evolutionary optimum in their shape (allometric and/or allom-free) data. To do this, they made various steps leading to tests performed on (morphological/phylogenetic) pairwise distances between species. At the end of the story, Figure 4 is graphically (i.e., qualitatively) evaluated to obtain some final inferences.

Now, the first issue with this procedure is that no references are provided in the manuscript in order to justify such a way to proceed (lines 245-258). I have never seen a similar framework used before and I think some explanations are required.

Perhaps even more importantly, the procedure suggested by the authors appears to be an indirect way to assess the presence of OU evolution without explicitely testing it. I do not see the point for using such an approach. To be more clear, I do not get the reason why the authors are not implementing in the manuscript model comparisons in order to assess the most likely model of evolution to describe their allometry or allom-free data. This is the standard way to proceed to validate the presence of an evolutionary optimum (i.e., OU evolution) or any other peculiar evolutionary condition, and it has been applied also in papers cited by the authors as Harmon et al. 2010 (but see for more recent theoretical discussions and examples on multivariate data papers like Adams and Collyer 2018; Clavel and Morlon 2020; Meloro and Tamagnini 2022; Bartoszek et al. 2022).

The authors need to implement explanations or alternative frameworks in order to validate this specific study hp, if they believe that is necessary for this manuscript, imo.

Dean C. Adams, Michael L. Collyer, Multivariate Phylogenetic Comparative Methods: Evaluations, Comparisons, and Recommendations, Systematic Biology, Volume 67, Issue 1, January 2018, Pages 14–31, https://doi.org/10.1093/sysbio/syx055

Julien Clavel, Hélène Morlon, Reliable Phylogenetic Regressions for Multivariate Comparative Data: Illustration with the MANOVA and Application to the Effect of Diet on Mandible Morphology in Phyllostomid Bats, Systematic Biology, Volume 69, Issue 5, September 2020, Pages 927–943, https://doi.org/10.1093/sysbio/syaa010

Carlo Meloro, Davide Tamagnini, Macroevolutionary ecomorphology of the Carnivora skull: adaptations and constraints in the extant species, Zoological Journal of the Linnean Society, Volume 196, Issue 3, November 2022, Pages 1054–1068, https://doi.org/10.1093/zoolinnean/zlab075

Krzysztof Bartoszek, Jesualdo Fuentes-González, Venelin Mitov, Jason Pienaar, Marcin Piwczyński, Radosław Puchałka, Krzysztof Spalik, Kjetil Lysne Voje, Model Selection Performance in Phylogenetic Comparative Methods Under Multivariate Ornstein–Uhlenbeck Models of Trait Evolution, Systematic Biology, Volume 72, Issue 2, March 2023, Pages 275–293, https://doi.org/10.1093/sysbio/syac079

**This comment (and others by both reviewers) have prompted us to re-write the entire introduction, as well as add more detailed analyses. This includes the use of Clavel’s package to assess mode-of-evolution and better referencing. We also agree that we have not taken the space to explain the rationale for our analyses, and this is now improved throughout. We opted to retain the morphological *versus* time distance plots because they represent a useful visualisation of the “spikes” of distances at times where an ecological specialisation occurred, but we have contextualised this appropriately as just a visualisation.**

**Comment to whole introduction**

N.B. I counted 13 cited papers in the entire Introduction section, with half of them that are mentioned in two sentences including lists describing previous papers on general topics (e.g., "This pattern, termed craniofacial evolutionary allometry (CREA), has been found in a diverse range of vertebrates representing 11 different orders, especially those of mammals (Bright, Marugán-Lobón, Cobb, & Rayfield, 2016; Cardini, 2019; Cardini et al., 2015)."; "This supports previous work suggesting that the strong allometry occurs as a result of stabilising selection on the rodent gnawing apparatus, which is highly specialized but allows for substantial dietary breadth (Druzinsky, 2015; Marcy et al., 2020; Zelditch & Swiderski, 2023).").

For me, there is a severe lack of references throughout the section: I think the authors should implement further literature, for instance, including different biological explainations that are suggested for CREA (see Cardini 2019 and references therein for some examples), clarifications concerning the assumptions they are making related to the application of specific PCMs (see my previous comment on the paragraph concerning Ornstein-Uhlenbeck), explainations concerning the importance of ecological specialisation and its interaction with allometry, etc..

**We have now added much more literature (20 references) to the paper, although we were cautious not to repeat the entire history of thoughts about CREA, which was subject to our recent review and would otherwise expand the manuscript unreasonably.**

**Comment 10- Pg 11, line 180-187, sentence starting “However, variation characterised through ordination or allometric analysis…”**

N.B. Here, you are pointing out that these two visualisations are "different visualisations of allometry". I disagree since as you are saying one merely aims to show the differences between the largest and the smallest species (if such species are far from your allometric trajectory you will see very different shape changes compared to those that are really due to allometry) and the other is simply the shape variation pattern associated with PC1.

**Agreed and clarified.**

**Comment 11- Pg 13, line 243**

See my comment on this set of analyses + related Intro/Discussion parts.

**See response there – this has been re-worked**

**Comment 12- Pg 13, line 280-282, sentence starting “However, removing the full shape PC1 – and the…”**

N.B. How did you perform such a Mantel test??? The two matrices you are trying to compare have different dimensions (n-1 x k for full versus n x k for residual) violating the conditions to apply a Mantel test.

**We dropped this comparison because it did not add much information to the test, but point out that the method is straightforward and had been described in the methods with a reference to the paper that introduced the analysis – the tests were not based on the PCs, but on the distance matrix between species based on the PCs, which is a legitimate means of testing if species are similarly distributed in overall morphospace based on different types of underlying data.**

**Comment 13- Pg 16, line 283-287, sentence starting “Nevertheless, the relationship between the full shape and shape residual…”**

N.B. Forgetting for a second the previous comment on Mantel test, this seems a very empirical way to proceed and to make assumptions. Can a simple correlation test dispute evidences you are obtaining from a Mantel test (if we assume that such a test is correctly performed and perfomable)? I do not think so, but I would like to see examples from the literature of similar approaches used in research using geometric morphometrics in the text (maybe implementing them in the Materials and Methods section).

**As above, these analyses were dropped.**

**Comment 18- Pg 22, line 425-427, sentence starting “For example, in the case of rodents, there are…”**

N.B. Concerning the role of gape angles on CREA, Tamagnini et al. 2023 recently demonstrated that extinct sabertoothed cats (possessing wider gape angles than their living counterparts) represent an exception to CREA, contrary to conical-toothed cats.

Tamagnini, D., Michaud, M., Meloro, C. et al. Conical and sabertoothed cats as an exception to craniofacial evolutionary allometry. Sci Rep 13, 13571 (2023). <https://doi.org/10.1038/s41598-023-40677-6>

**This paper is now in the manuscript in several places, alongside the other additional references.**

**Comment 19- Pg 25, line 479-494, Paragraph starting “Counter to our expectations…”**

See my comment on this set of analyses + related Intro/Discussion parts.

Furthermore, contrary to the rest of the Discussion that seems pretty reasonable to me, this paragraph is full of potential overstatemens introduced by arbitrary evaluations that are unlikely supported by your results (e.g., "Instead, the asymptotic divergence pattern of shape reinforces the concept of rodent skulls evolving around an optimal shape unless a substantial change in either size or cranial function evolves."; "Overall, the pattern of “spikes” of divergence in otherwise limited morphospace (as demonstrated by a plateau of diversification after 4.2-5.7 million years) suggests an evolutionary pattern most consistent with a mean-shift Ornstein-Uhlenbeck process of limited diversification around a local optimum (Harmon et al., 2010).").

Perhaps, my criticism can be solved by implementing a solid explaination of the analytical procedure behind this part of the manuscipt and, in this specific case, of the link between Harmon et al. 2010 and the type of approach behind Figure 4 in the present ms.

**Hopefully the addition of the evolutionary mode analysis will alleviate these concerns. In addition, we now focus more on the value of this figure as a visualisation and interpret it purely as that (as opposed to a formal analysis). But as argued above, it seems appropriate to show this plot because it serves as a way of visualising the numeric evidence for a relatively homogenous shape landscape with just a few spikes of diversification.**