Peer Review File

Manuscript Title: Fossoriality and evolutionary development in two Cretaceous mammaliamorphs

Editorial Notes:

Redactions – Third Party Material

Parts of this Peer Review File have been redacted as indicated to remove third-party material.

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

General technical comment

The diagnoses are abbreviated descriptions, which is no longer an acceptable mode. Measurements are meaningless at least for the tritylodontid because these synapsids often had an impressive size range (e.g., *Kayentatherium*; Hoffman and Rowe, 2018). A proper diagnosis should clearly identify autapomorphies for the taxon. The authors might want to supplement that with a differential diagnosis in the supplementary materials.

Specific technical comments

l. 30-31 “Mammaliamorpha comprises the last common ancestor …” To say “a group” is misleading as it is “the” group.

l. 61 The name is incorrectly formed. The Latin word for “to dig” is *fodere* and the correct nomen should be “*Fossoriomanus*”.

l. 69 The root of the zygomatic arch is located at the level of the mesial postcanine in some other tritylodontids as well (see Clark and Hopson, 1985).

l. 70 The alleged presence of a sutured mandibular symphysis requires further documentation because the symphysis of all other known tritylodontids is open and mobile (unlike, for example, in gomphodont eucynodonts). Could this not be the result of the considerable post-mortem crushing of the skull? Indeed, unless *Fossoriomanus* has a masticatory cycle unlike those of related taxa a sutured symphysis is unlikely.

l. 80 The claim that the tail is short is problematical. From the photographs, it appears that the tail is incomplete, lacking its distal portion. The tail was fairly long in other tritylodontids such as *Oligokyphus* and *Kayentatherium*.

l. 81 The correct term is “phalanx”, not “phalange”.

l. 91-92 This statement is factually incorrect – see Sues & Jenkins (2006). Note the distinctive shape of the ungual phalanges in the manus and the structure of the scapular blade. The unguals have large flexor tubercles and are blade-like distally rather than conical as in other non-mammalian eucynodonts. Sues (1984) also discussed fossorial adaptations in *Kayentatherium* at greater length.

Reference: H.-D. Sues. 1984. Feeding and locomotion in the Tritylodontidae (Synapsida); pp.231–236 in F. Westphal and W.-E. Reif (eds.), Second Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Attempto Verlag, Tübingen.

l. 182-183 There should be a comment that it is difficult to distinguish between fossorial and aquatic adaptations in the postcranial skeleton as many of them are identical or at least very

similar (e.g., structure of scapula). This was previously noted by various authors including Simpson and Hildebrand. At least *Kayentatherium* was semi-aquatic based on the structure of its tail (specimen at the Texas Memorial Museum), which is nearly identical with that of the semi-aquatic docodont *Castorocauda*, and this possibility should be discussed for the new Jeholtritylodontid as well.

Referee #2 (Remarks to the Author):

This paper describes more exciting new Cretaceous mammals from the Jehol biota. It is noteworthy on that ground alone because the exquisite preservation of many components of its ancient ecosystem elevate Jehol's importance to many disciplines beyond Mesozoic paleontologists. But the two animals described in the paper are themselves unique and add important pieces to our understanding of the ecological and morphological diversity of Cretaceous mammals at the time that the crown group originated. These new taxa are presented by the authors to have been diggers (fossorial), and the evidence strongly supports this interpretation (see comments below about the fine points of this argument with regard to the skull features). Because the morphological features associated with the fossorial lifestyle are closely tied to regionalization of the axial skeleton, the authors are able to discuss the specializations in the context of Hox gene expression patterns, including the implications for expression patterns in mammaliamorphs at their time of origin. All of this makes the paper suitable for Nature.

Overall, the paper is strong and the conclusions of the authors are supported by the evidence they present. In my opinion, it can be published with only minor revision. I have made a few suggestions about wording and grammar of particular passages and have one longer comment about which features in the skull may be related to fossoriality. The authors will need to make only a few changes to address them.

Note that I am not familiar enough with the details of other Mesozoic taxa to critique the phylogenetic topology presented in the paper, other than to say that the general phylogenetic placement of the two new species seems plausible.

Line 20: insert "a" in to "possess a high presacral count"

Line 81: change "phalange" to "phalanges" or "phalanx"

Line 86: change "synapsid" to "synapsids"

Figure 4: I suggest two changes. (1) if possible, place the tip names on the tree instead of a side key. (2) change the labels from homeotic and meristic "variations" to "changes" because "variations" suggest variability within tip taxa instead of evolutionary changes between ancestral condition and tip.

Lines 183-192: I find the limb and postcranial arguments for fossoriality to be strong, but I am less convinced about the features supporting the argument that the skull was also involved in digging. Vertebrates have several digging repertoires, which were reviewed by Wake (1993) [a paper that would be useful to cite here], some of which involve the skull and others which do not. Thus, it is possible that the animal could have been fossorial without particular specializations in the skull. I am not completely convinced that the skulls of these fossils were particularly large or blunt or that the orbits were especially small because their apparent shape is so distorted by the lateral splaying of the skulls due to compression and crushing. I am also not convinced that the tiny protuberances of the nasals are indicative of using the head in burrowing.

However, there are features of the skull that do seem to be convincing indicators of fossoriality, notably the seemingly thick bone and fused sutures over the braincase and the thick occipital areas with what seem to be heavy nuchal crests. Those are strongly in keeping with at least some use of the head for moving soil (see the Wake paper).

Overall, I think your interpretation of fossoriality is correct. The forelimbs have all the hallmarks of a digger: lever arms that produce a lot of torque at the elbows and wrist, broad flat manus, robust blunt claws. The long body is typical of mammals that dig with the front of their body (either forearms, teeth, or head) and then pass the debris underneath to where they can kick it back up the tunnel with their hindlimbs, the long flexible vertebral column aiding in that through flexion and extension, and a small tail that doesn't get in the way. Compare with the body proportions of a vole, gopher, or similar animal (the important difference being that those animals use their ever-growing incisors to dig, whereas this animal was clearly more like a mole in using its forelimbs). The thick roof of the braincase and strong nuchal crest are consistent with powerful shoulders and some use of the head to compact the roof of the tunnel. Compare with the illustrations of digging mechanics of the Golden Mole in Wake's Fig. 5.6 (which come from Gasc, 1986).

I suggest reorganizing this section of the paper to foreground the limb evidence by placing it in the first paragraph. In my opinion, the forelimb is almost indisputably that of a digger. Then continue in the second paragraph with the possibility that the head was also specialized for digging in the second, highlighting the thick braincase and robust occipital region.

Line 263: wording here is awkward. Maybe, "Developmental studies of extant mammals provide the grounds for developing hypotheses about developmental processes in fossils".

Line 290-291: the word "plastic" confuses me in these two sentences. I normally think of "plastic" as meaning non-genetic variation (sensu West-Eberhard) or at very least highly variable. I think you mean the latter. If so, then you might substitute "constrained" for "restricted plastic" in line 291.

Lines 303-304: in addition to being related to potential developmental genetic controls, the proportion of thoracic to lumbar may be related to differences in locomotor/fossorial strategy. In crown mammals the thoracic region is usually rigid so the lumbar region and pelvis tend to be longer in fossorials. I wonder if that logic holds true in these animals, where the thoracic region may have been more flexible if they were not parasagittal walkers? One can imagine that in Fossiomanus with its long thoracic region. In any event, the difference in regional proportion may be an indicator of different digging habits.

Line 294: sentence structure needs attention. I think you mean "the developmental system may be phylogenetically informative".

References cited:

Wake, M. H. 1993. The skull as a locomotor organ. Pp. 197-240 in J. Hanken and B. K. Hall (eds), The Skull Vol 3, Functional and Evolutionary Mechanisms. University of Chicago Press.

Referee #3 (Remarks to the Author):

A. Summary of the key results
The manuscript by Mao et al. introduce two new taxa of mamaliamorphs (a tritylodontid and a eutriconodontid) from the Chinese Early Cretaceous. This species are very distantly related but they develop similar features (particularly in the limbs) indicative of fossorial life. This is the first

time that this kind of lifestyle is proposed for these two groups of Mesozoic mammaliamorphs. The new tritylodontids shows unexpected postcranial features such as an unordinated number of presacral vertebrae (the maximum number in any synapsid). This is the most complete skeleton of a tritylodontid described thus far and is also one of the youngest representatives of the group.

B. Originality and significance: if not novel, please include reference
This is a remarkable contribution that expands greatly our knowledge on convergent adaptation evolved in distantly related groups and also expands the record of burrowing behaviour in Mesozoic clades. It is worth to mention that burrowing is also considered a very important life style represented in the therapsids of the Late Permian and Triassic (including dicynodonts, therocephalians and non-mammaliaform cynodonts). The authors in addition offer a possible explanation of the number of presacral vertebrae and vertebral formulae after meristic and homeotic changes.

C. Data & methodology: validity of approach, quality of data, quality of presentation
I consider the presentation and analysis the data as correct. The preservation of the specimens and the supplement with ct-scaning of the specimens provides as much information as possible. There is a near full description of the material in the supplementary information that is valuable. I cannot judge the Bayesian phylogenetic tip analysis as I don't know the methodology. The parsimony analysis seems to be accurate but I did not go through the data matrix. In the context of this analysis, relationships of the groups I am more familiar with (basal cynodonts) seems correct, although the sister-group relationships of lineages that include the cynodonts Massetognathus and Probainognathus,this is Cynognathia and Probainognathia, with the latter not including Pachygenelus, brasilodontids and mammaliamorph, is not represented in most recent analyses of basal cynodonts. In any case these are just very distant taxa in relation to the target species of the work and the supports of these lineages of cynodonts are poor in recent analyses. The same can be said of the sister group relationship of brasilodontids with tritylodontids resulting from the parsimony analysis (but not from the Bayesian).
The diagnosis offered for the two taxa are different. It is clearly comparative in the case of Jueconodon but not so in the case of Fossomanus. I encourage the authors to provide a more comparative diagnosis of the tritylodontid.
D. Appropriate use of statistics and treatment of uncertainties
See my comment above about Bayesian analysis.
E. Conclusions: robustness, validity, reliability
Considering that the taxonomic identification of the two taxa is indeed correct (as the evidence for this is quite strong), then the study is robust in the sense that the lineages compared are very distant, (near) contemporaneous and the morphological adaptations appears to be interpreted in a correct way (I am not totally convinced of the skull of Fossomanus showing adaptation to fossoriality, but the limbs clearly does). Therefore conclusions will likely maintain unaltered in a long run.
F. Suggested improvements: experiments, data for possible revision
My suggestions of change are minors and they are detailed in the annotated pdfs.
I think that would be worth to mention in the main text that burrowing adaptations are pervasive in therapsids. It is known in dicynodonts, therocephalians and non-mammalian cynodonts and in those cases they develop in non-related forms just like in the Liaoning fauna.
Something that the authors leave outside and I think it is also relevant is to discuss the ontogenetic age of Fossomanus. I think that evidence of the dentition (half of the upper dentition is not exposed apparently) and of the carpal bones (mostly rounded bones) is suggestive that the specimen is quite likely a juvenile.
G. References: appropriate credit to previous work?
References are up to date. I mentioned in the pdf some others that might be relevant to quote in the supplementary section.
If the authors agree to include as part of the text the fossoriality of basal therapsid groups I will suggest them to check in this work: Fontanarrosa G., Abdala F., Kummell S., Gess R. 2019. The manus of Tetracynodon (Therapsida: Therocephalia) provides evidence for survival strategies

following the Permo-Triassic extinction. Journal of Vertebrate Paleontology 38. doi.org/10.1080/02724634.2018.1491404. There is a recent discussion on fossoriality in therapsids.
H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions
The text is mostly clear for me. There were a few cases in which the messages did not come clear and I indicated this in the pdfs. The introduction is informative and the conclusions stated clearly.

I think that this contribution is appropriated for Nature as the implications of these new species in the evolution and bahaviour of mesozoic mammalamorphs,are very important.

Referee #4 (Remarks to the Author):

This paper includes descriptions and analyses of two new mammaliamorph skeletons from the Early Cretaceous of China. Both specimens are spectacularly preserved and informative regarding both fossoriality and developmental plasticity, so the subject matter is certainly appropriate for Nature. Both fossils are well illustrated, but some of the descriptions must be clarified. There are many missing words throughout the manuscript, so it still requires copy editing. I've listed several minor revisions below.

Line 77: Be explicit about how thoracic vertebrae are being defined given the difference in the number of thoracic vertebrae and ribs here and below. Cite the supplementary information here rather than below. Add "(see Supplementary Information for definitions of the vertebral regions)" here.

Line 81: Phalanx is singular and phalanges is plural. "Phalange" is incorrectly used in the supplementary information (p. 16) as well, so it must be corrected there too.

Line 82: Although forelimb is one word, hind limb should be two words. Correct the latter throughout the main text and supplementary information.

Line 82: Digit or ray? Was the metatarsal lost too? If the metatarsal was lost, then the entire ray (not just the digit) was lost. This must be clarified here and in the supplementary information.

Line 83: Was digit V or I lost? Digit V is indicated here, but this is not consistent with the text below (line 205) or the supplementary information (p. 17) where the first digit (I) is indicated. This must be clarified.

Line 84: What is meant by "latest evolutionary stage"? This should be clarified.

Lines 136-137: Again, "(see Supplementary Information for definitions of the vertebral regions)" should be cited above when thoracic and lumbar vertebrae are first discussed (see above).

Line 152: "CL" should be defined here when this abbreviation is first used.

Line 162 and Figure 4: The fossorial adaptation square should be added to Multituberculata, and the following new paper should be cited.

Weaver, LN, Varricchio, DJ, Sargis, EJ, Chen, M, Freimuth, WJ, and Wilson Mantilla, GP. 2021. Early mammalian social behaviour revealed by multituberculates from a dinosaur nesting site. Nature Ecology & Evolution 5: 32-37.

Line 164 and Figure 4: Both new taxa should be highlighted in Figure 4 to make them easier to find in the tree.

Line 173: What does "its" refer to? If eutriconodontans, then this should be changed to "their."

Lines 179-180 and Figure 4: Again, the Fossorial adaptation square should be added to Multituberculata (see Weaver et al. 2021 in Nature Ecology & Evolution).

Line 198: "medial and lateral epicondyles" are acceptable terms, but "entepicondyle" and "ectepicondyle" are used in the Figure 3 caption and Extended Data Figure 8 labels. The terms used in the text, figure caption, and figures should all be consistent with each other.

Line 200: What is meant by "strong"? Long? Robust? Both? This must be clarified because "strong" is not clear.

Line 202: Again, what is meant by "strong"? Long? Robust? Both? This must be clarified because "strong" is not clear.

Line 205: Was the first or fifth lost? The fifth was indicated in the diagnosis on line 83 (see above). This must be clarified.

Line 205: Again, was the "digit" or ray lost? Was the metatarsal lost too? If the metatarsal was lost, then the entire ray (not just the digit) was lost. This must be clarified here and in the supplementary information.

Line 294: Replace "of phylogenetic information" with "phylogenetically informative."

Line 418: The References should all be checked carefully. For example, reference 39 is incomplete. The complete book title is "Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay."

Line 489: Replace "cervical" with "caudal" because tail, not neck, vertebrae are in the close-up views.

Line 522: Hamate is misspelled here and in the supplementary information (p. 16) as well. Trapezium is also misspelled on p. 16 of the supplementary information.

Extended Data Figure 8: Are the capitate and trapezoid correctly identified in F? They look reversed.

Extended Data Figure 8: If the authors are using human anatomical terminology like capitate, then they should also use hamate rather than unciform for consistency. In other words, if they follow Terminologia Anatomica, then capitate and hamate should be used rather than magnum and unciform. Similarly, if they choose to use unciform rather than hamate, then they should also use magnum rather than capitate for consistency.

Author Rebuttals to Initial Comments:

Referees' comments and responses (in blue):

General responses: We are grateful for the reviewers in spending time to provide us their comments, suggestions, and edits - all being constructive and helpful. Some of the issues noted by the reviewers are at least partly due to the limited capacity for the paper. Given the subjects reported in this study, we have to focus on discussion on mammaliamorphs and cite

references that are essential. In the revision, we need to further condense the text to comply with *Nature*'s guide for authors so that our revision will not expand the subject material unless it's absolutely necessary.

Reviewer #1?. The following comments were from the pdf file attached along with the editor's email. We assume these comments were from reviewer #1. Although these comments appeared more or less rushed out, we greatly appreciate them in alerting us to carefully check the points raised.

General technical comment

The diagnoses are abbreviated descriptions, which is no longer an acceptable mode. Measurements are meaningless at least for the tritylodontid because these synapsids often had an impressive size range (e.g., *Kayentatherium*; Hoffman and Rowe, 2018). A proper diagnosis should clearly identify autapomorphies for the taxon. The authors might want to supplement that with a differential diagnosis in the supplementary materials.

Along with the comment from reviewer #3, we revised the diagnoses to make it more differential. We added additional comparison in the Supplementary Information to differentiate the new taxon.

The size range of *Kayentatherium* has been discussed in previous studies (e.g., Lewis, 1986), while the work by Hoffman and Rowe (2018) focused on perinates. Nonetheless, few specimens of tritylodontids have reliable measurements of the trunk and tail sizes, and we believe the size data are useful in establishing a new taxon.

Specific technical comments

l. 30-31 "Mammaliamorpha comprises the last common ancestor …" To say "a group" is misleading as it is "the" group.

This has been changed in the process making a concise summary.

l. 61 The name is incorrectly formed. The Latin word for "to dig" is *fodere* and the correct nomen should be "*Fossoriomanus*".

The Latin word, *fossio*, is a noun, meaning digging, while *fodere* is a verb; *fossori* (noun) means digger. We believe *fossio*, in combination with *manus*, correctly reflects what we want the generic name stand for.

l. 69 The root of the zygomatic arch is located at the level of the mesial postcanine in some other tritylodontids as well (see Clark and Hopson, 1985).

The comment is correct, but the difference is that the new species has a slender zygomatic arch, contrasting the deep arch of other species.

l. 70 The alleged presence of a sutured mandibular symphysis requires further documentation because the symphysis of all other known tritylodontids is open and mobile (unlike, for example, in gomphodont eucynodonts). Could this not be the result of the considerable post-mortem crushing of the skull? Indeed, unless *Fossoriomanus* has a masticatory cycle unlike those of related taxa a sutured symphysis is unlikely.

In Extended Data Figure 2A, C, the suture at the mandibular symphysis is clearly illustrated. As we described, it is "a zigzag suture", which means two things: First, it's difficult to form such a morphology by a post-mortem crushing. Second, similar to other tritylodontids, the symphysis is not fused. The difference is between a straight "suture" in other tritylodontids and a zigzag one in the new species; the latter is used as one of the diagnostic features for the new taxon. With the zigzag suture the mandibular mobility at the symphysis could be reduced, which may be a feature for fossorial adaptation. Regardless of interpretations, the zigzag suture is real.

l. 80 The claim that the tail is short is problematical. From the photographs, it appears that the tail is incomplete, lacking its distal portion. The tail was fairly long in other tritylodontids such as *Oligokyphus* and *Kayentatherium*.

As far as we can tell from the specimen, there is no evidence suggesting incomplete preservation of the caudal vertebrae. The short tail is not only recognized by the absolute length of the tail, but also by the length of each individual caudal vertebra. In other tritylodontids, such as *Oligokyphus* and *Kayentatherium*, the body of each caudal vertebra is considerably longer than its width, whereas in *Fossiomanus*, each caudal vertebra is notably shorter than the width; this is a compelling evidence for a short tail for any given number of caudal vertebrae. We made this clearer in the revised Supplementary Information.

l. 81 The correct term is "phalanx", not "phalange".

Changed.

l. 91-92 This statement is factually incorrect – see Sues & Jenkins (2006). Note the distinctive shape of the ungual phalanges in the manus and the structure of the scapular blade. The unguals have large flexor tubercles and are blade-like distally rather than conical as in

other non-mammalian eucynodonts. Sues (1984) also discussed fossorial adaptations in *Kayentatherium* at greater length.

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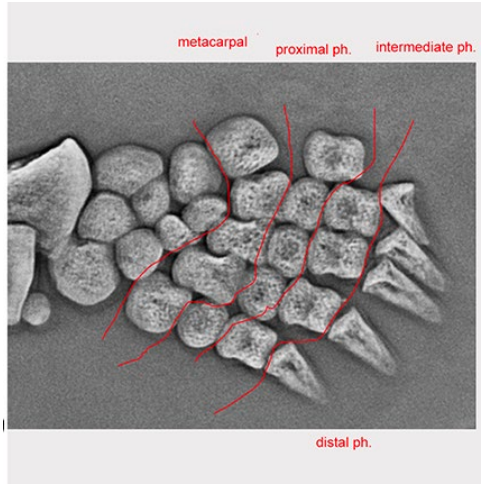
What we said was: "The long olecranon of the ulna in *Kayentatherium* was considered a fossorial feature (Sues & Jenkins, 2006), but other parts of the skeleton, such as the manus, are not so typical for fossorial adaptation." Although Sues and Jenkins described the unguals, as the reviewer mentioned, but they did not associate the manus with fossoriality. Compared the manus of *Kayentatherium* (the left one in the figure below) to that of *Fossiomanus* (on the right), the differences are obvious. For the scapula, Sues and Jenkins (2006: 144) said: "A postscapular fossa is not a universal mammalian feature. It occurs principally as a fossorial specialization (e.g., in some edentates) but also in forms with a powerful forelimb stroke (such as bears and pinnipeds) in which M. teres major, a humeral retractor, is hypertrophied. A similar functional inference may be made for the postscapular fossa of Kayentatherium." Based on the literature cited and figured morphologies in both species, our statement is accurate. Given the concern of the reviewer, we slightly reworded the sentence.

We were aware of the short paper by Sues (1984), which was more or less like an abstract. We think Sues and Jenkins (2006) is the up-to-date and data rich treatment of the subject, although it did not cite Sues (1984) either. We think we have cited the most relevant reference. [redacted]



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similar (e.g., structure of scapula). This was previously noted by various authors including Simpson and Hildebrand. At least *Kayentatherium* was semi-aquatic based on the structure of its tail (specimen at the Texas Memorial Museum), which is nearly identical with that of the

semi-aquatic docodont *Castorocauda*, and this possibility should be discussed for the new Jehol tritylodontid as well.

We are aware of some similarities between the semi-aquatic and fossorial species among Mesozoic mammals and kin. In addition to Hildebrand (1985), we also cited one of the most up-to-date studies analyzing structures and locomotion of Mesozoic mammaliamorphs (Chen and Wilson, 2015). The reviewer thought the limbs and scapula of *Kayentatherium* may indicate fossorial adaptation (see the preceding comment), but here the reviewer appears to advocate that *Kayentatherium* may be semi-aquatic animal based on caudal vertebral morphologies. Long transverse processes as one of such morphologies, for instance, can be seen in other specimens (e.g., USNM 317201 illustrated by Lewis [1986: fig. 2]). However, because *Fossiomanus* as a scratching digger is supported by skeletal evidence (recognized by other reviewers as well) and because *Kayentatherium* as a semi-aquatic animal, based on a specimen unavailable to us, was not discussed in literatures to our knowledge, discussing the possibility of *Kayentatherium* and/or *Fossiomanus* as semi-aquatic animals is beyond the scope of the current study that is restricted in length.

Referee #2 (Remarks to the Author):

This paper describes more exciting new Cretaceous mammals from the Jehol biota. It is noteworthy on that ground alone because the exquisite preservation of many components of its ancient ecosystem elevate Jehol's importance to many disciplines beyond Mesozoic paleontologists. But the two animals described in the paper are themselves unique and add important pieces to our understanding of the ecological and morphological diversity of Cretaceous mammals at the time that the crown group originated. These new taxa are presented by the authors to have been diggers (fossorial), and the evidence strongly supports this interpretation (see comments below about the fine points of this argument with regard to the skull features). Because the morphological features associated with the fossorial lifestyle are closely tied to regionalization of the axial skeleton, the authors are able to discuss the specializations in the context of Hox gene expression patterns, including the implications for expression patterns in mammaliamorphs at their time of origin. All of this makes the paper suitable for Nature.

Overall, the paper is strong and the conclusions of the authors are supported by the evidence they present. In my opinion, it can be published with only minor revision. I have made a few suggestions about wording and grammar of particular passages and have one longer comment about which features in the skull may be related to fossoriality. The authors will need to make only a few changes to address them.

Note that I am not familiar enough with the details of other Mesozoic taxa to critique the phylogenetic topology presented in the paper, other than to say that the general phylogenetic placement of the two new species seems plausible.

Line 20: insert “a” in to “possess a high presacral count”

Line 81: change “phalange” to “phalanges” or “phalanx”

Line 86: change “synapsid” to “synapsids”

All three above changed.

Figure 4: I suggest two changes. (1) if possible, place the tip names on the tree instead of a side key. (2) change the labels from homeotic and meristic “variations” to “changes” because “variations” suggest variability within tip taxa instead of evolutionary changes between ancestral condition and tip.

1. The tip names were on the original tree when the tree was generated, but we moved them to the side because the characters in the original figure are too small (smaller than font point 5 that *Nature* could accept) and too crowded to be clearly printed. So, we kept the figure as is.
2. We replaced “variations” with “changes”.

Lines 183-192: I find the limb and postcranial arguments for fossoriality to be strong, but I am less convinced about the features supporting the argument that the skull was also involved in digging. Vertebrates have several digging repertoires, which were reviewed by Wake (1993) [a paper that would be useful to cite here], some of which involve the skull and others which do not. Thus, it is possible that the animal could have been fossorial without particular specializations in the skull. I am not completely convinced that the skulls of these fossils were particularly large or blunt or that the orbits were especially small because their apparent shape is so distorted by the lateral splaying of the skulls due to compression and crushing. I am also not convinced that the tiny protuberances of the nasals are indicative of using the head in burrowing.

However, there are features of the skull that do seem to be convincing indicators of fossoriality, notably the seemingly thick bone and fused sutures over the braincase and the thick occipital areas with what seem to be heavy nuchal crests. Those are strongly in keeping with at least some use of the head for moving soil (see the Wake paper).

Overall, I think your interpretation of fossoriality is correct. The forelimbs have all the hallmarks of a digger: lever arms that produce a lot of torque at the elbows and wrist, broad flat manus, robust blunt claws. The long body is typical of mammals that dig with the front of their body (either forearms, teeth, or head) and then pass the debris underneath to where they can kick it back up the tunnel with their hindlimbs, the long flexible vertebral column aiding in that through flexion and extension, and a small tail that doesn’t get in the way. Compare with the body proportions of a vole, gopher, or similar animal (the important difference being that those animals use their ever-growing incisors to dig, whereas this animal was clearly more like a mole in using its forelimbs). The thick roof of the braincase and strong nuchal crest are consistent with powerful shoulders and some use of the head to compact the roof of the tunnel. Compare with the illustrations of digging mechanics of the Golden Mole in Wake’s Fig. 5.6 (which come

from Gasc, 1986).

I suggest reorganizing this section of the paper to foreground the limb evidence by placing it in the first paragraph. In my opinion, the forelimb is almost indisputably that of a digger. Then continue in the second paragraph with the possibility that the head was also specialized for digging in the second, highlighting the thick braincase and robust occipital region.

We appreciate the comments and suggestions. We have re-organized the text by putting the limb evidence first, added the suggested reference (Wake, 1993), and rephased the interpretation of the skull parts with a more cautious wording.

Line 263: wording here is awkward. Maybe, "Developmental studies of extant mammals provide the grounds for developing hypotheses about developmental processes in fossils".
Changed as suggested.

Line 290-291: the word "plastic" confuses me in these two sentences. I normally think of "plastic" as meaning non-genetic variation (sensu West-Eberhard) or at very least highly variable. I think you mean the latter. If so, then you might substitute "constrained" for "restricted plastic" in line 291.

We replaced "restricted" with "constrained".

Lines 303-304: in addition to being related to potential developmental genetic controls, the proportion of thoracic to lumbar may be related to differences in locomotor/fossorial strategy. In crown mammals the thoracic region is usually rigid so the lumbar region and pelvis tend to be longer in fossorials. I wonder if that logic holds true in these animals, where the thoracic region may have been more flexible if they were not parasagittal walkers? One can imagine that in Fossiomanus with its long thoracic region. In any event, the difference in regional proportion may be an indicator of different digging habits.

There may well be different reasons for why *Fossiomanus* had such a long thoracic region. We cited several studies, following lines 303-304, that identified functional/ecological factors that have potentially induced different vertebral counts, which answer the question raised by the reviewer.

Line 294: sentence structure needs attention. I think you mean "the developmental system may be phylogenetically informative".
Changed as suggested.

References cited:
Wake, M. H. 1993. The skull as a locomotor organ. Pp. 197-240 in J. Hanken and B. K. Hall

(eds), The Skull Vol 3, Functional and Evolutionary Mechanisms. University of Chicago Press.
Suggested reference cited in the revised manuscript.

Referee #3 (Remarks to the Author):

A. Summary of the key results
The manuscript by Mao et al. introduce two new taxa of mamaliamorphs (a tritylodontid and a eutriconodontid) from the Chinese Early Cretaceous. This species are very distantly related but they develop similar features (particularly in the limbs) indicative of fossorial life. This is the first time that this kind of lifestyle is proposed for these two groups of Mesozoic mammaliamorphs. The new tritylodontids shows unexpected postcranial features such as an unordinated number of presacral vertebrae (the maximum number in any synapsid). This is the most complete skeleton of a tritylodontid described thus far and is also one of the youngest representatives of the group.

B. Originality and significance: if not novel, please include reference
This is a remarkable contribution that expands greatly our knowledge on convergent adaptation evolved in distantly related groups and also expands the record of burrowing behaviour in Mesozoic clades. It is worth to mention that burrowing is also considered a very important life style represented in the therapsids of the Late Permian and Triassic (including dicynodonts, therocephalians and non-mammaliaform cynodonts). The authors in addition offer a possible explanation of the number of presacral vertebrae and vertebral formulae after meristic and homeotic changes.

C. Data & methodology: validity of approach, quality of data, quality of presentation
I consider the presentation and analysis the data as correct. The preservation of the specimens and the supplement with ct-scaning of the specimens provides as much information as possible. There is a near full description of the material in the supplementary information that is valuable. I cannot judge the Bayesian phylogenetic tip analysis as I don't know the methodology. The parsimony analysis seems to be accurate but I did not go through the data matrix. In the context of this analysis, relationships of the groups I am more familiar with (basal cynodonts) seems correct, although the sister-group relationships of lineages that include the cynodonts Massetognathus and Probainognathus,this is Cynognathia and Probainognathia, with the latter not including Pachygenelus, brasilodontids and mammaliamorph, is not represented in most recent analyses of basal cynodonts. In any case these are just very distant taxa in relation to the target species of the work and the supports of these lineages of cynodonts are poor in recent analyses. The same can be said of the sister group relationship of brasilodontids with tritylodontids resulting from the parsimony analysis (but not from the Bayesian).
The diagnosis offered for the two taxa are different. It is clearly comparative in the case of

Jueconodon but not so in the case of Fossomanus. I encourage the authors to provide a more comparative diagnosis of the tritylodontid.

We have modified the diagnosis to a more differential style for the tritylodontid *Fossiomanus*.

D. Appropriate use of statistics and treatment of uncertainties
See my comment above about Bayesian analysis.

E. Conclusions: robustness, validity, reliability
Considering that the taxonomic identification of the two taxa is indeed correct (as the evidence for this is quite strong), then the study is robust in the sense that the lineages compared are very distant, (near) contemporaneous and the morphological adaptations appears to be interpreted in a correct way (I am not totally convinced of the skull of Fossomanus showing adaptation to fossoriality, but the limbs clearly does). Therefore conclusions will likely maintain unaltered in a long run.

We have reworded the sentences describing the skull features adapting to fossoriality.

F. Suggested improvements: experiments, data for possible revision
My suggestions of change are minors and they are detailed in the annotated pdfs.
I think that would be worth to mention in the main text that burrowing adaptations are pervasive in therapsids. It is known in dicynodonts, therocephalians and non-mammalian cynodonts and in those cases they develop in non-related forms just like in the Liaoning fauna.

We were aware of the references related to non-mammaliamorph synapsids, but we think for the purpose of this study, the study by Kümmell et al., 2020, which we cited, is more relevant and up-to-date. We cannot expand to text to just mention other relevant forms and back the mention with additional references. With the reviewer's suggestion, we mentioned the fossorial adaptation of non-mammalian cynodonts and cited proper papers in the Supplementary Information.

Something that the authors leave outside and I think it is also relevant is to discuss the ontogenetic age of Fossomanus. I think that evidence of the dentition (half of the upper dentition is not exposed apparently) and of the carpal bones (mostly rounded bones) is suggestive that the specimen is quite likely a juvenile.

The tooth eruption in tritylodontids is sequential so that the distal ones push forward to replace the mesial ones, and the mesial ones shed after worn. So, in different species, only five or six are erupted and functional while the distal ones are forming in the bone in a continuous sequence. Our CT rendered dentition includes the erupted one, which bear considerable tooth wear, and those still contained in the maxilla; this is certainly not an

indicator of a juvenile individual. Given the reviewer's concern, we explained this in more detail in the Supplementary Information to clarify the tooth eruption condition and make it clear that this is not a juvenile individual. The carpal bones are primitively less delimited by contact facets, a common primitive condition is many non-mammaliamorph cynodonts, as shown in Kümmell et al. (2020).

G. References: appropriate credit to previous work?
References are up to date. I mentioned in the pdf some others that might be relevant to quote in the supplementary section.
If the authors agree to include as part of the text the fossoriality of basal therapsid groups I will suggest them to check in this work:

Fontanarrosa G., Abdala F., Kummell S., Gess R. 2019. The manus of Tetracynodon (Therapsida: Therocephalia) provides evidence for survival strategies following the Permo-Triassic extinction. Journal of Vertebrate Paleontology 38.

doi.org/10.1080/02724634.2018.1491404. There is a recent discussion on fossoriality in therapsids.
We cited Fontanarrosa et al. (2019) and several others in the Supplementary Information.

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

The text is mostly clear for me. There were a few cases in which the messages did not come clear and I indicated this in the pdfs. The introduction is informative and the conclusions stated clearly.
I think that this contribution is appropriated for Nature as the implications of these new species in the evolution and bahaviour of mesozoic mammalamorphs,are very important.
The reviewer also left some comments in the annotated pdf files of the manuscript. We have incorporated the comments into the revised manuscript and made changes wherever necessary. We greatly appreciate all the helpful and constructive comments and the time the reviewer spent.

Referee #4 (Remarks to the Author):

This paper includes descriptions and analyses of two new mammaliamorph skeletons from the Early Cretaceous of China. Both specimens are spectacularly preserved and informative regarding both fossoriality and developmental plasticity, so the subject matter is certainly appropriate for Nature. Both fossils are well illustrated, but some of the descriptions must be clarified. There are many missing words throughout the manuscript, so it still requires copy editing. I've listed several minor revisions below.

Line 77: Be explicit about how thoracic vertebrae are being defined given the difference in the number of thoracic vertebrae and ribs here and below. Cite the supplementary information here rather than below. Add "(see Supplementary Information for definitions of the vertebral regions)" here.
Changed as suggested.

Line 81: Phalanx is singular and phalanges is plural. "Phalange" is incorrectly used in the supplementary information (p. 16) as well, so it must be corrected there too.
Changed.

Line 82: Although forelimb is one word, hind limb should be two words. Correct the latter throughout the main text and supplementary information.
Changed.

Line 82: Digit or ray? Was the metatarsal lost too? If the metatarsal was lost, then the entire ray (not just the digit) was lost. This must be clarified here and in the supplementary information.

A good catch! This should be a ray. Changed in the main text and clarified in the SI.

Line 83: Was digit V or I lost? Digit V is indicated here, but this is not consistent with the text below (line 205) or the supplementary information (p. 17) where the first digit (I) is indicated. This must be clarified.

It is ray-I that had been lost. Corrected.

Line 84: What is meant by "latest evolutionary stage"? This should be clarified.

In recent years, the Jehol Biota was considered to have three evolutionary stages. For instance, one study we cited (Yang et al., 2020) stated: "The Jehol Biota experienced early, middle, and late stages of evolution, which were correlated to the fossil assemblages from the Dabeigou, Yixian, and Jiufotang formations, respectively (33, 34)." We have directed the reader to the Supplementary Information for reference. With the concern of the reviewer, we further detailed this point in the Supplementary Information, but we felt it is unnecessary to elaborate this in the main text.

Lines 136-137: Again, "(see Supplementary Information for definitions of the vertebral regions)" should be cited above when thoracic and lumbar vertebrae are first discussed (see above).
Changed.

Line 152: “CL” should be defined here when this abbreviation is first used.
Defined.

Line 162 and Figure 4: The fossorial adaptation square should be added to Multituberculata, and the following new paper should be cited.

Weaver, LN, Varricchio, DJ, Sargis, EJ, Chen, M, Freimuth, WJ, and Wilson Mantilla, GP. 2021. Early mammalian social behaviour revealed by multituberculates from a dinosaur nesting site. Nature Ecology & Evolution 5: 32-37.

We were unaware of this work when we submitted our work; we added it in the revised manuscript. However, we cited the paper in the Supplementary Information, not in the main text, for the reason that we are out of the reference limit. In. the figure caption, we direct the reader to the SI where we proved the relevant references.

Line 164 and Figure 4: Both new taxa should be highlighted in Figure 4 to make them easier to find in the tree.
New taxon names high-lighted.

Line 173: What does “its” refer to? If eutriconodontans, then this should be changed to “their.”
Changed.

Lines 179-180 and Figure 4: Again, the Fossorial adaptation square should be added to Multituberculata (see Weaver et al. 2021 in Nature Ecology & Evolution).

Added.

Line 198: “medial and lateral epicondyles” are acceptable terms, but “entepicondyle” and “ectepicondyle” are used in the Figure 3 caption and Extended Data Figure 8 labels. The terms used in the text, figure caption, and figures should all be consistent with each other.
We changed “medial and lateral epicondyles” to “entepicondyle and ectepicondyle”.

Line 200: What is meant by “strong”? Long? Robust? Both? This must be clarified because “strong” is not clear.

We changed “strong” to “long”,

Line 202: Again, what is meant by “strong”? Long? Robust? Both? This must be clarified because “strong” is not clear.
We changed “strong” to “robust”.

Line 205: Was the first or fifth lost? The fifth was indicated in the diagnosis on line 83 (see above). This must be clarified.

It is the first ray that got lost, as we responded above.

Line 205: Again, was the "digit" or ray lost? Was the metatarsal lost too? If the metatarsal was lost, then the entire ray (not just the digit) was lost. This must be clarified here and in the supplementary information.

It is the first ray that was lost – it is consistently stated now in the main text and Supplementary Information.

Line 294: Replace "of phylogenetic information" with "phylogenetically informative."
Changed.

Line 418: The References should all be checked carefully. For example, reference 39 is incomplete. The complete book title is "Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay."
Book title corrected.

Line 489: Replace "cervical" with "caudal" because tail, not neck, vertebrae are in the close-up views.
Changed.

Line 522: Hamate is misspelled here and in the supplementary information (p. 16) as well. Trapezium is also misspelled on p. 16 of the supplementary information.

Spelling corrected.

Extended Data Figure 8: Are the capitate and trapezoid correctly identified in F? They look reversed.
It is indeed mis-labelled, and now corrected.

Extended Data Figure 8: If the authors are using human anatomical terminology like capitate, then they should also use hamate rather than unciform for consistency. In other words, if they follow Terminologia Anatomica, then capitate and hamate should be used rather than magnum and unciform. Similarly, if they choose to use unciform rather than hamate, then they should also use magnum rather than capitate for consistency.

We have replaced unciform with hamate in Extended Data Figure 8.

The reviewer also left some comments in the pdf file of the Supplementary Information. We have incorporated those comments in the revised Supplementary Information.