

## **A new varanopid synapsid from the early Permian of Oklahoma and the evolutionary stasis in this clade**

Sigi Maho, Bryan M. Gee and Robert R. Reisz

### **Article citation details**

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### **Review timeline**

Original submission: 25 July 2019  
Revised submission: 11 September 2019  
Final acceptance: 24 September 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

## Review History

### RSOS-191297.R0 (Original submission)

#### Review form: Reviewer 1 (Christian F. Kammerer)

**Is the manuscript scientifically sound in its present form?**

Yes

**Are the interpretations and conclusions justified by the results?**

Yes

**Is the language acceptable?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Have you any concerns about statistical analyses in this paper?**

No

**Recommendation?**

Accept with minor revision (please list in comments)

**Comments to the Author(s)**

See attached file (Appendix A).

## Review form: Reviewer 2

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## Decision letter (RSOS-191297.R0)

03-Sep-2019

Dear Dr Maho

On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-191297 entitled "A new varanopid synapsid from the early Permian of Oklahoma and the evolutionary stasis in this clade" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and handling editors have recommended publication, but also suggest some minor

revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

- Ethics statement

If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

- Data accessibility

It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (<http://datadryad.org/>), or modify your current submission to dryad, please use the following link:  
<http://datadryad.org/submit?journalID=RSOS&manu=RSOS-191297>

- Competing interests

Please declare any financial or non-financial competing interests, or state that you have no competing interests.

- Authors' contributions

All submissions, other than those with a single author, must include an Authors' Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:

AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

- Acknowledgements

Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

- Funding statement

Please list the source of funding for each author.

Please ensure you have prepared your revision in accordance with the guidance at

<https://royalsociety.org/journals/authors/author-guidelines/> -- please note that we cannot publish your manuscript without the end statements. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before 12-Sep-2019. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/rsos> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision." You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". You can use this to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees. We strongly recommend uploading two versions of your revised manuscript:

- 1) Identifying all the changes that have been made (for instance, in coloured highlight, in bold text, or tracked changes);
- 2) A 'clean' version of the new manuscript that incorporates the changes made, but does not highlight them.

When uploading your revised files please make sure that you have:

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- 2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format);
- 3) Included a 100 word media summary of your paper when requested at submission. Please ensure you have entered correct contact details (email, institution and telephone) in your user account;
- 4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript. Make sure it is clear in your data accessibility statement how the data can be accessed;
- 5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (<https://rs.figshare.com/>). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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If your manuscript is newly submitted and subsequently accepted for publication, you will be asked to pay the article processing charge, unless you request a waiver and this is approved by Royal Society Publishing. You can find out more about the charges at <http://rsos.royalsocietypublishing.org/page/charges>. Should you have any queries, please contact [openscience@royalsociety.org](mailto:openscience@royalsociety.org).

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,  
Andrew Dunn  
Royal Society Open Science Editorial Office  
Royal Society Open Science  
[openscience@royalsociety.org](mailto:openscience@royalsociety.org)

on behalf of Dr Julia Brenda Desojo (Associate Editor) and Kevin Padian (Subject Editor)  
[openscience@royalsociety.org](mailto:openscience@royalsociety.org)

Reviewer comments to Author:  
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## Author's Response to Decision Letter for (RSOS-191297.R0)

See Appendix B.

## Decision letter (RSOS-191297.R1)

24-Sep-2019

Dear Ms Maho,

I am pleased to inform you that your manuscript entitled "A new varanopid synapsid from the early Permian of Oklahoma and the evolutionary stasis in this clade" is now accepted for publication in Royal Society Open Science.

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## Appendix A

These are beautiful and anatomically very informative specimens, which are well described and figured by the authors. In general this is an important contribution to our knowledge of varanopid anatomy and diversity in American Permian faunas.

Regarding the argument that these fossils indicate remarkable morphological stasis in a Permian tetrapod, I think the authors are probably correct that *Mesenosaurus* was long ranging. However, this argument is rendered highly uncertain by the essentially unknown date of the Russian Mezen assemblage. Historically considered upper Permian due to the presence of therapsids and mostly considered middle Permian now, this assemblage is dominated by parareptiles and pelycosaurids and has a very archaic aspect. The therapsid components are also exceedingly plesiomorphic, probably near the divergence of the major therapsid groups. I would not be surprised if the Mezen fauna was substantially older than usually thought, potentially filling in Olson's Gap to some degree. With that said, a date as old as Artinskian (as for Richards Spur) is unlikely, and *Mesenosaurus* likely did range through several stages of the Permian. Relevant to this topic and unremarked upon by the authors (although the paper is cited) is the cross-continental presence of the nycteroleterid tetrapod *Macroleter*, previously known from the Mezen River and later recognized in seemingly earlier Permian strata in Oklahoma. This is an intriguingly comparable scenario to the present discovery of *Mesenosaurus* and warrants discussion, as it suggests broader spatial distribution of Mezen-style taxa (and again raises the issue of how much temporal separation there really is between these faunas).

Although a historically-used variant and acceptable transliteration, "Mesen" is usually spelled "Mezen" in Latin script (Google search recovers <200 hits for "Mesen" vs. nearly 8000 for "Mezen") and this should be followed here.

Minor edits:

Line 3: change "extending from" to "whose range extends from"

Line 8: change "from fragmentary disarticulated material" to "from fragmentary disarticulated material at Richards Spur" (as these taxa are known from complete skulls at other localities)

Line 62: change "that do not extend" to "that does not extend"

Line 102: "are partially represented to complete" is somewhat awkward, I recommend changing this to "range from partial to complete"

Lines 244–245: change "exposing only on the dorsal surfaces" to "with only the dorsal surfaces exposed"

Line 278: change "to from a" to "to form a"

Line 312: delete the extraneous "on the"

Lines 328–329: add commas after "features" and "positions"

Line 333: change "relatively short" to "is relatively short"

Lines 344–345: change "certainly not sufficient to argue for taxonomic distinction above the species level" (although I agree this is the case) to "and we would argue insufficient for taxonomic distinction above the species level"

# Appendix B

## Response to Reviewers

We thank the three reviewers and the editor for their constructive feedback on this manuscript. Below are our point-by-point responses to the comments raised during review.

### Reviewer: 1

- Regarding the argument that these fossils indicate remarkable morphological stasis in a Permian tetrapod, I think the authors are probably correct that Mesenosaurus was long ranging. However, this argument is rendered highly uncertain by the essentially unknown date of the Russian Mezen assemblage. Historically considered upper Permian due to the presence of therapsids and mostly considered middle Permian now, this assemblage is dominated by parareptiles and pelycosaurids and has a very archaic aspect. The therapsid components are also exceedingly plesiomorphic, probably near the divergence of the major therapsid groups. I would not be surprised if the Mezen fauna was substantially older than usually thought, potentially filling in Olson's Gap to some degree. With that said, a date as old as Artinskian (as for Richards Spur) is unlikely, and Mesenosaurus likely did range through several stages of the Permian. Relevant to this topic and unremarked upon by the authors (although the paper is cited) is the cross-continental presence of the nycteroleterid tetrapod Macroleter, previously known from the Mezen River and later recognized in seemingly earlier Permian strata in Oklahoma. This is an intriguingly comparable scenario to the present discovery of Mesenosaurus and warrants discussion, as it suggests broader spatial distribution of Mezen-style taxa (and again raises the issue of how much temporal separation there really is between these faunas).
  - We added a few brief comments on this in the discussion.
- Although a historically-used variant and acceptable transliteration, "Mesen" is usually spelled "Mezen" in Latin script (Google search recovers <200 hits for "Mesen" vs. nearly 8000 for "Mezen") and this should be followed here.
  - We made the spelling modification throughout the manuscript.
- Line 3: change "extending from" to "whose range extends from"
  - We made the requested edit.
- Line 8: change "from fragmentary disarticulated material" to "from fragmentary disarticulated material at Richards Spur" (as these taxa are known from complete skulls at other localities)
  - We made the requested edit.
- Line 62: change "that do not extend" to "that does not extend"
  - We made the requested edit.
- Line 102: "are partially represented to complete" is somewhat awkward, I recommend changing this to "range from partial to complete"
  - We made the requested edit.
- Lines 244–245: change "exposing only on the dorsal surfaces" to "with only the dorsal surfaces exposed"



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- We made the requested edit.
- Line 278: change “to from a” to “to form a”
  - We made the requested edit.
- Line 312: delete the extraneous “on the”
  - We made the edit.
- Lines 328–329: add commas after “features” and “positions”
  - We added a coma after “positions” but don't believe that one is grammatically warranted after “features.”
- Line 333: change “relatively short” to “is relatively short”
  - We made the requested edit.
- Lines 344–345: change “certainly not sufficient to argue for taxonomic distinction above the species level” (although I agree this is the case) to “and we would argue insufficient for taxonomic distinction above the species level”
  - We made the requested edit.

### **Reviewer: 2**

- line 12: typo in ‘others’
  - We made the correction.
- line 47: semi-colon should be lightface
  - We made the correction.
- line 69: an individual gnathostome has a single mandible (composed of left and right rami)
  - We made the correction.
- line 153: change ‘while’ to ‘whereas’
  - We made the requested edit.
- lines 162-163: the entrance of the lacrimal duct (lacrimal puncture or puncti) should be labelled (as some of our colleagues are using the lateral expression of this opening as a phylogenetic character)
  - We added the additional label to the figures.
- line 229: what exactly is ‘it’ ?
  - We clarified the language here.
- line 244: delete the word ‘on’ near end of sentence

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- We made the correction.
- lines 246-257: any evidence for a tympanic flange?
  - We added additional comments to this end.
- line 306: the angular generally articulates dorsally with the surangular
  - We made the correction.
- line 309: the surangular generally articulates ventrally with the angular; also, close up the space following the figure citation
  - We made the corrections.
- line 324: change ‘nares’ to ‘naris’
  - We made the requested edit.
- lines 360-361: do you mean that *Basicranodon fortsillensis* can be distinguished from neither *Mycterosaurus longiceps* nor *Mesenosaurus romeri* ?
  - We clarified the language here.
- lines 352, 354: ‘*M. longiceps*’ should be ‘*My. longiceps*’
  - We made the requested edit.
- line 442: the term ‘equatorial exposures’ is somewhat misleading. Do you mean ‘palaeoequatorial localities’?
  - We made the requested edit.
- line 450: for ‘explanator’ do you mean ‘hypothesis’?
  - We made the requested edit.

### Reviewer: 3

- Diagnosis - line 64 - ‘lack of contact between postorbital and supratemporal bones’. It would appear from the figures, and particularly from Fig 5, that the postorbital and supratemporal in *M. efremovi* are in contact, and that this contact distinguishes the new taxon from *M. romeri*, where these bones do not make contact (Reisz and Berman 2001). This view is indeed confirmed by the authors in lines 193-195. However, the same apparent error is made by the authors in the Discussion, lines 336-337. This requires clarification and amendment.
  - We clarified the language throughout the manuscript.
- Skull roof - line 119 - is the premaxilla transversely (mediolaterally) narrow?
  - We clarified the details.
- Skull roof - line 120 - are the authors able to note the narial shelf is smoothly rounded between the medial and lateral surface off the premaxilla? This might be worth noting as it has been proposed as a synapomorphy of varanopids (Reisz and Berman 2001).

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- We added additional details.
- Maxilla - line 138/139 - does the dorsal process extend posterior to the dorsal process of the jugal? In 73500 it appears to do so I left dorsolateral view, but in right lateral view it appears to be level with the dorsal process of the jugal. In line 146 authors note that the suborbital process of the maxilla terminates at the posterior orbital margin, which is probably slightly anterior to the dorsal process of the jugal.
  - We clarified the language.
- Maxilla - line 144 - 'proximity of the anterior orbital margin', perhaps authors could be more specific here, as in Reisz and Berman (2001), in describing the anterior extent of the lacrimal in respect to the snout, i.e. 40% between the orbit and the naris?
  - We clarified the language and added additional details.
- Maxilla- line 147 - is the anterior-most foramen larger than the posterior foramina? This might be of diagnostic interest in the wider sense.
  - We clarified the language.
- Marginal dentition - line 155 - authors note in line 152 that there are four distinct, enlarged teeth in the caniniform region. In line 155 they note the region covers positions 4-6, i.e only three teeth.
  - We clarified the language.
- Lacrimal - line 164 - is the lacrimal excluded from the naris bed contact of the maxilla with the nasal and the prefrontal?
  - We clarified the language.
- Nasal - line 165 - should read 'with the premaxilla anteriorly.'
  - We made the requested edit.
- Nasal - line 166 - and with the prefrontal posterolaterally?
  - We made the edit.
- Prefrontal - line 175-177 - the prefrontal does articulate with the frontal medially, but not with the parietal or postfrontal or postorbital. I think there is some confusion here between the pre- and post-frontals.
  - We made the correction.
- Prefrontal - line 178 - this might be better described as a sharp right-angled transition between the lateral and dorsal surfaces of the prefrontal, as in other mycterosaurines.
  - We made the requested edit.
- Frontal - line 180 - '....in both species of Mesenosaurus' might be more explanatory.
  - We made the requested edit.

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- Squamosal - is there a small posterodorsal process on the squamosal? The drawing of 73500 in right lateral seem to show a small process, which is interesting in respect to the more distinct processes on *Elliotsmithia* (Modesto et al. 2001). Without a close look at the specimen it's difficult to judge from the photo.
  - We added additional details.
- Vomer - line 237/238 - it's difficult to see in Fig 4 that the vomer, palatine and pterygoid articular in the way described. In Fig.4, I think the labelling on the lower of the two pterygoids (pt) is incorrect, and this should be the palatine. Nevertheless, although the text describes a typical palatal layout, it's difficult to see this in the illustration.
  - We made the changes to the description regarding sutural contacts but have double-checked the identifications and believe the figure was labeled correctly. The figured profile appears to show two separate ossifications, but they are exposed as a single ossification in views that were difficult to photograph.
- Vomer - line 239m - it's interesting to see the anterior vomers are bifurcated. Are they formed asymmetrically in the same way as *M. romeri*, with the longer medial spur?
  - We added additional information.
- Pterygoid - line 247 - does the palatal rami of the pterygoid articulate with the ectopterygoid anterolaterally or posterolaterally?
  - We checked the original interpretation and verified that it was anterolateral.
- Pterygoid - line 254/255 - are the teeth on the transverse flange isodont, or is the posterior-most row composed of larger teeth?
  - It was not possible to assess size patterns for this region in any specimen.
- Pterygoid - line 256/257 - Fig 4 doesn't show any contact between the quadrate ramus of the pterygoid and the quadrate. It just appears to end at the squamosal. In all it contacts the anterior flange of the quadrate, but this can't be seen in the figure.
  - We clarified the language.
- Exoccipital - line 275- the exoccipitals are paired elements but rarely meet their partner along the midline since they are often separated by the basioccipital (ventrally) and by the supraoccipital (dorsally) as in the case of *M. Romeri* (see Reisz and Berman Fig 4). Do the authors mean that each exoccipital is formed of two elements sutured along the sagittal midline?
  - We clarified the language.
- Stapes - line 298 - I'm not sure what the authors mean by the stapedial foramen piercing the columella 'anteroposteriorly to the footplate'. Perhaps this could be expanded upon.
  - We clarified the language.
- Dentary - line 293 - the dentary forms the anterodorsal margin of the mandible.
  - We made the edit.

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- Coronoid - line 304 - ‘...frame the coronoid process form within’, I suspect that authors mean that the coronoid has a mainly medial (lingual) exposure.
  - We clarified the language.
- Angular - line 306m- doesn’t the angular articulate with the surangular dorsally (Fig 5) rather than anteriorly?
  - We made the correction
- Surangular - line 309 - Fig 5 seems to show the surangular articulating with the dentary anterodorsally and the angular ventrally.
  - We made the corrections.
- Discussion - line 329 - are the authors sure that premaxillary teeth are absent in other mycterosaurines? Or is it that other mycterosaurines have less than 5 premaxillary teeth?
  - We clarified the language.
- Discussion - line 360 - the authors note that the parasphenoid described by Vaughn (1958) cannot be distinguish from *M. efremovi* and *Mycterosaurus*, and should be considered a nomen dubium. This may well be the case, however, the median ventral ridge on the basal plate described by the authors (lines 269/270) does not appear to be present in the parasphenoid described by Vaughn, where the anterolateral ridges (crista ventrolaterales?) form a shelf at their anterior point of confluence rather than a medial ridge (line 270). Vaughn describes medial ridges posterior to this shelf, in the concavity between the posteriorly diverging crista ventrolaterales. Perhaps the authors could consider a close-up drawing or illustration of the parasphenoid. It would be very useful for comparative purposes with other early amniotes.
  - We have clarified some of the details of the description of our taxon; there is a medial ridge in the concavity, but it is largely obscured by dislodged elements. A comparison with Vaughn’s figures did not indicate any appreciable difference in the anterior confluence of the ridges (i.e. no distinct shelf), and we attribute the apparent difference to word choice. We are working on CT data of the parasphenoid of the specimen that will be published in the future that will more clearly illustrate some of the relevant features in all anatomical profiles.
- Phylogenetic results - line 370 - MPTS should be MPTs
  - We made the edit.
- Phylogenetic results - line 380 - is the difference in tooth count qualitative in nature, or quantitative?
  - We clarified the language.
- Phylogenetic results - line 420 - did the authors consider adding *Cabarzia* to the Brocklehurst et al. matrix? Although only postcranial material is available for this taxon, postcranial data is available for *M. Romeri* (same paper, Spindler et al. 2018).
  - We did consider this option, but this would still fail to fully test the relationship of the three taxa, as the issue is the lack of skeletal overlap between the new taxon

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that we describe here and *Cabarzia*. Adding *Cabarzia* to the matrix that we used would essentially provide a single-taxon case study for partitioned datasets (i.e. does postcranial or cranial anatomy exert more influence on this specific relationship), which is something already tested by Benson (2012), which was the framework for the Brocklehurst et al. matrix.