nature research

Peer Review File

Manuscript Title: Enigmatic dinosaur precursors bridge the gap to the origin of Pterosauria

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:

Referee #1 (Remarks to the Author):

The authors propose a new sister group of pterosaurs, one of the most unusual vertebrates groups to ever evolve, whose origins (both phylogenetic and how they acquired flight) have been the subject of considerable debate. Their analyses, which include new fossils and new CT data, place lagerpetids as the closest pterosaur relatives. Previously these small archosaurs were one node over on the family tree, as the earliest dinosauromorphs (sister taxon to more derived dinosauriforms). It is a small move on the phylogeny, but it has larger implications.

This is strong, scrupulous, admirable work, and an example of how to do phylogenetic analysis right. In my view, this is the best study of early archosaur and 'stem-dinosaur' relationships yet attempted, as it builds on previous important phylogenetic work by some of the authors (notably Ezcurra's PhD thesis dataset and Nesbitt and team's work on North American lagerpetids), adds new taxa and characters, and produces a dataset that the authors then analyse not only by parsimony but also with the latest Bayesian techniques (the Bayesian work is fantastic). The results are convincing. The weight of current evidence strongly groups lagerpetids with pterosaurs, and not closer to dinosaurs. With their analyses, their description of characters, and their figures, the authors have done a highly credible job of making this link, and I am confident that it is the best hypothesis.

I find myself comparing this study to another recent Nature paper 'shaking up' the base of the archosaur family tree [Redacted]. Although the exact aims were different, this current manuscript eclipses that earlier study in every way: the quality of the character data, the scrupulousness of describing and figuring synapomorphies, and the care in using multiple phylogenetic methods to test the robustness of results. The authors must be commended for this. It is impressive.

What the new pterosaur-lagerpetid result does is provide a search image for where to look in the fossil record for additional evidence on pterosaur origins. What it doesn't do, yet, is shed light on the fundamental questions of how pterosaurs developed their unique body plan and through which intermediate stages or selective regimes they became the first vertebrates to achieve powered flight. Although lagerpetids and pterosaurs share many synapomorphies that link them on the phylogeny, lagerpetids do not—as of yet—show any signs of forelimb modifications related to flight, or other body plan modifications hinting at aerial behaviour. The new relationship also only partially fills the long ghost lineage of early pterosaur evolution. This is no fault of the authors; the transitional fossils don't exist yet. In that sense, I don't know if I'd call the lagerpetid-pterosaur link 'revolutionary', although I understand we all need to occasionally use such language in Nature papers! It reminds me of the debate on bat origins. Phylogenetic work puts bats among the laurasiatheres, so we know what their closest relatives are. But we're still missing the transitional

fossils telling us how bats changed from a terrestrial animal into a flier. The fossil record, c'est la vie.

The CT data on ear labryinths and the flocculus is intriguing and very welcome, providing important new insight into the senses of lagerpetids. This is the one part of the anatomy of lagerpetids that *might* give insight into the origin of flight. But there are some uncertainties. There do seem to be similarities between lagerpetids and pterosaurs (large flocculus and tall labyrinth with a tall and arching anterior canal), but I'm not yet convinced these are synapomorphic, or tell us much about the origin of flight. First, when labyrinth shape data is used as a phylogenetic character on its own, the resulting trees do not group lagerpetids and pterosaurs based on synapomorphic shapes, regardless of which taxon is used to root the tree (extended data figures 9-10). Instead, there seems to be considerable convergence between many basal archosaur groups, including some early dinosaurs that have similar ear shapes. Second, it is known that many different behaviours affect flocculus size and ear shape; both are likely related to agility in general, rather than flight specifically, and the work of Walsh and colleagues has recently argued that there isn't much ecological or behavioural signal in flocculus size. Therefore, even if pterosaurs and lagerpetids had similar flocculus and ear shapes, it might simply be because both were agile animals and not because lagerpetids were showing 'pre-adaptations' for flight. Previous workers have described lagerpetids as highly mobile, perhaps hopping animals. Might this be why they have a large flocculus and looping semicircular canals? There's also the issue that only two pterosaurs—both derived Jurassic taxa that lived more than 50 million years after the ancestral pterosaurs—are included in the ear dataset. Again, c'est la vie: the earliest pterosaurs don't preserve these regions in 3D, so the authors have done all they can—which is already the best analysis of ear shape in early archosaurs yet attempted, worthy of publication in its own right. But this sampling issue does increase the probability of convergence and long-branch attraction making the ear shapes of lagerpetids and pterosaurs similar—if indeed they *are* uniquely similar to each other. I think the authors should augment this section of the manuscript: make it clear what lagerpetids and pterosaurs actually share uniquely, either in a phylogenetic sense or using a non-phylogenetic shape morphospace, and discuss convergences and behavioural implications in more detail. Tricky with the limited space available, I know.

To conclude, I'm ready to crown lagerpetids as the closest (known) extinct relatives to pterosaurs, would like more detailed discussion of the ear and brain features, and await the discovery of a lagerpetid with long arms and other forelimb features that can help understand the origin of pterosaur flight. I think these fossils will be found before too long, and some of the authors of this paper will probably be the people to find them. Good luck!

Referee #2 (Remarks to the Author):

I have reviewed many manuscripts for NATURE and other top journals over the years, and in summary I will say that this is the most interesting and important in my experience.

Powered flight (we are reminded tirelessly in reviews and popular presentations) evolved only three times in vertebrates. Of the Pterosaurs, who first evolved it, we know the least. This manuscript establishes that pterosaurs evolved from small bipedal Triassic archosaurs related to dinosauromorphs, and shows that these animals already had the basis of the neuromuscular system that characterizes flying animals. Although the functional problems of the phylogenetic evolution of flight are not solved here, this is not the problem of the present manuscript. What we have is a strong demonstration of why pterosaurs are a major clade of archosaurs related to dinosaurs, and why a very interesting and elusive clade of Triassic archosaurs (lagerpetids) are their closest relatives. The features of lagerpetids provide huge clues to the origin of flight in pterosaurs at the very least by eliminating the putative distribution of features supporting hypotheses to the contrary. This manuscript also puts paid to some fantastical alternative phylogenies [Redacted]. And it lays the foundation for future studies of the mosaic evolution of

flight-related adaptations in pterosaurs.

It's not just this. Evolving powered flight is one of the biggest bugaboos that creationists lob at science. No transitional forms or features, they say. Well, here you are, honeys. This paper can be a major assault on anti-science, anti-methods. Agreed that the authors have not attempted the functional-evolutionary questions. That is not their remit. Any more than one can reproach a paper on cancerous anatomy without complaining that the cause of cancer was not solved.

This is a great contribution and I hope it will be treated as such.

Referee #3 (Remarks to the Author):

The origin of pterosaurs is poorly understood and any progress towards resolving their broader relationships can be a significant advance. This manuscript presents new information in the form of additional material of lagerpetids and new phylogenetic analyses to outline a new hypothesis for the origin of pterosaurs. I congratulate the authors on a very interesting idea: I found the arguments quite intriguing. Certainly the hypothesis is deserving of greater scrutiny and I would very much like to see the results of their work published.

While this is novel research, the same relationship was at least hinted at in the recent description of Kongonophon so this manuscript seems to be the logical next stage in marshalling these ideas together. As such this is a step change, but perhaps not a significant leap forward towards a better understanding of the early evolution of pterosaurs.

I did not feel that the evidence was presented in as compelling and coherent a fashion as might have been. Having set the scene in the opening two paragraphs, lines 93 – 120 lacked a clear narrative. The text rather jumps into the details of the various taxa without giving any background and I felt that the concepts are not particularly well presented. I believe for the non-specialist this is going to be rather hard to understand and follow. At the outset some clearer signposting of which taxa are the lagerpetids and which the early pterosaurs would help to really focus the arguments. At this point in the narrative there is no clear indication of what Ixalerpeton is currently considered to be. Why should the reader worry that Ixalerpeton has a well-developed antorbital fossa? Adding to these issues of clarity, figures 1 and 2 are also very busy and difficult to readily decipher, particularly in designating particular taxa to the individual elements. I am not sure of the value of all the elements in each figure as currently presented. For example, in fig 1a it is very difficult to determine the key features of the partial skull roof, or in fig. 1k what does the scale model of the partial maxilla purport to show? What is the reconstructed skeleton based upon? I also failed to see how it was contributing to a clearer understanding of the hypothesis. Including both Ixalerpeton (fig. 1q,r,s) and Lagerpeton pelvic elements in these two figures doesn't seem to be making the best use of the limited space. As a consequence, I think the main points the authors are trying to make can be quite easily lost. I appreciate that it is the cumulative evidence from all the different characters that is important to the main argument, but I feel that it might be better to do a good job of highlighting fewer of these in the main figures. Perhaps the remaining detail could be moved to the Supplementary data?

The authors have cast their net wide in making their comparisons and this is an appropriate approach. The consideration of tanystropheids is important here, although it is unfortunate that the authors are in some ways forced to give credence to the concepts as presented by Peters. That, of course, is in no way the fault of the current authors. Likewise Scleromochlus was also partly considered. Obviously this is difficult to include as the interpretation of the individual elements in the various specimens are very controversial. Even so, I wonder if the different interpretations and subsequent different scorings were considered? I am not asking the authors to provide any more detail at this stage though.

Looking at the individual characters in a bit more detail, it is possible to break down some of the lines of evidence and counteract them bit by bit. For instance, the authors do admit that the absence of both a posterior groove on the astragalus and a calcaneal tuber while shared by pterosaurs and lagerpetids, presumably independently arose in silesaurids and some early dinosaurs.

The lack of interdental plates in both groups is suggestive, but again loss of a feature is somewhat equivocal, particularly when there are one or two instances of this in other Triassic archosauriforms.

The nature of the puboischiatic plate is cited as another similarity between lagerpetids and basal pterosaurs, (fig, 2h and i). While I agree there is a deep contact between pubis and ischium, I wonder how different the lagerpetid condition is from, say, the allokotosaur Pamelaria? For me it is not so dissimilar from Lagerpeton as illustrated in fig. 2h.

I also question the putative deltopectoral crest similarity. Yes it is enlarged in lagerpetids but does not lie in the same proximal position as in pterosaurs.
Some of the other characters such as the tooth count and morphology, and the anterior shape and edentulous nature of the anterior dentary could be linked to similarities in diet rather than indicators of phylogenetic closeness.

As I have already said, I do accept that it is the overall body of evidence taken together that is important but it would be more compelling if there were one or two really convincing features and for me the authors have not highlighted anything in particular.

I found the manuscript mostly free from typos and errors of grammar, but I was intrigued by the term in l.65 "lateralized" glenoid fossa. What kind of word is this? Can any noun be verbed?

In summary, this is a very interesting hypothesis that deserves to be published, but I think it can be presented in a more compelling way.

Author Rebuttals to Initial Comments:

Referee #1 (Remarks to the Author):

What the new pterosaur-lagerpetid result does is provide a search image for where to look in the fossil record for additional evidence on pterosaur origins. What it doesn't do, yet, is shed light on the fundamental questions of how pterosaurs developed their unique body plan and through which intermediate stages or selective regimes they became the first vertebrates to achieve powered flight. Although lagerpetids and pterosaurs share many synapomorphies that link them on the phylogeny, lagerpetids do not—as of yet—show any signs of forelimb modifications related to flight, or other body plan modifications hinting at aerial behaviour. The new relationship also only partially fills the long ghost lineage of early pterosaur evolution. This is no fault of the authors; the transitional fossils don't exist yet. In that sense, I don't know if I'd call the lagerpetid-pterosaur link 'revolutionary', although I understand we all need to occasionally use such language in Nature papers! It reminds me of the debate on bat origins. Phylogenetic work puts bats among the laurasiatheres, so we know what their closest relatives are. But we're still missing the transitional fossils telling us how bats changed from a terrestrial animal into a flier. The fossil record, c'est la vie.

We have deleted the word ‘revolutionary’ to address the reviewer’s comment.

The CT data on ear labryinths and the flocculus is intriguing and very welcome, providing important new insight into the senses of lagerpetids. This is the one part of the anatomy of lagerpetids that *might* give insight into the origin of flight. But there are some uncertainties. There do seem to be similarities between lagerpetids and pterosaurs (large flocculus and tall labyrinth with a tall and arching anterior canal), but I’m not yet convinced these are synapomorphic, or tell us much about the origin of flight. First, when labyrinth shape data is used as a phylogenetic character on its own, the resulting trees do not group lagerpetids and pterosaurs based on synapomorphic shapes, regardless of which taxon is used to root the tree (extended data figures 9-10). Instead, there seems to be considerable convergence between many basal archosaur groups, including some early dinosaurs that have similar ear shapes. Second, it is known that many different behaviours affect flocculus size and ear shape; both are likely related to agility in general, rather than flight specifically, and the work of Walsh and colleagues has recently argued that there isn’t much ecological or behavioural signal in flocculus size. Therefore, even if pterosaurs and lagerpetids had similar flocculus and ear shapes, it might simply be because both were agile animals and not because lagerpetids were showing ‘pre-adaptations’ for flight. Previous workers have described lagerpetids as highly mobile, perhaps hopping animals. Might this be why they have a large flocculus and looping semicircular canals? There’s also the issue that only two pterosaurs—both derived Jurassic taxa that lived more than 50 million years after the ancestral pterosaurs—are included in the ear dataset. Again, c’est la vie: the earliest pterosaurs don’t preserve these regions in 3D, so the authors have done all they can—which is already the best analysis of ear shape in early archosaurs yet attempted, worthy of publication in its own right. But this sampling issue does increase the probability of convergence and long-branch attraction making the ear shapes of lagerpetids and pterosaurs similar—if indeed they *are* uniquely similar to each other. I think the authors should augment this section of the manuscript: make it clear what lagerpetids and pterosaurs actually share uniquely, either in a phylogenetic sense or using a non-phylogenetic shape morphospace, and discuss convergences and behavioural implications in more detail. Tricky with the limited space available, I know.

To conclude, I’m ready to crown lagerpetids as the closest (known) extinct relatives to pterosaurs, would like more detailed discussion of the ear and brain features, and await the discovery of a lagerpetid with long arms and other forelimb features that can help understand the origin of pterosaur flight. I think these fossils will be found before too long, and some of the authors of this paper will probably be the people to find them. Good luck!

We agree with the reviewer and recognize the uncertainties about phylogenetic signal. To examine the information in another way, we have generated a morphospace of the semicircular canals (SCCs) of the labyrinth using a Principal Components Analysis based on the 3D morphometric geometric data. In this morphospace, we recovered the SCCs of lagerpetids and pterosaurs close to one another (PC1 is plotted against PC2; what explains more than 50% of the variation in SCCs geometry), occupying a region of the morphospace distinct from that of other archosaurs. We have modified the text to describe, first, the morphology of the inner ear of lagerpetids and pterosaurs, which is unique among archosaurs and represents a non-homoplastic synapomorphy of

Pterosauromorpha (Lagerpetidae + Pterosauria). Subsequently, we describe the degree of curvature of the anterior semicircular canal (ASC) of the inner ear, which is also a synapomorphy of Pterosauromorpha, but has appeared convergently in at least one early saurischian dinosaur. Finally, we discuss the behavioural implications of the increased ASC curvature radius of lagerpetids and its implications in pterosauromorph evolution.

Referee #3 (Remarks to the Author):

While this is novel research, the same relationship was at least hinted at in the recent description of *Kongonaphon* so this manuscript seems to be the logical next stage in marshalling these ideas together. As such this is a step change, but perhaps not a significant leap forward towards a better understanding of the early evolution of pterosaurs.

We would like to point out that our manuscript is the result of a research project completely independent to that of *Kongonaphon*. Indeed, our analyses are based on a much more complete phylogenetic matrix than the one that was used in the *Kongonaphon* paper (e.g. we are including a comprehensive sample of Triassic pterosaurs) and we recovered the results that we report here (a pterosaur + lagerpetid clade) before the publication of this new lagerpetid taxon and its inclusion in our dataset. *Kongonaphon* is too incomplete to allow drawing the same conclusions we did here and the phylogenetic matrix produced a pterosaur + lagerpetid clade only in some of the alternative optimal trees (the other ones show the typical position of lagerpetids closer to dinosaurs than to pterosaurs). Indeed, this is stressed by the authors of the *Kongonaphon* paper (Kammerer et al., 2020: page 3), stating that it is "based on very limited evidence" and "the support for lagerpetids-as-pterosauromorphs generally is weak and rendered problematic by extensive missing data for the majority of lagerpetid taxa. More complete and better-preserved specimens are needed to further test the position of Lagerpetidae in avemetatarsalian phylogeny. At present, we consider their placement equivocal…". Thus, we have independently found more complete evidence that allows recovering a robust position for lagerpetids in the early pan-avian phylogeny and bridging the gap between the highly specialized pterosaur body plan and that of other archosauromorphs.

I did not feel that the evidence was presented in as compelling and coherent a fashion as might have been. Having set the scene in the opening two paragraphs, lines 93 – 120 lacked a clear narrative. The text rather jumps into the details of the various taxa without giving any background and I felt that the concepts are not particularly well presented. I believe for the non-specialist this is going to be rather hard to understand and follow. At the outset some clearer signposting of which taxa are the lagerpetids and which the early pterosaurs would help to really focus the arguments. At this point in the narrative there is no clear indication of what Ixalerpeton is currently considered to be. Why should the reader worry that Ixalerpeton has a well-developed antorbital fossa?

We thank the reviewer for this constructive observation. We have modified the beginning of that paragraph to give a general statement of the lagerpetid body plan, list currently valid lagerpetid taxa, and explain why we are describing some aspects of the lagerpetid anatomy and why we are comparing them mainly with early pterosaurs: "Lagerpetids are small to medium-sized (usually

below 1 meter long), gracile and cursorial reptiles known from Middle-Upper Triassic rocks of South and North America and Madagascar[23,24]. Previous knowledge of lagerpetid anatomy was mostly limited to vertebrae, hindlimbs, and a few cranial bones. Our new data are based on improved observations across the entire skeleton, plus the neuroanatomy, of multiple lagerpetid taxa (*Lagerpeton*, *Ixalerpeton*, *Kongonaphon*, *Dromomeron* spp.; Fig. 1), which inform on their relationship to pterosaurs (Fig. 2)".

We have also removed a few sentences of these paragraphs because they were describing features (e.g. presence of a maxillary antorbital fossa in *Ixalerpeton*) that were not directly related in the phylogenetic relationship of lagerpetids to pterosaurs.

Adding to these issues of clarity, figures 1 and 2 are also very busy and difficult to readily decipher, particularly in designating particular taxa to the individual elements. I am not sure of the value of all the elements in each figure as currently presented. For example, in fig 1a it is very difficult to determine the key features of the partial skull roof, or in fig. 1k what does the scale model of the partial maxilla purport to show? What is the reconstructed skeleton based upon? I also failed to see how it was contributing to a clearer understanding of the hypothesis. Including both Ixalerpeton (fig. 1q,r,s) and Lagerpeton pelvic elements in these two figures doesn't seem to be making the best use of the limited space. As a consequence, I think the main points the authors are trying to make can be quite easily lost. I appreciate that it is the cumulative evidence from all the different characters that is important to the main argument, but I feel that it might be better to do a good job of highlighting fewer of these in the main figures. Perhaps the remaining detail could be moved to the Supplementary data?

We have removed some images from Figures 1 and 2 and moved some others to a new Extended Data Figure 3 (we have merged together the original Extended Data Figures 3 and 4). Now, figures 1 and 2 are less crowded, giving us the opportunity to enlarge some relatively small images that show phylogenetically important features. For example, we have moved the partial skull of *Dromomeron gregorii* (originally in fig. 1a) and the hemipelves of *Lagerpeton* and *Dimorphodon* (originally in fig. 2h, i) to the new extended data figure. We have also removed the images of the cervical, sacral and caudal vertebrae of *Ixalerpeton* from figure 1 because they were not informing on the phylogenetic affinities between lagerpetids and pterosaurs. Overall, we think that figures 1 and 2 are now more readable and they haven't lost relevant information for the main goal of this manuscript.

The authors have cast their net wide in making their comparisons and this is an appropriate approach. The consideration of tanystropheids is important here, although it is unfortunate that the authors are in some ways forced to give credence to the concepts as presented by Peters. That, of course, is in no way the fault of the current authors. Likewise Scleromochlus was also partly considered. Obviously this is difficult to include as the interpretation of the individual elements in the various specimens are very controversial. Even so, I wonder if the different interpretations and subsequent different scorings were considered? I am not asking the authors to provide any more detail at this stage though.

We considered alternative interpretations at the time of scoring these problematic taxa, but we ultimately based the scorings on our personal, first-hand observations of the specimens (based on the independent observations of two or more co-authors). In particular, we have tried to be as conservative as possible in the case of scoring *Scleromochlus*; when a character-scoring has been matter of intense debate, we have opted to score it as a question mark. Despite this conservative approach, which inflates the amount of missing data, the phylogenetic position recovered for *Scleromochlus* is relatively robust and consistent with our character observations and optimizations.

Looking at the individual characters in a bit more detail, it is possible to break down some of the lines of evidence and counteract them bit by bit. For instance, the authors do admit that the absence of both a posterior groove on the astragalus and a calcaneal tuber while shared by pterosaurs and lagerpetids, presumably independently arose in silesaurids and some early dinosaurs.

Previous authors have described the presence of extensive homoplasy along the early evolution of Archosauria (Nesbitt, 2011; Ezcurra, 2016) and, as a result, we have tried to give honest statements about the presence of convergences between apomorphies of Pterosauromorpha and other archosaur groups, mainly dinosaurs and their most immediate relatives (silesaurids). The interpretation of these similarities as synapomorphies or convergences is based on the results of our phylogenetic analyses, but the presence of homoplasy is not evidence to disprove our hypothesis. For example, pterosauromorphs, silesaurids, and dinosaurs lack a posterior groove and a calcaneal tuber on the proximal tarsus. However, there are several taxa in the early pan-avian phylogeny that retain both features, showing that it is more parsimonious to interpret that the loss of these conditions occurred independently three times in the clade. This latter inference is based on the analysis of the other c. 800 characters. Ultimately, character construction and coding are hypotheses of homology that are tested via phylogenetic analyses of the entire dataset – that, after all, is the power of modern phylogenetic inference. We have conducted the so far most comprehensive analysis to test pterosaur relationships. Our analyses recover these character states as homologous apomorphies that indicate an exclusive common ancestry between pterosaurs and lagerpetids.

The lack of interdental plates in both groups is suggestive, but again loss of a feature is somewhat equivocal, particularly when there are one or two instances of this in other Triassic archosauriforms.

The loss of interdental plates occurred a few times in archosauriforms (e.g. pterosauromorphs and ornithischians), but this part of the tree of life comprises more than 400 currently valid species. Some degree of homoplasy, in a clade where homoplasy is common (see above), is to be expected. Nevertheless, our analysis shows that the absence of interdental plates is synapomorphic for pterosauromorphs among early archosaurs.

The nature of the puboischiatic plate is cited as another similarity between lagerpetids and basal pterosaurs, (fig, 2h and i). While I agree there is a deep contact between pubis and ischium, I wonder how different the lagerpetid condition is from, say, the allokotosaur *Pamelaria*? For me it is not so dissimilar from Lagerpeton as illustrated in fig. 2h.

The presence of such ventrally extended puboischiatic plate is plesiomorphic for Archosauromorpha and it seems to have been retained by most non-archosauriform archosauromorphs (including *Trilophosaurus*, a close relative of *Pamelaria*, although the latter taxon has a more dorsally restricted puboischiatic contact) and proterosuchids. However, the contact between pubis and ischium becomes more dorsally restricted within Archosauriformes and it is strongly restricted at the base of Archosauria. There are several taxa showing a rather stepwise series of transformations between the ancestral archosauromorph condition and that of archosaurs. As a result, the presence of such a ventrally extended puboischiatic plate in lagerpetids and pterosaurs, resembling the condition in the earliest archosauromorphs, is optimized by the phylogenetic analysis as an apomorphic reversal supporting the pterosauromorph clade.

I also question the putative deltopectoral crest similarity. Yes it is enlarged in lagerpetids but does not lie in the same proximal position as in pterosaurs.

We haven't proposed that the shape and size of the deltopectoral crest of lagerpetids is similar to those of pterosaurs. Indeed, the deltopectoral crest of lagerpetids is very similar to that of other early pan-avians.

Some of the other characters such as the tooth count and morphology, and the anterior shape and edentulous nature of the anterior dentary could be linked to similarities in diet rather than indicators of phylogenetic closeness.

It is true that these characters are very likely linked to diet, but this is not a reason to consider them potentially phylogenetically uninformative. Indeed, some dental features, such as the presence of multicusped tooth crowns, are very rare among archosauromorphs, but occur in both lagerpetids and most Triassic pterosaurs. Additionally, the combination of an edentulous and tapering anterior end of dentary, procumbent first dentary tooth, and multicusped tooth crowns is unique to lagerpetids and Triassic pterosaurs (e.g. *Seazzadactylus*, *Raeticodactylus*, *Carniadactylus*).

As I have already said, I do accept that it is the overall body of evidence taken together that is important but it would be more compelling if there were one or two really convincing features and for me the authors have not highlighted anything in particular.

We added to the main text a list of selected features that have been recovered as synapomorphies of Pterosauromorpha (Lagerpetidae + Pterosauria) and are absent in other early archosaurs: "Some of these synapomorphies are unique to pterosauromorphs among early archosaurs, including the subtriangular and dorsoventrally tall floccular fossa of the braincase, height-anteroposterior length ratio of the SCCs of the inner ear >0.90, reduced to absent splenial, strongly ventrally extended pubo-ischiatic plate, and hook-shaped femoral head (complete list of synapomorphies in Supplementary Information)".

I found the manuscript mostly free from typos and errors of grammar, but I was intrigued by the term in l.65 “lateralized” glenoid fossa. What kind of word is this? Can any noun be verbed?

We have changed this part of the sentence from “a lateralized glenoid fossa” to “a laterally facing glenoid fossa”.

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

I thank the authors for robustly addressing my comments, particularly those relating to the inner ear. The PCA is a most welcome addition and I am now convinced that there is unique similarity (synapomorphy) in the tall, curved semicircular canals of lagerpetids and pterosaurs. Same with the greatly enlarged flocculus. There is still the issue of potential long-branch atttraction, as the two pterosaurs in the dataset are much younger than the Triassic lagerpetids, but there is nothing the authors can do about this becuase high quality 3D scannable fossils filling the gap do not yet exist. The authors have done all they can, and I have no further suggestions before publication. Nice work and congratulations. The authors may know my identity: Steve Brusatte.

Referee #2 (Remarks to the Author):

The other two reviewers offered interesting and excellent comments, and I think that the authors have responded well to them. I have only some minor suggestions for the text, indexed by line numbers:

46: Do you want to add “bipedal” in front of “cursorial”? Would clarify.

65: For “enlarged coracoid and”, substitute “elongated coracoid braced to sternum;”

93: For “below” read “less than”

97: “several” for “multiple”

98: “elucidate” for “inform on”

115: remove hyphen in “mesiodistally-aligned”

135: can you tell if the forearm is longer than the humerus in any lagerpetids? This is a synapomorphy of pterosaurs that is also shared by Scleromochlus.

138: “at least one has a trenchant claw” for “have at least one trenchant claw”

139: insert after “By contrast,” : “like all other archosaurs,”

142: “ischiadic” for “ischiatic”? I’ve seen it both ways but usually the former in our literature.

161: omit “for”

170: for “height-“ read “height to”

172: again, "ischiatic"?

181: "evolution" for "acquisition"; in 182, for "evolutionary" substitute "taxonomic" or "morphological"?

185: for "interrelationships" read "phylogenetic reconstructions".

186: "much higher than in" for "very high relative to"

193: omit "of"

194: "not well supported" for "strongly suboptimal"

201: "discretization" is not a word, as far as I can tell. Could you say "forcing more subjective discrete character-states on such a complex structure"?

203: "that supports" for "supporting"?

206: "evolution" for "acquisition"

213-214: "which convergently evolved"

222: "hypothesized," unless you use British spelling throughout. Same with "behaviour" in 231 and 241.

241: "evolution" for "acquisition"

246: "because" for "as"

248: "millions of years" for "million years"

250: "resource zone" for "ecological niche"

Referee #3 (Remarks to the Author):

I appreciate the effort of the authors to respond to the comments of the referees. Overall, I think the authors have made a very good attempt to address the concerns, and to my mind the manuscript is now a whole lot tighter and presented in a simpler and widely accessible manner. I am sure that the manuscript, once published, will be highly-cited and the authors are to be highly commended for their efforts.

Author Rebuttals to First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

I thank the authors for robustly addressing my comments, particularly those relating to the inner ear. The PCA is a most welcome addition and I am now convinced that there is unique similarity (synapomorphy) in the tall, curved semicircular canals of lagerpetids and pterosaurs. Same with the greatly enlarged flocculus. There is still the issue of potential long-branch atttraction, as the two

pterosaurs in the dataset are much younger than the Triassic lagerpetids, but there is nothing the authors can do about this becuase high quality 3D scannable fossils filling the gap do not yet exist. The authors have done all they can, and I have no further suggestions before publication. Nice work and congratulations. The authors may know my identity: Steve Brusatte.
Thank you.

Referee #2 (Remarks to the Author):

The other two reviewers offered interesting and excellent comments, and I think that the authors have responded well to them. I have only some minor suggestions for the text, indexed by line numbers:

46: Do you want to add “bipedal” in front of “cursorial”? Would clarify.
We think that adding “bipedal” here will complicate the narrative of the manuscript because there is currently no consensus about the locomotion style of lagerpetids and we discussed this issue more deeply several paragraphs later in the text.

65: For “enlarged coracoid and”, substitute “elongated coracoid braced to sternum;”
We have added “elongated coracoid braced with the sternum”.

93: For “below” read “less than”
Changed to “<”.

97: “several” for “multiple”
Changed.

98: “elucidate” for “inform on”
Changed.

115: remove hyphen in “mesiodistally-aligned”
Removed.

135: can you tell if the forearm is longer than the humerus in any lagerpetids? This is a synapomorphy of pterosaurs that is also shared by Scleromochlus.
Indeed, the lagerpetid *D. romeri* possesses a forearm longer than the humerus. This information has been added to the text.

138: “at least one has a trenchant claw” for “have at least one trenchant claw”
Changed to “at least one digit has a trenchant claw”.

139: insert after “By contrast,” : “like all other archosaurs,”
We inserted “like other archosauromorphs”.

142: “ischiadic” for “ischiatic”? I’ve seen it both ways but usually the former in our literature.
Changed.

161: omit “for”

Deleted.

170: for “height-“ read “height to”
Changed.

172: again, “ischiatic”?
Changed.

181: “evolution” for “acquisition”; in 182, for “evolutionary” substitute “taxonomic” or “morphological”?
We prefer to keep “acquisition” instead of “evolution” in order to not repeat the word again later in the sentence, and also keep “evolutionary” because it is the most common use of this kind of analyses (i.e. “evolutionary rates”).

185: for “interrelationships” read “phylogenetic reconstructions”.
Changed.

186: “much higher than in” for “very high relative to”
Changed.

193: omit “of”
Deleted.

194: “not well supported” for “strongly suboptimal”
Changed to “a poorly supported”.

201: “discretization” is not a word, as far as I can tell. Could you say “forcing more subjective discrete character-states on such a complex structure”?

Changed to “in an attempt to avoid subjective discrete character-states on such a complex structure”.

203: “that supports” for “supporting”?
Changed.

206: “evolution” for “acquisition”
Changed.

213-214: “which convergently evolved”
Changed.

222: “hypothesized,” unless you use British spelling throughout. Same with “behaviour” in 231 and 241.
We have checked the text throughout and we have modified “hypothesised” to follow a British spelling. No changes were required for “behaviour”.

241: “evolution” for “acquisition”

Changed.

246: “because” for “as”
Changed.

248: “millions of years” for “million years”
Changed.

250: “resource zone” for “ecological niche”
We have deleted this part of the sentence in order to reduce the word count.

Referee #3 (Remarks to the Author):

I appreciate the effort of the authors to respond to the comments of the referees. Overall, I think the authors have made a very good attempt to address the concerns, and to my mind the manuscript is now a whole lot tighter and presented in a simpler and widely accessible manner. I am sure that the manuscript, once published, will be highly-cited and the authors are to be highly commended for their efforts.
Thank you.