

A Jurassic Mammaliaform Swimmer and Transformation of the Mammalian Pharynx

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Any redactions in this file are there to maintain patient confidentiality, the confidentiality of unpublished data, or to remove third-party material.

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

Thank you for the opportunity to review the manuscript by Li et al. This paper describes a spectacular new mammaliaform fossil from the Middle Jurassic of China, *Megacauda sungei*. The fossil preserves very fine details of the skeletal and soft tissue anatomy of this docodontan, and its highly specialised dentition, which together provide an intricate picture of its life as a swimming, carnivorous “pre-mammal” 165 million years ago. This fossil represents a new genus and species of docodontans; it is included in a comprehensive phylogenetic analysis resulting in a new family being erected for it and its slightly younger sister taxon *Castorocauda lutrasimilis*. With key postcranial systems also studied and discussed in depth, *Megacauda* provides compelling new, very detailed evidence of a semiaquatic lifestyle in docodontans, and expands understanding about the exploitation of a wide range of ecological niches long before the evolution of crown mammals. Of equal significance in this fossil discovery is the detailed information provided by the rare preservation of soft tissue imprints of the pharyngeal vault (throat) and its skeletal supporting apparatus (throat bones) in *Megacauda*, structures that are key for swallowing and suckling in mammals. The latter behaviour was previously thought of as being a hallmark of therian (advanced) mammals but is now interpreted by the authors as having evolved well before the rise of crown mammals, in the common ancestor of docodontans and mammals. The fossil enables the authors to trace the functional evolutionary transformation of the pharyngeal vault across the cynodont-to-mammal transition.

The fossil has enabled an exceptional depth of detailed information to be assembled and assessed by the authors - a dissertation or more. Striking the balance between leading with swimming mammaliaform versus evolution of the pharyngeal vault in cynodonts/mammals is tricky, but the authors have found a good balance in the main paper, videos and supplementary information. This study will be a landmark contribution to this field. The results presented will be of great interest to a wide audience of scientists, including palaeontologists, mammalogists, anatomists, evolutionary biologists, geneticists, phylogeneticists, etc., and in presenting an extraordinary new fossil the content will also be of interest to non-scientists, including journalists.

The methodology is standard and the study very well documented. In terms of statistical treatment, the estimation of body mass and body proportions is straightforward, using widely accepted published formulae, and the authors offer a range of possible values. Where extrapolation of information from other specimens has been used to reveal potential details in *Megacauda*, the approach has been explicit.

In terms of phylogenetic analysis to place the new species, and revision of interrelationships between docodontans, is appropriate and thorough. Erection of the new family appears to be warranted and well argued. However, detailed information about part of the results appears to be missing from the files. For example, I have not found the normally-reported data such as the type of consensus tree shown, number of most parsimonious trees, tree length, consistency indices, support values (bootstrap or other), etc. A sentence or two rationalising the use of maximum parsimony analysis over Bayesian analysis would be welcome.

Expression is good and mostly consistent throughout the manuscript. I have suggested below a few places where rephrasing would help clarify certain points. The abstract, introduction and conclusions are informative and clear, accurately reflect the content of the manuscript, with key results covered succinctly and the significance of the research made plain. The conclusions and data interpretation are robust, valid and reliable. The references credit other studies appropriately. The figures are all necessary, and of good quality. The stereo pairs in the Extended data figures are excellent. I have suggested below that an inset in either Figure 5 (the phylogeny) or in a supplementary figure would be helpful to indicate

where Docodonta fits within the broader cynodont-mammal tree, particularly with respect to Theria (since specific comparisons with crown/modern mammals are made throughout the ms).

Specific comments

Line 33: Insert: "a" therian-like pharyngeal vault
Line 34: Invert order and no hyphen: hyoid skeletal anatomy (throat bones)
Line 54: swimmers (plural)
Line 63: Insert: "the docodontan" Castorocauda (at first mention in ms)
Line 69: Rephrase: E.g. "Phylogenetic analysis of a matrix of dental and"
Line 75: Does the highly apomorphic dentition of Megacauda (multi-rooted canine, independent pseudotribosphenic cheektooth morphology) provide insight on the evolution of a key mammalian character? Rephrase slightly?
Line 104: The upper canine is unique in three features if you include its 3 roots.
Lines 121-126: Seems to be some repetition with respect to the serrate series of cusps; please review or rephrase to simplify message.
Line 190: similar to many living placental mammals. Add reference/s
Line 194: Define definitive mammalian middle ear for the non-specialist reader, or add reference/s.
Line 210: Define cynodonts at first mention for non-specialist readers.
Line 226-227: Rephrase as: "from the palatine pyramidal process by a recessed (concave) area of the palatine."
Line 252: (passageway between the oral cavity and the esophagus). Move to line 85 (first mention of pharynx)
Line 347: macropodid, macropodoid, otherwise kangaroo
Line 358-360: Rephrase? Something like: In tail outline, megacaudids are more similar to the giant otter *Pteronura* (87) than to the rounded distal tail of the platypus and beaver species (*Castor*), and probably also lack the full capacity of propulsive force provided by the distally rounded tails.
Line 416: Extant semiaquatic mammals use shelters
Line 428: ecologically diverse
Line 435: This ecological history
Line 447: early-diverging docodontans?
Line 757: Bold c1 and c2
Line 763: Add "of un-named docodont SDUST-V0007"
Line 765: Remove "of un-named docodont"
Line 766: Add "platypus" *Ornithorhynchus*
Line 767: Add "short-beaked echidna" *Tachyglossus*
Line 774-775: It would be good to show (in inset to Fig. 5? Or in supplementary figure?) where Docodonta fits within the broader cynodont-mammal tree, particularly with respect to Theria (since specific comparisons with crown/modern mammals are made throughout the ms).
Line 787: Add? "Small arrows on posterior-most haemal arches on the tail (in a and b)."
Fig. S8e: Correct spelling of Docofossor in figure
Line 927: Insert: unique in having/displaying/exhibiting a fully ossified sternal segment
Supplementary info doc
Line 410-411: Update platypus size range? E.g., from Van Dyck et al. 2013, *Mammals of Australia*. Adult length: 400-630 mm (males), 370-550 mm (females) (Van Dyck et al. 2013)
Adult weight: 0.8-3.0 kg (males), 0.6-1.7 kg (females) (Van Dyck et al. 2013).
Line 1616: Insert "un-named docodontan" before SDUST-V0007
Line 1668: Insert missing information: "From Ca16 to the tail" end/tip/distal margin?
Line 1697-1697: Platypus uses/curls its tail to carry nesting materials to its den/shelter. Any thoughts on potential curling/prehensile ability in Megacauda (at least as suggested by inferred tail musculature)?
Line 2000. iliopectineal process. Alternative term possibly used previously in ms? Please check.
Line 2842. Three types of vertebrae with respect to pelvis? Otherwise rephrase (see also line 2844).
Line 2862: Common name for *Pteronura* varies in ms (giant otter, Amazon river otter, giant Brazilian otter, etc.), make consistent unless referring to specific populations which is also possible. Please check.
Line 2938. hold the hindlimb close to the pelvis/body
Line 2975 and 2977. Close to the pelvis?
Line 3031. Spelling of *Kryoryctes*
Line 3047. The infraorbital foramen/nerve/vibrissae are discussed; can the authors also make a comment about the size of the mandibular canal in Megacauda (cf. platypus where this canal/nerve is enlarged, associated with electroreception)?

Sincerely,
Suzanne J. Hand (Sue)

Referee #2

(Remarks to the Author)
Nature Review

General Comments:

Our expertise as reviewers is in the evolution of feeding and cranial/orofacial anatomy of mammals, and therefore we are less able to comment on the evolution of the postcranial anatomy, and locomotion.

A. Summary of the key results

This is a new fossil with extraordinary preservation that permits inference about the common ancestors of Docodonta and Mammalia, and therefore about the origin and evolution of these taxa.

B. Originality and significance: if not novel, please include reference

The description and interpretation of this fossil is both original and significant. The preservation of the oral cavity and pharynx of this fossil is remarkable, and the interpretation of these authors is strong.

C. Data & methodology: validity of approach, quality of data, quality of presentation: Excellent, no concerns.

D. Appropriate use of statistics and treatment of uncertainties

The authors are sure of themselves, but from our perspective (knowing oropharyngeal anatomy extremely well), they are within reasonable limits of interpretation.

E. Conclusions: robustness, validity, reliability

As above for D. the authors are making inferences about function that are consistent with the material they have studied and reconstructed.

F. Suggested improvements: experiments, data for possible revision

Please find more fossils. Also, the tongue is sadly neglected in this paper, and we appreciate that it is an entirely muscular organ, and not amenable to preservation. However, given that styloglossus, hyoglossus and palatoglossus are critical and interesting extrinsic tongue muscles for formation of the seals that permit efficient liquid transport in both infants and adults, might there be some room for some inference about them?

G. References: appropriate credit to previous work?

Yes. While there is much more detailed work on the anatomy of the hyoid, pharynx and mandible, as well as variation in pharyngeal and palatal muscle anatomy across mammals (one audience for this paper), it is possible, but not necessary to include that literature in this paper.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The paper is well written, and easy to follow. The extended figures, especially the video are very useful for three-dimensional perception and understanding.

Specific comments from Reviewers.

The preservation of oropharyngeal anatomy, including the hyoid, is remarkable, and the authors are commended on their descriptions. We agree that these structures support the hypothesis that suckling could have evolved in this lineage. In turn, this supports the idea that mammalian swallowing, critical to the evolution of endothermy, likely occurred in the common ancestor of mammals. Further the dental features, particularly the post-canine teeth are fascinating. The authors' interpretations bring a modern evolutionary interpretation and context to this work.

The authors do spend time discussing the implications for suckling, but it is also important (at least to us) how this anatomy impacts our understanding adult mammalian drinking. The muscles of the palate are critical for drinking, and the authors allude to this in their discussion of the pterygopharyngeus muscle (lines 280-290).

While there is an extensive and historical literature on diversification of mammalian mastication, there is very little comparative and evolutionary work on adult drinking. Because drinking is not dependent on the dentition, and thus not informed by the ubiquitous fossilization of teeth, it has received less attention than mastication. Some adult mammal drinking is through a mechanism similar to suckling, with a change in head position (e.g. pigs, primates). But others appear to use a different mechanism (carnivores). There is value to applying the results of this study to broader evolutionary issues.

From a perspective of endothermy, the standard evolutionary argument is that airway protection & continuous respiration is critical in mammals, but less so for ectotherms. The evolution of the soft palate and fleshy precisely controlled tongue is often couched in this perspective. But the work of these authors suggests that the mammalian soft palate may predate, in evolution, the need for airway protection.

Hopefully this paper will spark some interest in understanding the evolution of mechanisms used for liquid transport across adults. And it will be a critical source for understanding how mammalian drinking evolved and how much is based on that functional morphology that powers suckling.

Even more specific comments:

Line 183-187 – there is some debate in the literature as to the prevalence of ossified stylohyals (bats, sloths, carnivores). This result supports the non-ossification as the primitive state, as well as the configuration of the ventral hyoid elements.

The description of the pharynx starting at line 203 is good. Should this be the “pharyngeal vault” or just “pharynx”? Is there

an anatomical or evolutionary distinction the authors are making?

Fig 2 is well done. We appreciate that this is a paper replete with figures, however, perhaps adding a lateral view of the reconstruction of these bones would help readers understand the 3-dimensional nature of this space. The additional supplemental figures (and video) are very useful.

Line 274 – As the authors say, the soft palate muscles are critical for suckling, but they are also critical for transport of liquids and masticated/triturated solids in adults (St I and St II – see Hiiemae and Crompton & lengthy comment above). The authors do a good job outlining the role of the soft palate during suckling, and the role of the pterygopharyngeus during swallowing.

Line 278 – could this trough be indicated on fig 2? It is a complex figure, but it would help the reader to see this specific area (in main figures –there was more in the supplemental figures).

The text, starting at line 251, "Inference..." is a good review of comparative anatomy. However, at line 292 – the authors bring a functional/biomechanical perspective that then carries on at line 297. The para after this contains more function. Consider a new section header at 291/292 including the para that starts at 297 to delineate some functional capacity of the anatomy (as the previous sections are more anatomical, rather than synthetic). Some of the literature on in vivo movements of the soft palate (there are several papers about this in animal models), rather than hypothetical inferences would strengthen these (very good) arguments.

It would also be possible/valuable to expand this section (line 292 & paragraph from 297 – 306) to hypothesize that if these features are present, it would indicate two distinct behaviors. Firstly, that these animals were swallowing/capable of swallowing heavily processed/homogenized foods, a hallmark of mammalian masticatory behaviors. This is also supported by the apomorphic dental features. Secondly, that other oropharyngeal structures, such as a tongue capable of curling around a nipple and generating suction, may have been present at this time as we suggest in co-reviewer & German (citation 58).

In this section, the authors could also hypothesize about the anatomical origin/insertion of other tongue musculature data (i.e. styloglossus, palatoglossus hyoglossus). The completeness of this specimen would lend credence to mapping the evolution of those muscles, which are as important as the velum to mammalian feeding and swallowing.

The remainder of the manuscript is interesting, well written, and outside of our expertise.

Rebecca German and Co-reviewer

Referee #3

(Remarks to the Author)

I co-reviewed this manuscript with one of the reviewers who provided the listed reports.

Referee #4

(Remarks to the Author)

This new paper on a swimming mammaliaform, *Megacauda*, and the evolution of the pharynx by Li et al., describes a large-bodied platypus-analogue from the Jurassic, with exceptionally well preserved features of the throat. There is a lot in this paper, it's rich and exciting. The authors outline multiple lines of convergence between this taxon and later therians, in the teeth, hyoid, pelvis, and overall ecology of this animal. It once again proves that early mammals are surprisingly 'advanced', and that docodontans are a fascinating trial run of later therian life.

The reconstruction and analysis of the hyoid, and how this relates to suckling, is extremely exciting. While the anatomy of the throat was previously mentioned in the paper on *Microdocodon* (Zhou et al. 2019), this specimen allows for much more definitive statements about muscle attachment and the structure of the region, and how this relates to suckling. In the teeth, the identification of a carnassial analogue to modern carnassial teeth and shearing (the 'pseudo-carnassial' and prevallum-postvallid shearing), is extremely well presented, adding another astonishing feather in the cap of early mammals, indicating this was a large-bodied predator at a time when most mammals were thought to be quite tiny.

The visualisations are clear and will be of enormous value to future researchers to reference. The detailed anatomical description and comparison is ideal, and they have employed all the expected methods to estimate body mass, and appropriately analyse the taxon phylogenetically. The references are thorough and appropriate. It is also written with clarity and focus, and includes a wealth of supplementary material for those who wish to dive deeper.

Based on the evidence presented here, there is currently not enough support for the erection of a new genus in my opinion. The main differences presented between *Castorocauda* and *Megacauda* are size – which is well known as being very unreliable for differentiating taxa – and the dental formula. The reason the dental formula differs, is because of the author's reinterpretation of *Castorocauda* from i4/c1/p5/m6 (same as *Megacauda*) to i4/c1/p6/m5. Their argument for this is based on the interlock of the m1-m2, which seems sound enough. The additional differences of cusps being slightly smaller, cingulid less visible and tooth slope reduced on some molars in *Megacauda* (see supplementary) is not completely convincing though - these features are not clearly figured for *Castorocauda*, and so rely on an interpretive diagram rather than 'direct'

observation of the micro CT data (the same issue goes for the interpretation of the m1-m2 interlock). They may actually be signs of wear in an older (=larger, as we know docodontans did not have determinate growth like modern mammals) individual. These differences are maybe species-level, as supported by the results of the phylogenetic analysis, but not genus-level. The authors themselves repeatedly demonstrate how similar *Castorocauda* and *Megacauda* are, to the exclusion of other docodontan taxa. Their postcranial anatomy is apparently the same - and one might even have thought they were the same taxon entirely.

While it is a stunning specimen and has been visualised beautifully, a lot of the message here is not new. We already know mammaliaforms grew large (Li et al. 2000; Hu et al. 2005; Ji et al. 2006), that they had mammal-like hyoids (Zhou et al. 2019) that allowed them to suckle, that they included semi-aquatic taxa (Ji et al. 2006) and were more ecologically diverse than previously thought (Luo 2007 onwards), plus this is not convincingly a new genus (above). While I think it's a really fantastic study, I am not sure that there is enough novelty for *Nature*, but certainly for another imprint of the *Nature* group. This is because the information on hyoid evolution, and the incredible monotreme-like stance demonstrated for this taxon – along with a wealth of other information contained herein - will be of enormous interest to palaeontologists, mammalogists, anatomists, and many others. The quality of the figures and videos also make it incredibly useful for other researchers – all too often such studies are sparse in terms of detail, but this one is quite the opposite, and will aid interpretation in multiple future studies.

Some small edits:

Line 51 - provides change to provide

Line 53 - Refs currently run from number 6 to number 15, they should be sequential in order of appearance

Line 75 - change to new insights into

Line 127 - but because *Megacauda*

Line 128 - it is feasible

Line 218 - the pyramidal process

Lines 337-338 - Repetition of the previous sentence, the two should be combined

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The authors have carefully and consistently addressed my concerns and suggestions in their revised manuscript, and I look forward to seeing the paper in print.

Referee #2

(Remarks to the Author)

Having read through the manuscript and the extensive response to reviewers, I find these authors have addressed every comment I made. They made nearly every change suggested, which I believe has strengthened this manuscript significantly. The few changes they did NOT make result from the limits that *NATURE* imposes (limits on figures, etc). I appreciate such constraints.

Referee #3

(Remarks to the Author)

I co-reviewed this manuscript with one of the reviewers who provided the listed reports.

Referee #4

(Remarks to the Author)

The authors have addressed the comments raised in my first review, and I thank them for doing so. The changes, especially clearer highlighting of the anatomical differences between these taxa, are thorough, and as I said in my previous review, these, along with the excellent figuring and videos, will be extremely useful to future researchers.

I am still not entirely convinced that this is a new genus (rather, a new species of *Castorocauda*). The fact that *Castorocauda* is mostly figured previously using drawings, and that there are not good micro-CT or even many photographic images provided by previous authors, make it hard to evaluate it against *Megacauda*. However, the authors' justification for erecting a new genus is synthesised more clearly now and given in detail, and I very much appreciate the comparative images of the two taxa to make it easier to see how they differ.

Clarifying that this is a largest mammaliaform (rather than mammal) is also important, I thank the authors for taking this comment into account in their revision. The revisions have emphasised the unique features of the specimen, and functional and evolutionary implications.

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In cases where reviewers are anonymous, credit should be given to 'Anonymous Referee' and the source.

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A Jurassic Swimming Mammaliaform and Early Evolution of the Mammalian Pharynx (Nature Ms. 2026-04-10515A(R1))

Explanation on Revision & Clarification for Review Comments

By Li, Li, Neander, Zhang, Zhou, Martin, and Luo

Summary (July 3, 2026)

We greatly appreciate the effort and time by all four referees to check through our manuscript. We are grateful for the many supportive statements and appraisal from the referees.

In response to the review comments and queries, we improved four major areas of the paper:

1) For a fuller presentation on details of parsimony and Bayesian phylogenetic analyses. We expanded the Fig. 5 caption and added Bayesian details to Supplementary Information, in response to Prof. Hand's comment. Fig. 5 is also made more reader-friendly, with full details, according to Prof. Hand's suggestion.

2) For better introductory text on pharynx soft-tissue and bony pharyngeal structure (Comments from Profs. German, co-reviewer and Hand). A more balanced explanation of pharyngeal function both for airway protection and for swallowing. "Swallowing" now covers both the masticated food and fluids ("drinking").

3) To accommodate the suggestions and editorial requests (from Profs. German and co-reviewer), we rearranged the text on pharyngeal osteology (fossil), anatomy (extant mammal comparison) and functional interpretation. We believe the changes prompted by referees have improved the accessibility for nonexpert readers to better grasp the evolutionary significance of this fossil for the mammalian pharyngeal structures.

4) Toward a fuller taxonomic justification and a better explanation why *Megacauda* is a new genus (Referee 4). To clarify for Referee 4 and to better explain our justification for a wider readership, we have now expanded the manuscript:

- (a) **a short summary of diagnostic features in *main text***, highlighting the longer text in Supple-Info.
- (b) **a new Extended Data Fig. S6** to provide integrative characters like Supple-Info Table of (Supple-Info)
- (c) **new paragraph in Supple-Info to explain the skeletal differences** of *Megacauda* and *Castorocauda*.
- (d) **a new stratigraphical illustration** to explain that Bed 4 of *Megacauda* (lower horizon) and Bed 9 of *Castorocauda* (higher in horizon) are separated by 60 meters of sedimentary in the Haifanggou Formation that is only 90 m thick in its entirety in Daohugou area. *Megacauda* is much older than *Castorocauda*.

We believe we have addressed all review comments. Thank you for the help to improve this paper!

Note of Thanks for Appraisals from Referees

Prof. Sue Hand: "...a spectacular new mammaliaform fossil from the Middle Jurassic of China..which together provide(s) an intricate picture of its life as a swimming, carnivorous "pre-mammal" 165 million years ago...*Megacauda* provides compelling new, very detailed evidence of a semiaquatic lifestyle...in the exploitation of a wide range of ecological niches long before the evolution of crown mammals.... Of equal significance in this fossil discovery is .. the rare preservation of soft tissue imprints of the pharyngeal vault (throat) and its skeletal supporting apparatus (throat bones)..key for swallowing and suckling in mammals."

Profs. Rebecca German & co-reviewer: "This is a new fossil with extraordinary preservation that permits inference about the common ancestors of Docodonta and Mammalia...The description and interpretation of this fossil is both original and significant... The preservation of the oral cavity and pharynx of this fossil is

remarkable, and the interpretation...is strong...There is value to applying the results of this study to broader evolutionary issues...Hopefully this paper will spark some interest in understanding the evolution of mechanisms used for liquid transport across adults...functional morphology that powers suckling.”

Referee 4 “The reconstruction and analysis of the hyoid, and how this relates to suckling, is extremely exciting...this specimen allows for much more definitive statements about muscle attachment and the structure of the (pharyngeal) region...relates to suckling...identification of a carnassial analogue to modern carnassial teeth and shearing (the ‘pseudo-carnassial’...shearing), is extremely well presented, adding another astonishing feather in the cap of early mammals.... The quality of the figures and videos also make it incredibly useful for other researchers...will aid interpretation in multiple future studies.”

Authors Response: We are grateful for an overall very supportive appraisal by Referees. Many positive comments are specific to the content of this new fossil and our analysis – these are real substance from our scientific peers. Their suggestions for improvement and prodding for changes are insightful and valuable. We greatly appreciated all of these.

We are also thankful to the referees (e.g. Prof. Sue Hand) for their effort to check through both the manuscript text and the lengthy supplementary information (text, graphics, and videos). We are indebted to their help and dedication in improving the quality of our manuscript. And this debt can only be re-paid by serious revision on our part, in response to each query, to answer each question with constructive clarification in this “response and explanation for revision” document, the best we can.

FROM REFEREE 1 (Prof. Susan Hand)

Major Revision 1 (Ref 1) Request for details on phylogenetic analysis (3 related comments)

(Ref 1) - “detailed information about ...the results (‘normally-reported data’) missing from the files: the type of consensus tree, # of most parsimonious trees, tree length, consistency indices, support values (bootstrap or other), etc.”

(Ref 1) - “a sentence or two rationalising the use of maximum parsimony analysis over Bayesian analysis would be welcome.”

(Ref 1) - “I have suggested below that an inset in either Figure 5 (the phylogeny) ... would be helpful to indicate where Docodonta fits within the broader cynodont-mammal tree, particularly with respect to Theria”

Authors: These are excellent suggestions for us to develop better presentation on the analyses that we had already done. It was our oversight that details are not provided in Fig. 5 caption in previous draft. Thank you Referee 1!

Authors’ Explanation (1): It was our negligence that the previous Fig. 5 caption omitted the details of the consensus tree and most parsimony trees (these were in the Supplementary Information, but not in Fig 5 caption). In revision, we have now listed the details of both parsimony analyses results, and the Bayesian analysis. The revised Fig. 5 caption has: a) type of consensus tree, b) # of most parsimonious trees, c) consistency (CI) and Retention (RI) indices. Fig. 5B now shows Bremer and bootstrap values.

The Supplementary Information is also expanded accordingly: we expanded file on the log file of PAUP, and TNT results on the bootstrap and the bremer index values. We also included the summary of the Bayesian analyses (the 50%-rule consensus of 14983 post burn-in trees).

Authors’ Explanation (2): The revision has included Bayesian analyses (to complement the PAUP searches). In revised Supplementary Information, we presented the results of Bayesian analysis. To clarify this briefly: further Bayesian analyses also recovered the key clades of PAUP analyses:

the clade (*Dsungarodon*(*Megacauda*, *Castorocauda*), the clade Docodontidae (*Haldanodon* + *Docodon* + *Docofossor*), and the clade Tegotheiidae. The “Borealestid clade” ((*Borealestes* + *Krusatodon*) *Dobunnodon*), was weakly supported in PAUP results; it shows a different clustering in the Bayesian maximum compatibility tree, and collapsed into polytomy in 50% majority-rule consensus tree.

We interpret that, given our matrix of docodontans, PAUP appears to recover some weakly supported clades (e.g. borealestids), more so than the Bayesian. The key clades of Docodontidae, Megacaulidae and Tegotheiidae are corroborated in both PAUP and Bayesian results.

Authors’ Explanation (3) Re “Figure 5 should show where Docodonta fits within the broader cynodont-mammals-therians tree”: This is an excellent suggestion from Prof. Hand. We have now added an general evolutionary tree (= New Fig. 5A) that shows the position of docodontans in the broader cynodont-mammaliaform phylogeny. We improve on the graphics (e.g., logos of mammaliaforms) to make the content more accessible for a wider audiences.

Revision 2 (Ref. 1) – Updating the Literature Source on Monotreme Body Size
(Ref 1) “Line 410-411: Update platypus size range? E.g., from Van Dyck et al. 2013, Mammals of Australia. Adult length: 400-630 mm (males), 370-550 mm (females) (Van Dyck et al. 2013) Adult weight: 0.8-3.0 kg (males), 0.6-1.7 kg (females) (Van Dyck et al. 2013).”

Authors: Thank you for an excellent suggestion. We have now revised the discussion on body mass estimates for Megacauda and Castorocauda vis-à-vis to the body mass data of the platypuses by Van Dyck et al. (2013). The SI paragraph on this content is also expanded with Van Dick et al. (2013).

We like to thank Referee 1 for bringing this reference to our attention for improvement the SI.

Revision 3 (Ref. 1) Tail Functional Morphology of Platypus
(Ref 1) “L. 1697-1697: Platypus uses/curly its tail to carry nesting materials to its den/shelter. Any thoughts on potential curling/prehensile ability in Megacauda (at least as suggested by inferred tail musculature)?”

Authors: A big thank you to Referee 1 for an insightful comment and a good suggestion for us to explore this the tail function in nesting behavior of the platypus. We have now added a new paragraph in supplementary information about nest-building behavior of the platypus in carrying nesting materials by curling of the tail, as described by Jessica Thomas et al (2018, 2019). We commented that megacaulid docodontans likely were capable of similar capacity to curl the tails, as monotremes, in a new paragraph in supple information.

We are thankful for referee’s suggestion of this tail function we did not know. Addition of this new content has augmented the comparative inference of possible tail functional of megacaulid docodontans.

Revision 3 (Ref. 1) Explanation of Anatomy and Cladistic Terminology (4 comments)

Authors: Thank you to Referee 1 for prompting us to explain each anatomical or phylogenetic term at its first appearance: “bony” pharyngeal vault; “muscular” pharynx; cynodonts; DMME – the definitive mammalian middle ear. These are added or revised to improve accessibility for non-expert readers.

Line-by-line corrections requested by Referee 1

(Ref 1) Line 33: Insert: “a” therian-like pharyngeal vault

Authors: changed

(Ref 1) Line 34: Invert order and no hyphen: hyoid skeletal anatomy (throat bones)

Authors: revised as suggested

(Ref 1) Line 54: swimmers (plural)

Authors: changed.

(Ref 1) Line 63: Insert: “the docodontan” Castorocauda (at first mention in ms)

Authors: revised as suggested

(Ref 1) Line 69: Rephrase: E.g. “Phylogenetic analysis of a matrix of dental and”

Authors: the whole sentence was revised as suggested

(Ref 1) Line 75: “Does the highly apomorphic dentition of Megacauda (multi-rooted canine, independent pseudotribosphenic cheektooth morphology) provide insight on the evolution of a key mammalian character? Rephrase slightly?”

Authors: This sentence was re-arranged. Rephrased as suggested by the referee.

(Ref 1) Line 104: “The upper canine is unique in three features if you include its 3 roots.

Authors: Our sentence was awkward. It is rephrased. Thank you for prompting for us to improve.

(Ref 1) Lines 121-126: “Seems to be some repetition with respect to the serrate series of cusps; please review or rephrase to simplify message.”

Authors: These sentences were re-organized and streamlined, during revision.

(Ref 1) Line 190: “similar to many living placental mammals. Add reference/s”

Authors: References were added in this location. The sentence is also slightly rephrased.

(Ref 1) Line 194: “Define definitive mammalian middle ear for the non-specialist reader, or add reference/s.”

Authors: this sentence was expanded to explain DMME. Allin & Hopson (1992) was added here.

(Ref 1) Line 210: “Define cynodonts at first mention for non-specialist readers.”

Authors: good prompt. We added explanation of cynodonts. Cynodonts now labeled in Fig. 5A.

(Ref 1) Line 226-227: “Rephrase as: ‘from the palatine pyramidal process by a recessed (concave) area of the palatine.’...”

Authors: changed according to referee’s suggestion.

(Ref 1) Line 252: “(passageway between the oral cavity and the esophagus). Move to line 85 (first mention of pharynx)”

Authors: This was re-arranged according to Referee’s suggestion.

(Ref 1) Line 347: “macropodid, macropodoid, otherwise kangaroo”

Authors: Correction made. Sorry for the typo.

(Ref 1) Line 358-360: “Rephrase? Something like: In tail outline, megacaudids are more similar to the giant otter Pteronura (87) than to the rounded distal tail of the platypus and beaver species (Castor), and probably also lack the full capacity of propulsive force provided by the distally rounded tails.”

Authors: These sentences were re-organized and streamlined according to Referee’s suggestion.

(Ref 1) Line 416: Change to “Extant semiaquatic mammals use shelters”

Authors: correction made.

(Ref 1) Line 428: Change to “ecologically diverse”

Authors: correction made.

(Ref 1) Line 435: Change to “**This** ecological history”

Authors: changed.

(Ref 1) Line 447: Change to “early-diverging docodontans?”

Authors: edited “early-divergent” to “early-diverging.” Thank you for catching an awkward wording.

(Ref 1) Line 757: Bold c1 and c2

Authors: changed. Thank you for catching this inconsistency.

(Ref 1) Line 763: Add “of ‘un-named docodont’ SDUST-V0007”

Authors: changed.

(Ref 1) Line 765: Remove “of un-named docodont”

Authors: changed.

(Ref 1) Line 766: Add “ ‘platypus’ Ornithorhynchus”

Authors: changed.

(Ref 1) Line 767: Add “ ‘short-beaked echidna’ Tachyglossus”

Authors: changed.

(Ref 1) Line 774-775: “It would be good to show (in inset to Fig. 5? Or in supplementary figure?) where Docodonta fits within the broader cynodont-mammal tree, particularly with respect to Theria (since specific comparisons with crown/modern mammals are made throughout the ms).”

Authors: Figure 5 was expanded, according to this good suggestion. Thank you!

(Ref 1) Line 787: Add? “Small arrows on posterior-most haemal arches on the tail (in a and b).”

Authors: Done. Thank you for catching this inconsistency.

(Ref 1) Fig. S8e: Correct spelling of “Docoforssor (Docofossor) in figure S9

Authors: typo corrected. Thank you for catching the typo!

(Ref 1) Line 927: Insert: “unique in having/displaying/exhibiting a fully ossified sternal segment”

Authors: Thank you for catching it. It was changed, and the sentence is complete.

FROM REFEREES 2 & 3 (Profs. Rebecca German & Christopher co-reviewer)

Major Suggestion 1 (several interrelated comments)

Profs. German and co-reviewer offer very thoughtful comment/suggestion (spanning 3 paragraphs), encouraging the authors to broaden the introduction/preview of functional significance of the soft-palate-pharynx. We fully appreciate their emphasis that this system is also for respiratory airway protection (in both neonates and adults) and adult drinking (fluid swallowing), beyond swallowing of masticated food, and suckling. Their prompt is for us to balance the drinking (“fluid swallowing”), with the somewhat oversimplified “suckling-swallowing” shorthand mention, in our introductory text and functional interpretation of the ‘soft-palate-pharynx’ musculoskeletal system, in thinking about the new osteological features of *Megacauda*.

Authors: We totally agree with this insight from referees. “Suckling-swallowing” has been a tight focus by previous functional interpretations. This “single-mindedness” was constrained by the fact that

teeth and jaws are well preserved in early mammal fossils and the “tooth-jaw” function was better understood. Therefore it is more tangible to focus on the masticated food in general. In revision (also mindful of Nature’s limit on word count), we added text on adult drinking and respiratory airway protection in 3 places (pp. 6 and 7, and abstract), for a more comprehensive explanation of the function.

Major Suggestion 2

Profs. German and co-reviewer suggest that we should high-light the functional inference of “soft-palate-pharyngeal muscles” by consolidating the related contents together (via their 3 related comments)

Authors’ revision: This is an excellent suggestion. We have re-arranged the texts, and consolidated the texts into two sections with differentiated subtitles “Reconstruction of pharyngeal musculoskeletal structure” and “Inference of Pharyngeal Function”. After revision, the text has a three-tier presentation:

- ➔ osteological description of bony pharyngeal vault and mesocranium
- ➔ Reconstruction of musculoskeletal structure
- ➔ Inference of pharyngeal function

Prof. Sue Hand (Ref 1) also suggested that we move the common-language explanation of the technical terms “bony pharyngeal vault” and “pharynx” to their first appearance. Thus these paragraphs are also tweaked to improve the narrative.

Line-by-Line explanation for referees 2 and 3

(Refs. 2 & 3) “While there is an extensive and historical literature on diversification of mammalian mastication, there is very little comparative and evolutionary work on adult drinking.... Hopefully this paper will spark some interest in understanding the evolution of mechanisms used for liquid transport across adults... for understanding how mammalian drinking evolved, and how much of that (=drinking) is based on that functional morphology ... of suckling.”

Authors: We fully agree with Profs. German and co-reviewer on this. Thank you for the high expectation of the future work that will grow from this!

(Refs. 2 & 3) Lines 183-187 – “there is some debate in the literature as to the prevalence of ossified stylohyals (bats, sloths, carnivores). This result supports the non-ossification as the primitive state, as well as the configuration of the ventral hyoid elements.”

Authors: We revised this sentence, in the light of the alternative wording suggested by referees

(Refs. 2 & 3) Line 203 “ Should this be the “pharyngeal vault” or just “pharynx”? Is there an anatomical or evolutionary distinction the authors are making?

Authors’ explanation: Thank you to Referees for prompting us to clarify. In this location the words “the ‘pharyngeal vault’ and pterygoid hamulus” are meant for osteological features.

We have changed this content to “the **bony** pharyngeal vault and pterygoid hamulus.” Two lines down, we have also tweaked the sentences to “**soft-tissue anatomy of the pharynx, which is the critical muscular pathway for food, liquid, and air**, for mammalian feeding and **respiration...**”. These changes clarify the term “Pharyngeal vault” refers to osteology, while the term “pharynx” refers to musculature.

Thank you for a great pointer for us to preemptively explain. This also syncs well with Prof. Hand’s suggestion to explain “pharyngeal vault” and “pharynx” at the first mention of these terms.

(Refs. 2 & 3) Line 203 “Fig 2 is well done. We appreciate that this is a paper replete with figures, however, perhaps adding a lateral view of the reconstruction of these bones would help readers understand the 3-dimensional nature of this space.” The additional supplemental figures (and video) are very useful. “

Authors’ explanation: We certainly understand why Referees suggest this. With the abundant illustrations so far our manuscript is already up to the limits imposed Nature: 5 text figs, 10 extended data figures. We will not be able to add more illustration in lateral view.

We are glad that referees 2 and 3 found the supplementary videos useful. The rotation movies Supplementary SI Video S1 already shows this. Referees can check **S1 Video: 00:34-00:59**.

Schematic illustrations from different angles for the pharyngeal musculoskeletal reconstruction of *Megacauda* will have to be done, with side-by-side illustration of *Didelphis*. This will have to be covered by another longer paper. Here we are under Nature’s format constraint (≥ 10 Ext Data Displays).

(Refs. 2 & 3) Line 274 – “As the authors say, the soft palate muscles are critical for suckling, but they are also critical for transport of liquids and masticated/triturated solids in adults (St I and St II – see Hiimeae and Crompton & lengthy comment above). “

Authors: Good comment. In revision, we expanded to include adult drinking and respiratory airway protection, for a more comprehensive explanation of functional significance, as prompted by referees.

(Refs. 2 & 3) Line 278 “– could this trough be indicated on fig 2? It is a complex figure, but it would help the reader to see this specific area (in main figures –there was more in the supplemental figures).”

Authors: It was our lapse that we did not label the pterygopalatal trough (pt-pa trough) in Fig. 2. In revision, we have now labelled both the pterygo-palatal trough (pt-pa trough) and the pterygoid-palatal ridge (pt-pa ridge) in Fig. 2.

(Refs. 2 & 3) Comments on Lines 251-292; 297-306. ” The text, starting at line 251, ‘Inference...’ is a good review of comparative anatomy. However, at line 292 – the authors bring a functional/biomechanical perspective that then carries on at line 297...Consider a **new section header** at 291/292 including the para that starts at 297 to delineate some functional capacity.”

Authors: This is an excellent suggest to improve the narrative. We have re-arranged and consolidated these texts into two sections, each with differentiated subtitles: “Reconstruction of pharyngeal musculoskeletal structure” and “Inference of Pharyngeal Function”. Thank you for a good suggestion to streamline this content, and to delineate the functional discussion by sub-header.

(Refs. 2 & 3) Under Criterion D. “...given that styloglossus, hyoglossus and palatoglossus are critical and interesting extrinsic tongue muscles for formation of the seals that permit efficient liquid transport in both infants and adults, might there be some room for some inference about them? ”

Lines 296-297 ”....that other oropharyngeal structures, such as a tongue capable of curling around a nipple and generating suction, may have been present at this time as we suggest in co-reviewer & German (citation 58)... In this section, the authors could also hypothesize about the anatomical origin/insertion of other tongue musculature data (i.e. styloglossus, palatoglossus hyoglossus).“

Authors: We appreciate the strong encouragement from Profs. German and co-reviewer, for us to discuss more about how the tongue and the muscular pharynx together, and to integrate these two. They meant well, and pushed even further for functional significance, than we had presented so far on the pharyngeal musculoskeletal system. We are grateful that Profs. German and co-reviewer have confidence in our work.

In revised text, we expanded the text to touch on that tongue muscles are required for suckling and also cited the references. We re-phrased this in this part of the text, in response to the prompt by referees. Because the main text of Nature paper is under a tight length requirement, the room to discuss this content is limited. Instead, we added a more expanded text in Supplementary Information to this effect.

FROM REFEREE 4

Major Revision

(Ref. 4) – “...These differences are maybe species-level, as supported by the results of the phylogenetic analysis, but not genus-level.... This is not convincingly a new genus (above).”

Authors Response: We welcome Referee 4’s question. It is a normal part of peer-review process on taxonomy, for referees to criticize our classification of *Megacauda* as a new genus - the onus is on us to respond and explain why the dental and skeletal differences of these fossils, and how we can justify *Megacauda* as a new genus.

The referee’s query is all reasonable, largely because of our mediocre presentation on the key character differences of *Megacauda-Castorocauda*. These differences were not illustrated in a clear way for the readers. Our graphics were separated in 2 figs. This content is haphazardly mentioned in the text, poorly linked to our formal taxonomy. We did not do a good job in making the graphics/text accessible.

The first deficiency is our lack of an illustration on Mega-Casto differences in occlusal view. Secondly, the lingual-view graphics on teeth were scattered in two separate figures – this is not reader-friendly! Likewise our text on the critical differences of Mega-vs-Casto was scattered, in supplementary information. Our interpretations were buried by a large amount of new data on other aspects of the new fossil, inconvenient for referees to pick out, and not easy for nonexpert readers to digest.

To clarify for referee 4, and more importantly to be more effective in demonstrating the Mega-Casto differences to non-expert readers, we rectified this weakness, with the following changes:

- ◆ **New Extended Data Fig. S6 & Supplementary Table 1**– the new figure has now combined (1) graphics on the *Megacauda* and *Castorocauda* differences in the ultimate premolar; (2) graphics of the Mega-n-Casto differences in m1; (3) juxtaposed lingual views of *Megacauda* and *Castorocauda* in m2-4; (4) occlusal views of *Megacauda* and *Castorocauda*, with their differences in m2-4 side-by-side. The main dental character differences labeled in this figure corresponds, vis-à-vis, to the itemized list of these character differences in Supplementary Table 1.
- ◆ **Main manuscript text is augmented with more information on dental characters:** we added a sentence (mindful of Nature’s word limit) “*Megacauda* is clearly distinguishable from *Castorocauda* in over 15 characters of the posterior lower premolars and molars (Ext. Dat. Fig S6; Supplementary Table 1), and in several skeletal characters (Fig. 1, Ext. Dat. Fig S8 and Supplementary Information).”
- ◆ **Full Diagnosis in Systematic Paleontology (SI) are expanded and reorganized** to offer a more detailed justification of *Megacauda* as a new genus and species, and its separation from *Castorocauda*:
 - **new text paragraph** on diagnostic characters separating *Megacauda* from *Castorocauda*;
 - **full list of different dental characters (SI Table 1 in red font)** of *Megacauda* vs. *Castorocauda*;
 - **a new paragraph on differences postcranial character (red font in revised SI)** of *Megacauda* vs. *Castorocauda*
- ◆ Under “**Systematic Paleontology**” in “**Locality and Stratigraphy**”, we have newly described the stratigraphical difference between the Bed 4 of the *Megacauda* Locality and Bed 9 of the *Castorocauda* Locality, in the Haifanggou Formation (using Huang et al. 2016 figures). These fossiliferous horizons are separated by 60 meters of stratigraphical section. By comparison, the whole formation has a total thickness of about 90 meters in the field outcrops in the Daohugou Museum

Locality area. In the actual outcrop, the *Megacauda* horizon (Bed 4) is near the bottom of this formation, while the *Castorocauda* horizon (Bed 9) is from the top of this formation. This is an important indication that highlights *Megacauda* to be stratigraphically much older than *Castorocauda*, within the same formation. This complements our argument *Megacauda* is a new genus because it is older geologically than *Castorocauda*, despite that both were found in the same formation.

With these efforts to improve the presentation our justification of *Megacauda* as new genus, we believe we have clarified for Referee 4.

(Ref. 4) Re: mentioning of age/developmental status of the holotypes of these taxa.

Authors: Both *M. sungei* type and *C. lutasimilis* type are fully-grown adults by age-indicating dental and dentary features. This assessment is explained in red-font text in supplementary information.

(Ref. 4) General comment that “We already know mammaliaforms grew large (Li et al. 2000; Hu et al. 2005; Ji et al. 2006)...” Likely Referee 4 meant here to refer to the body size of *Repenomamus*.

Authors: We revised to be more precise Re: “*Megacauda* had a ‘much larger body mass than other **Jurassic** mammaliaforms” (revised Lines 169-170) and “**the largest of Jurassic mammaliaforms** (abstract).” *Repenomamus* with its massive size clearly played a paleoecological role in Cretaceous Jehol biota, which is 40 ma younger than Mid-Jurassic Yanliao Biota. We clarify that the Jehol biota and the Yanliao biota are temporally separate ecosystems with iterative paleoecological patterns - our emphasis is on the latter pattern, and why docodontans is so disparate among the early-diverging mammaliaform clades.

Referee 4. Line-by-Line changes and response

(Ref. 4) Line 51 – “provides” change to “provide”

Authors: correct grammatic error, as prompted.

(Ref. 4) Line 53 – “Refs currently run from number 6 to number 15, they should be sequential in order of appearance”

Authors: We apologize for losing Refs 7-14 at this location. This likely occurred in the last round of edits before April 2026 submission. We are grateful that Ref. 4 helps to catch this!

(Ref. 4) Line 75 - change to new insights “into” (from “on”

Authors: changed as suggested by referee 4.

(Ref. 4) Line 127 - but “because” *Megacauda*

Authors: We decided to cut these two sentences out - this is to control for the length (because of Nature’s tight length limit). Thank you just the same to Referee 4 for suggesting.

(Ref. 4) Line 128 – “it is” feasible

Authors: We have cut these two sentences short, to control for the length (because of Nature’s tight length limit). Thank you just the same to Referee 4 for pointing this out, for editing

(Ref. 4) Line 218 – “the” pyramidal process

Authors: added “the”. Thank you for pointing out this omission.

(Ref. 4) Lines 337-338 – “Repetition of the previous sentence, the two should be combined.”

Authors: we eliminated the repetitive mentions of “monotremes” in these two sentences. We also shortened and simplified the second sentence. Thank you for pointing this out.

Thanks to All Referees for Their Reviews and Suggestions for Improvement

Explanation and edits re. specifics of the Manuscript (from Dr. Henry Gee's 07/28 email):

1. Please reduce the length of the title to 75 characters (with spaces) or less, so that it fits on two lines in the final layout.

Authors revision: Yes we have now shortened the title to 75 characters, exactly.

2. Please add references to the abstract (if applicable).

Authors revision: Yes we have now moved refs 1-3 into the abstract (red font).

3. The number of references should generally not exceed 60. Currently you have 85 references.

Authors revision: Yes we have now reduced the references to 60 (changed refs in red font)..

4. Please create a separate reference list for any methods references, making sure that the numbering continues from the main text references.

Authors revision: Yes we have organized Methods section, with its references 61-70 (red font).

5. Please reduce subheadings to 40 characters (with spaces) or less.

Authors revision: we shortened all subheadings – they are all 40 characters or less.

6. Please provide titles/legends for the supplementary videos.

Authors revision: we have added a title to each of the two Supplementary Videos (red font).

7. There are potential third party rights issues in the figures. Please check the sources of illustrations and clarify whether permissions are needed to adapt or reproduce them. Return the 3rd party rights table.

Authors revision: we completed Nature's 3rd party rights table, and clarified the relevant details re. permissions to adapt or reproduce them.

8. Please make sure to provide a third party rights table (more information below) when you resubmit.

Authors revision: we have now completed Nature's 3rd party rights table, and upload it

9. Please provide a data availability statement in the main text of the manuscript.

Authors revision: we have now added data availability statement (red font).

10. Please provide a competing interest statement in the main text of the manuscript.

Authors revision: we have now added a competing interest statement (red font).

11. Please provide an author contributions statement in the main text of the manuscript.

Authors revision: we have now added a detailed statement on author contributions (red font).

12. Please ensure that the text size in all figures is at least 5 pt Arial.

Authors clarification: all text labels for figures are 6pt or higher.

14. Funding section is not present, please provide it as separate section.

Authors clarification: we added a section on funding (red font).

15. The formal taxonomy of the animal must be placed in the main text, not supplementary information.

Revision: we have now added the formal taxonomy at the beginning of main-text (red font).

However, we like to explain that the Systematic Paleontology, in all its formality, requires a lot more words. Thus the Systematic Paleontology takes up 380 words! Even after we had cut 200 words elsewhere on dental characteristics, this expansion on Systematic Paleontology made our manuscript exceed, slightly, over the suggested length of 5000 words. I hope this is OK with Nature colleagues.