

The oldest lepidosaur and origins of lepidosaur feeding adaptations

Corresponding Author: Professor Michael Benton

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

This manuscript describes a new fossil lepidosaur from the Triassic of the southern UK. Originating from the Anisian, this would be the oldest lepidosaur known to date and could therefore play a key role in elucidating the early evolutionary history of lepidosaurs.

The evidence presented to support *Agriodontosaurus* as a Rhynchocephalian is quite compelling. Certainly the fossil is very intriguing and the dentition seems to be very unusual and rather surprising in a tetrapod that is so small.

I have two main points to raise:

Firstly the authors need to clarify the size of the specimen. On l. 85 they say the skull is estimated to be 14 mm long, yet based on the scale bar in Figure 3 the complete skull would be more like 25+mm long. While still a tiny animal, this is a significant difference for the authors claim of a diet of large insects. For the most part “large” insects from the Triassic include some blattoids, orthopterans and hemipterans which might be up to 15mm long – quite a mouthful for an animal with a 14 mm long skull and a pretty rigid skull and difficult to really imagine. Even at 25 mm long it would be quite a task. However, the authors actually take it a step further on l. 410 and 411, and suggest it may have tackled insects with a 150mm wing length. That does seem to be an extraordinary claim! Tackling a large prey item that was its equal in size is difficult to conceive - even if scavenging could an animal with a 14 mm mandible bite into and break into chunks such a large keratinised body? I really doubt it.

The second point concerns the nature of the palate. In the analyses there appears to be no evidence for a palatal dentition and this lies at the centre of their discussions. However, I would like to understand how well preserved the specimen is – it does seem possible that the palatine bones are incomplete. The reconstruction of the palatines and ectopterygoid (Figure 3i) seem to be more definitive than the 3 D model (Figure 3b) would suggest. What evidence do the authors have that what is preserved of the skull is in good condition with finished bone surfaces. An examination of the image of the block that is included in the supplementary data indicates some areas of the skeleton are more fragmentary than others. Indeed on l. 159, 160 the authors even state that “the sutures between elements are obscure and cannot be discerned.....partially because of skull deformation .”

As a result, I don't necessarily think the authors have provided strong evidence to support their claim for a lack of palatal teeth, including an enlarged row of teeth on the palatine. Absence of evidence is not evidence of absence.

More minor comments

Abstract l. 15 refers to the Otter Sandstone. Why not Helsby Sandstone Formation, as used in l. 79

l. 31 does the gap between the jugal and quadrate allow the muscles to bulge. Don't the temporal fenestrae play a more significant role?

L 245. In what way are the teeth flanged? There are very clear descriptions of flange size and orientation of flanges on mandibular and maxillary teeth in many other rhynchocephalians. Does the pattern match any of these? The remarkable size of the teeth requires a little more detail in the description. Are these slicing and what is the distribution of wear facets on these teeth? This is not clearly shown.

l. 307 Delete “of”

l. 347 states that the skull is less robust in the postorbital region than *Gephyrosaurus* and *Diphydontosaurus*. Doesn't this therefore speak against a powerful bite?

Referee #2

(Remarks to the Author)

This is a really interesting discovery that confirms previous suggestions that lepidosaurs arose in the Early or early Middle Triassic. The new taxon has some intriguing features such as the mode of tooth implantation.

Generally, the paper is excellent with a nice, concise description of the material. I have made a few comments on the review copy, mostly concerning proper anatomical terminology.

Figure 3 is much too dark and might be unintelligible in the reduced printed version. Subfigure 3e has several points that should be fixed: The teeth do not resemble those in the scan images and even those that are not en echelon are tightly packed together. The squamosal is rendered too small and the quadrate-quadratojugal is incorrectly oriented, both creating an odd-looking suspensorial region. You might want to consult reconstructions of the skulls of other early-diverging rhynchocephalians such as *Diphydontosaurus* (Whiteside, 1986).

Comments on text

l. 16 'oldest currently known', not 'current oldest'

l. 18 delete 'giant' – the small size of the skull would not allow capturing a titanopteran

l. 151 'quadratojugal foramen' is the generally used term (e.g., Whiteside, 1986)

l. 194 Tetrapods have only one mandible, which comprises two 'mandibular rami' or hemimandibles. Only arthropods have 'mandibles'.

l. 226 There is no such thing as 'lateral mandible'. Do you mean 'lateral surface of the mandibular ramus'?

l. 255-256 The mode of a tooth implantation is very different from other early rhynchocephalians such as *Diphydontosaurus* and *Wirtembergia*, in which the anterior teeth have pleurodont tooth implantation and the posterior ones have acrodon attachment.

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l.431-432 This sentence is unsupported by a palaeobiogeographical analysis and, in any case, meaningless as Europe did not exist as a geographical entity during the Triassic Period. Please delete this sentence.

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Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

Many thanks for the opportunity to review the revised version of this very interesting manuscript. I am pleased to see that the authors have made every effort to address my initial suggestions and concerns.

I still question the absence of palatal teeth, but I thank the authors for providing further clarification on their original reasoning. I accept they have made as good a case as they can with the provision of new scans and some clarifications around the absence of tooth wear facets. This is very helpful and it does strengthen their case. While I still consider the presence or absence of palatal teeth to be a key part of the manuscript, the support the authors have provided for their point of view is reasonable.

Referee #2

(Remarks to the Author)

Thank you for fully addressing the comments from my previous review.

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Dear Mike

Your manuscript, "The oldest lepidosaur and origins of lepidosaur feeding adaptations", has now been seen by two referees, whose comments are attached below. While they find your work of potential interest, as do we, they have raised important concerns that in our view need to be addressed before we can consider publication in Nature.

We work through these concerns and provide detailed responses to each, below.

Should further work allow you to address these criticisms, we would be happy to consider a revised manuscript (unless something similar has been accepted at Nature or appeared elsewhere in the meantime). We hope to receive your revised paper within four to six months. If you cannot complete the required revisions within this time frame, please let us know when you would anticipate being able to submit a revised manuscript.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if there are specific requests from the reviewers that you believe are technically impossible or unlikely to yield a meaningful outcome.

In the meantime, we hope that you will find our referees' comments helpful. Please do not hesitate to contact me if there is anything you would like to discuss.

Yours sincerely

Henry

Dr Henry Gee

Senior Editor Biological Sciences

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<http://www.nature.com/nature>

See Nature's new guide to authors at www.nature.com/nature/submit

Referees' comments:

Referee #1 (Remarks to the Author):

This manuscript describes a new fossil lepidosaur from the Triassic of the southern UK. Originating from the Anisian, this would be the oldest lepidosaur known to date and could therefore play a key role in elucidating the early evolutionary history of lepidosaurs.

The evidence presented to support Agriodontosaurus as a Rhynchocephalian is quite compelling. Certainly the fossil is very intriguing and the dentition seems to be very unusual and rather surprising in a tetrapod that is so small.

Many thanks for the positive remarks

I have two main points to raise:

Firstly the authors need to clarify the size of the specimen. On l. 85 they say the skull is estimated to be 14 mm long, yet based on the scale bar in Figure 3 the complete skull would be more like 25+mm long. While still a tiny animal, this is a significant difference for the authors claim of a diet of large insects. For the most part "large" insects from the Triassic include some blattoids, orthopterans and hemipterans which might be up to 15mm long – quite a mouthful for an animal with a 14 mm long skull and a pretty rigid skull and difficult to really imagine. Even at 25 mm long it would be quite a task. However, the authors actually take it a step further on l. 410 and 411, and suggest it may have tackled insects with a 150mm wing length. That does seem to be an extraordinary claim! Tackling a large prey item that was its equal in size is difficult to conceive - even if scavenging could an animal with a 14 mm mandible bite into and break into chunks such a large keratinised body? I really doubt it.

The 10 mm scale bar noted in the caption of Figure 3 was in error and has been corrected to 5 mm. Apologies for this error. We have also checked all other scale bars and size indications to ensure there are no other such bloopers.

We have omitted the comment on lines 410-412 regarding the largest Mesozoic insects to avoid the interpretation described by the reviewer. It is indeed extremely unlikely that the **largest** representatives of these groups were the prey items of choice for *Agriodontosaurus* and this was not the intended suggestion. Thank you for raising this.

In terms of dealing with smaller prey up to 15 mm as mentioned by the reviewer, we suggest in l. 404 that this animal was a lingual feeder like *Sphenodon* which itself has an immobile skull and that a mobile skull was less important for prey prehension in *Agriodontosaurus*.

The second point concerns the nature of the palate. In the analyses there appears to be no evidence for a palatal dentition and this lies at the centre of their discussions. However, I would like to understand how well preserved the specimen is – it does seem possible that the palatine bones are incomplete. The reconstruction of the palatines and ectopterygoid (Figure 3i) seem to be more definitive than the 3D model (Figure 3b) would suggest. What evidence do the authors have that what is preserved of the skull is in good condition with finished bone surfaces. An examination of the image of the block that is included in the supplementary data indicates some areas of the skeleton are more fragmentary than others. Indeed on l. 159, 160 the authors even state that “the sutures between elements are obscure and cannot be discerned... partially because of skull deformation.”

As a result, I don't necessarily think the authors have provided strong evidence to support their claim for a lack of palatal teeth, including an enlarged row of teeth on the palatine. Absence of evidence is not evidence of absence.

As a result of the reviews, we looked at the slices across the palate to include the region lying medially of the maxilla teeth at the point of occlusion with the dentary teeth (images now included in Supplements 2, 3). We can clearly recognise the large maxillary teeth and the occluding dentary teeth on the right-hand side of the skull. Bones of the palate, including the palatine and the pterygoid are recognisable but there are no large teeth on the palatine or pterygoid. This corresponds with our recognition that there are no wear facets on the lingual sides of the dentary teeth. Lingual tooth wear facets are found on the dentary in rhynchocephalians that have a lateral tooth row on the palatine, e.g. in clevosaurs.

To further address the reviewer's concerns, we have produced a series of images (PDF files) through the palate (in dorso-ventral and in coronal slices) to demonstrate our conclusion that *Agriodontosaurus* lacks large palatal teeth. These include annotated images through the ESRF scan that was used initially as well as a brand-new image stack acquired from Diamond Light Source Ltd, Oxfordshire, for the purposes of this response. We also include an MP4 file of the image stack for the benefit of the reviewers, to be included in conjunction with the extended data and the annotated slices.

We are aware that ‘absence of evidence does not mean evidence of absence’, and we cannot therefore rule out that *Agriodontosaurus* had palatal teeth. However, we can indicate two lines of evidence: (1) absence of lingual tooth wear facets from putative palatal teeth on dentary teeth; and (2) re-investigation now from two micro-CT studies, one from ESRF and a new one from Diamond, where we identify the palatine and pterygoid bones, but find no hint of teeth.

We reword and expand this section.

More minor comments

Abstract l. 15 refers to the Otter Sandstone. Why not Helsby Sandstone Formation, as used in l. 79

Amended

l. 31 does the gap between the jugal and quadrate allow the muscles to bulge. Don't the temporal fenestrae play a more significant role?

We removed this remark; it's enough to say the open lower temporal bar is essential for cranial kinesis.

L 245. In what way are the teeth flanged? There are very clear descriptions of flange size and orientation of flanges on mandibular and maxillary teeth in many other rhynchocephalians. Does the pattern match any of these? The remarkable size of the teeth requires a little more detail in the description. Are these slicing and what is the distribution of wear facets on these teeth? This is not clearly shown.

We have provided more detail on the flanges of the posterior teeth of *Agriodontosaurus*. We now make clear that the maxillary and dentary posterior teeth each have a postero-lingual flange but lack mesial flanges (Fig. 3F–G; Extended Data Fig. 2E–H) which are present in clevososaurs such as *C. hudsoni*. We also reference the wear facets found on the labial side of the dentary that occluded with the large, flanged maxillary teeth.

I. 307 Delete “of”

corrected to “of the pterygoid”

I. 347 states that the skull is less robust in the postorbital region than *Gephyrosaurus* and *Diphydontosaurus*. Doesn't this therefore speak against a powerful bite?

We have improved the reconstruction of *Agriodontosaurus* reducing the area (in lateral view) of the lower temporal fenestra and made the squamosal more robust, although it is somewhat less robust than in *Diphydontosaurus*. There are strong wear facets on the dentary teeth which we have annotated in the Extended data Figure 2 and such wear facets will be caused by hard biting of dentary against maxillary teeth. We show the precise occlusion between the dentary and maxillary teeth in the CT slices of the additional data.

Referee #2 (Remarks to the Author):

This is a really interesting discovery that confirms previous suggestions that lepidosaurs arose in the Early or early Middle Triassic. The new taxon has some intriguing features such as the mode of tooth implantation.

Generally, the paper is excellent with a nice, concise description of the material. I have made a few comments on the review copy, mostly concerning proper anatomical terminology.

Many thanks for these overview comments.

Figure 3 is much too dark and might be unintelligible in the reduced printed version. Subfigure 3e has several points that should be fixed: The teeth do not resemble those in the scan images and even those that are not en echelon are tightly packed together. The squamosal is rendered too small and the quadrate-quadratojugal is incorrectly oriented, both creating an odd-looking suspensorial region. You might want to consult reconstructions of the skulls of other early-diverging rhynchocephalians such as *Diphydontosaurus* (Whiteside, 1986).

We thank the reviewer for raising these points. We have lightened Fig. 3. This has been addressed by further information from CT slices and scrutiny of the scans, and we have reorientated the quadrate suspensorium so that it accords with the reconstructions of basal rhynchocephalians such as *Diphydontosaurus* and *Gephyrosaurus*.

We have superimposed our reconstruction of the maxillary teeth over the scans as shown in Figs. 3a–d and they correspond exactly so we regard our reconstruction (Fig. 3e, h, i) as accurate. We based our reconstructions of the maxilla and lower jaw on the left-hand elements which are less disturbed by skull deformation. The right-hand side does have looser teeth, but this is a result of deformation.

Comments on text

I. 16 ‘oldest currently known’, not ‘current oldest’

amended

I. 18 delete ‘giant’ – the small size of the skull would not allow capturing a titanopteran

amended

I. 151 'quadratojugal foramen' is the generally used term (e.g., Whiteside, 1986)

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I. 194 Tetrapods have only one mandible, which comprises two 'mandibular rami' or hemimandibles. Only arthropods have 'mandibles'.

amended

I. 226 There is no such thing as 'lateral mandible'. Do you mean 'lateral surface of the mandibular ramus'?

amended to "lateral surfaces of the mandible"

I. 255-256 The mode of a tooth implantation is very different from other early rhynchocephalians such as *Diphydontosaurus* and *Wirtembergia*, in which the anterior teeth have pleurodont tooth implantation and the posterior ones have acrodont attachment.

We now clarify this, by writing 'The shape and mode of implantation of the teeth support a rhynchocephalian affinity, being primarily acrodont as in *Clevosaurus*, *Sphenodon* and others, even though *Wirtembergia* and *Diphydontosaurus* have pleurodont anterior teeth and acrodont posterior teeth.'

I. 347 Do you mean 'less robust posterior portion of the skull'?

yes, amended

I. 414 There are clear scouring marks on some jaws of *Wirtembergia* – they do not 'appear' to be there.

amended

I.431-432 This sentence is unsupported by a palaeobiogeographical analysis and, in any case, meaningless as Europe did not exist as a geographical entity during the Triassic Period. Please delete this sentence.

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As above; corrected.

9th June 2025

Dear Mike

This is the letter I warned you about. Make some fresh coffee. You might need to bring sandwiches.

Your manuscript, "The oldest lepidosaur and origins of lepidosaur feeding adaptations", has now been seen by our referees, and in the light of their advice I am delighted to say that we can in principle offer to publish it. First, however, we would like you to revise your paper to address any remaining points made by the referees, and to make some editorial changes to your paper so that it is as brief as possible and complies with our [Guide to Authors](#). No peer reviewed data should be removed altogether when making these changes.

Many thanks for the final Referee comments and the other information. We respond individually to all the items listed. In that the Referees did not request further changes to the MS, we have made no further changes. We did however check it line by line and are happy with the structure and content of the last version you have. It can be passed to copy-editing.

SOME SPECIFIC ISSUES:

1. Please remove the main figures from the article file and re-supply them individually in an acceptable format such as EPS, AI, PS, PDF, PPT, PSD or XLS (for graphs) with editable vector files. All removed from MS and provided in pdf format. Can provide editable svg too if required.
2. You have duplicate accounts on our content management system, ejp. Please resolve this if you can. If not, just yell. I linked the floating account to my main account.
3. Please provide a supplementary information guide. Our SI guide is on Page 1 of S1, but we can supply this as a separate document if required.
4. There are potential third-party rights issues in the figures - please check sources or if permissions are needed for the fossils, A. helsbypetrae, skull, animal silhouettes etc illustrations in the figures. We checked all figures in main text, extended data and supplement, and find nothing with third-party rights. For example, in Figure 1, all the little skulls are redrafted by us from multiple sources, including generic images without known authorship. In Figure 4, we used silhouettes from phylopic, and we chose their copyright-free option, and cite the artists of all the used images. The other images of the specimen and reconstructions, cladograms, and scan images are by lead author Dan Marke.
5. Please ensure that the text size in all figures is at least 5 pt Arial. All checked.
6. Please re-supply the Extended data figures individually in EPS, JPEG or TIF format. All provided as jpg files; can provide as editable svg as well, if required.
7. For any Supplementary Figures, please check and confirm that:
 - * If data is presented as bar charts, individual data points are shown using overlaid dot plots.
 - * The n number (i.e. the sample size used to derive statistics) is provided and defined as a precise value (not a range), using the wording "n=X samples/cells/independent experiments" etc. where applicable.

- * Any chart axis, error bars, scale bars, symbols and colour scales are defined.
- * Any statistical tests used for data analysis are specified and exact p-values are provided either on the figures themselves, in the legend or in the Source Data file.
- * Wherever representative data such as micrographs are shown, the legend indicates how many times the experiment was repeated with the same results.

None of these issues is relevant to our paper.

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No suggestions for redactions.

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I think this is done – we all have ORCID numbers and hope we provided them somewhere. Mike Benton, as Corresponding author, is 0000-0002-4323-1824. David Whiteside is 0000-0003-1619-747X.

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statistical reporting (as discussed [here](#)) are sound before the paper is published, we have reviewed your Reporting summary and Editorial policy checklist editorially. I have attached two documents: one listing specific issues related to your manuscript and one containing an annotated version of the Reporting summary. Please ensure that, as well as the more general points below, the points highlighted in the attached documents are addressed in full, both on these forms and within the manuscript. Both forms should be uploaded as a “Related Manuscript” file type. The Reporting summary will be published with your paper. **We revised the two documents and upload the revised versions.**

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MAIN TEXT: If further introductory material is necessary, the main text can begin with up to 500 words of introduction expanding on the background to the work (some overlap with the summary is acceptable), before proceeding to a concise, focused account of the findings, and ending with 1 or 2 short paragraphs of discussion. Sections are separated with subheadings (up to 40 characters including spaces) to aid navigation. **We believe we have followed all these suggestions.**

REFERENCES: As a guideline, most papers should include no more than 50 main text references; all additional references can be cited in (and listed after) the Methods section, as detailed below. **We have 46 references for the main text, and 77 in total, when Methods referencing is also included.**

FIGURE LEGENDS: These should be listed sequentially after the main text references and not in the figure files. Each legend should begin with a brief title for the whole figure and continue with a short description of each panel and the symbols used. Legends should not exceed 300 words each. Each figure legend should contain, for each panel where relevant, the following information:

- * the exact sample size (n) for each experimental group/condition, given as a number, not a range;
- * a description of the sample collection allowing the reader to understand whether the samples represent technical or biological replicates (including how many animals, litters, cultures, etc);
- * a statement of how many times the experiment shown was replicated;
- * definitions of statistical methods and measures:

- * very common tests (e.g. t-test, simple Chi-square tests, Wilcoxon and Mann-Whitney tests) can be identified by name only, but more complex techniques should be described in the Methods;
- * whether tests are one-sided or two-sided;
- * whether there are adjustments for multiple comparisons;
- * the statistical test results (e.g., P values);
- * the definition of 'center values' as median or average;
- * the definition of error bars as s.d. or s.e.m.

Descriptions that are too long for the figure legend should be included in the Methods section. **Our figure descriptions follow these suggestions; they do not include any illustrations of statistical tests, and so the mentioned guidelines are not applicable.**

METHODS: The Methods section, which provides the full, step-by-step instructions that would allow other researchers to replicate the results, is included after the main text figure legends. The Methods section will not appear in print but will appear online in the full-text HTML and PDF versions. The Methods section should be written as concisely as possible but should contain all elements necessary to allow interpretation and reproduction of the results. If there are additional references (in the Methods section, Supplementary Information, etc), their numbering should continue from the last entry in the main text reference list, and they should be listed following the Methods section. Specialized methods that require chemical structures, figures, or tables cannot be accommodated in the Methods section of the main text file. If such information is part of the Methods, the entire Methods section must instead be included within a Supplementary Information text file. **We have followed all these suggestions.**

MAIN TEXT STATEMENTS: Several statements (which will not appear in print but will appear online in the full-text HTML and PDF) are required after the Methods (and additional references, if present). First, there should be an Acknowledgements section, listing grant/financial support. Next, we require a detailed Author Contribution statement; the specific contributions of each author, particularly in terms of which authors performed which specific experiments, must be listed. This is followed by a Competing Interest statement. Financial and non-financial interests should be noted here, as well as any patents; patent information should include at a minimum patent number, what is covered by the patent, and who submitted the patent application. Finally, an Additional Information statement should include information regarding reprints and permissions and name the author(s) to whom correspondence and requests for materials should be addressed. Formatting details and an example are available [here](#). **We included all these post-text statements, following the guidelines.**

DATA AND CODE AVAILABILITY STATEMENTS: Any manuscript reporting original research must include a Data Availability statement that makes transparent to the reader the conditions of access to the "minimum dataset" that is necessary to interpret, verify and extend the research in the article. This minimum dataset may be provided through deposition in public community/discipline-specific repositories, custom proprietary repositories (for certain types of datasets), or general repositories like Figshare, Zenodo and Dryad. We strongly discourage providing large datasets in Supplementary Information; the preferred approach is to make data available in

repositories. More information on Nature Portfolio's reporting standards and guidance on preparing your Data Availability statement can be found [here](#). **We provide modest additional data in the Extended data and Supplementary information sections, and provide the original scan data through a doi at the ESRF repository; all detailed in the 'Data Availability Statement'.**

For all studies using custom code or mathematical algorithms that are deemed central to the conclusions, a Code Availability statement must be included, indicating whether and how the code or algorithm can be accessed, including any restrictions to access. The Code Availability statement is listed as a separate section after the Data Availability statement but before any additional references. Code should be deposited in a DOI-minting repository such as Zenodo, Gigantum or Code Ocean and cited in the reference list. Authors are encouraged to manage subsequent code versions and to use a license approved by the open source initiative. Additional details can be found [here](#). **Not relevant to our paper.**

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Yours sincerely

Henry

Dr Henry Gee

Senior Editor Biological Sciences

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Referees' comments:

Referee #1 (Remarks to the Author):

Many thanks for the opportunity to review the revised version of this very interesting manuscript. I am pleased to see that the authors have made every effort to address my initial suggestions and concerns.

I still question the absence of palatal teeth, but I thank the authors for providing further clarification on their original reasoning. I accept they have made as good a case as they can with the provision of new scans and some clarifications around the absence of tooth wear facets. This is very helpful and it does strengthen their case. While I still consider the presence or absence of palatal teeth to be a key part of the manuscript, the support the authors have provided for their point of view is reasonable.

Many thanks; no action.

Referee #2 (Remarks to the Author):

Thank you for fully addressing the comments from my previous review.
Many thanks; no action.