

Functional constraints during development limit jaw shape evolution in marsupials

Anne-Claire Fabre, Carys Dowling, Roberto Portela Miguez, Vincent Fernandez, Eve Noirault and Anjali Goswami

Article citation details

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Review timeline

Original submission: 6 February 2021
Revised submission: 22 March 2021
Final acceptance: 29 March 2021

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

Review History

RSPB-2021-0319.R0 (Original submission)

Review form: Reviewer 1

Recommendation

Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Good

General interest: Is the paper of sufficient general interest?

Good

Quality of the paper: Is the overall quality of the paper suitable?

Excellent

Is the length of the paper justified?

Yes

Should the paper be seen by a specialist statistical reviewer?

Yes

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?

Yes

Is it clear?

Yes

Is it adequate?

Yes

Do you have any ethical concerns with this paper?

No

Comments to the Author

Unlike eutherian (placental) mammals, metatherian (marsupial) mammals are born before the end of embryonic development and complete their ontogeny outside of the body. This results in adaptation to the craniofacial skeleton and jaw to ensure feeding is possible at birth. This interesting article investigates the unique life history of marsupials results in developmental constraints limiting the potential morphologies of the lower jaw bone.

I find the data and arguments made clear and convincing, and the paper well written. Therefore I have no major revision requests.

Minor comments:

The diets corresponding to the box colours should be re-stated in figure 2 for ease of reading. This can be either in the legend or, preferably, in the figure itself.

One striking feature of the marsupial jaw compared to that of eutherians is the medially inflected angular process. Whilst mentioned in passing, I am surprised that this feature does not appear to alter the position and the morphospace more, particularly for hard food specialist feeders. perhaps a sentence or two could be added to discuss this.

Review form: Reviewer 2 (Vera Weisbecker)

Recommendation

Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?

Excellent

General interest: Is the paper of sufficient general interest?

Excellent

Quality of the paper: Is the overall quality of the paper suitable?

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Is the length of the paper justified?

No

Should the paper be seen by a specialist statistical reviewer?

No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.

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This study uses a sophisticated pipeline of geometric morphometric and phylogenetic methods to provide the best-supported comparative investigation of the claim that marsupial mammals have a developmentally constrained jaw and are therefore potentially less “adaptable”. The paper is very well written and clear, with excellent analyses, so that I have very few comments and no substantial issues at all. I love the availability of extensive code scripts!

The introduction is simple, clear, well-argued, and well-referenced. I have no suggestions for improvements.

The base methods are mostly following well-established protocols, but the phylogenetic methods are much more sophisticated than what is usually done, e.g. phylogenetic linear models that not just depend on an assumption of Brownian motion, and the excellent phylogenetic ridge regression for convergence. The BayesTraits pipeline is wonderful, it is so sad that this can't be implemented in R (yet).

A minor method/results clarity issue – at first I was looking for a reproductive mode variable in Table S1, but in the code “reproductive mode” seems to refer to the infraclass variable (i.e. metatherians vs. eutherians), rather than an actual reproductive mode – I also later found this in the text but it could be easier to understand if “reproductive mode” was replaced with “infraclass”, and perhaps an explanation that the main distinction assumed is between birth maturities.

The discussion is also clear and comprehensive.

The roughly page-long passage that raises validity concerns with Martin-Serra and Benson's paper might need some shortening, it seems out of scope because it deals with broader issues of serial homology and differential constraints in limbs, which this study is not addressing.

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P. 4, line 36: comma after "gestation"

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P. 14, line 249 – primate (not primates)

P. 17, Acknowledgements – it is *Tarsipes rostratus* (not *rostratum*).

I would recommend using a more precise term than "functional pressures", which sounds a bit like evolutionary selection pressure but is here used in the context of the evolution of individual development. Maybe "jaw function"?

Vera Weisbecker

Decision letter (RSPB-2021-0319.R0)

18-Mar-2021

Dear Dr Fabre:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into <http://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (<https://royalsociety.org/journals/ethics-policies/>). You should pay particular attention to the following:

Research ethics:

If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:

If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:

It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (<https://royalsociety.org/journals/authors/author-guidelines/#data>). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (<https://royalsociety.org/journals/ethics-policies/data-sharing-mining/>). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link [http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document%20not%20available)), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

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Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. 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. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr John Hutchinson, Editor
mailto:proceedingsb@royalsociety.org

Associate Editor
Comments to Author:

We have now received two thoughtful reviews of this manuscript. I am delighted to share the news that both reviewers found the manuscript interesting and well assembled. Both reviewers have provided a few simple recommendations/queries, and I suggest the authors address all of these. I agree with the reviewers that this is an excellent study and manuscript.

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Referee: 1

Comments to the Author(s)

Unlike eutherian (placental) mammals, metatherian (marsupial) mammals are born before the end of embryonic development and complete their ontogeny outside of the body. This results in adaptation to the craniofacial skeleton and jaw to ensure feeding is possible at birth. This interesting article investigates the unique life history of marsupials results in developmental constraints limiting the potential morphologies of the lower jaw bone.

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P. 14, line 249 – primate (not primates)

P. 17, Acknowledgements – it is *Tarsipes rostratus* (not *rostratum*).

I would recommend using a more precise term than “functional pressures”, which sounds a bit like evolutionary selection pressure but is here used in the context of the evolution of individual development. Maybe “jaw function”?

Vera Weisbecker

Author's Response to Decision Letter for (RSPB-2021-0319.R0)

See Appendix A.

Decision letter (RSPB-2021-0319.R1)

29-Mar-2021

Dear Dr Fabre

I am pleased to inform you that your manuscript entitled "Functional constraints during development limit jaw shape evolution in marsupials" has been accepted for publication in Proceedings B. No further revisions are required. Congratulations!

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. 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.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Dr John Hutchinson

Editor, Proceedings B

mailto: proceedingsb@royalsociety.org

Appendix A

Zurich, the 20th of March 2021,

Dear Dr Hutchinson,

We are pleased to submit our revised manuscript “Functional constraints during development limit jaw shape evolution in marsupials” (RSPB-2021-0319) by Anne-Claire Fabre, Carys Dowling, Roberto Portela Miguez, Vincent Fernandez, Eve Noirault and Anjali Goswami for publication in *Proceedings of the Royal Society B*. We would like to thank both reviewers, the associated editor and yourself for the positive and constructive review of our paper, and we feel that the comments and suggestions provided have greatly strengthened this work. Among the major changes, we re-did figure 2 by adding the colour categories as a legend. We have included the rewording and all the supplementary information required in the comments and suggestions of both reviewers. We would like to thank you once again for the positive and constructive reviews and hope that our paper is now suitable for publication in the *Proceedings of the Royal Society B*. Below you will find a detailed point-by-point reply to the comments of both referees.

Please feel free to contact us if there are any questions concerning this manuscript submission.

Sincerely,

Dr. Anne-Claire Fabre

Associate Editor

Comments to Author:

We have now received two thoughtful reviews of this manuscript. I am delighted to share the news that both reviewers found the manuscript interesting and well assembled. Both reviewers have provided a few simple recommendations/queries, and I suggest the authors address all of these. I agree with the reviewers that this is an excellent study and manuscript.

OUR REPLY: We thank the associated editor for this positive review and we have modified the manuscript in the light of the comments of both reviewers

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

Unlike eutherian (placental) mammals, metatherian (marsupial) mammals are born before the end of embryonic development and complete their ontogeny outside of the body. This results in adaptation to the craniofacial skeleton and jaw to ensure feeding is possible at birth. This interesting article investigates the unique life history of marsupials results in developmental constraints limiting the potential morphologies of the lower jaw bone.

I find the data and arguments made clear and convincing, and the paper well written. Therefore I have no major revision requests.

OUR REPLY: we thank the reviewer this really positive and constructive review.

Minor comments:

The diets corresponding to the box colours should be re-stated in figure 2 for ease of reading. This can be either in the legend or, preferably, in the figure itself.

OUR REPLY: we agree with the reviewer that the diet corresponding to the box colours was missing and we now added a legend to the figure.

One striking feature of the marsupial jaw compared to that of eutherians is the medially inflected angular process. Whilst mentioned in passing, I am surprised that this feature does not appear to alter the position and the morphospace more, particularly for hard food specialist feeders. perhaps a sentence or two could be added to discuss this.

OUR REPLY: thanks for this really good suggestion, we added one sentence to mention this striking result in the discussion

Referee: 2

Comments to the Author(s)

This study uses a sophisticated pipeline of geometric morphometric and phylogenetic methods to

provide the best-supported comparative investigation of the claim that marsupial mammals have a developmentally constrained jaw and are therefore potentially less “adaptable”. The paper is very well written and clear, with excellent analyses, so that I have very few comments and no substantial issues at all. I love the availability of extensive code scripts!

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OUR REPLY: we thank the reviewer for her really positive comment about our paper, and we are glad that she enjoyed our study as well as the availability of all the scripts and data. We think that nowadays, it is really important to share methodological pipelines as well as data sets with the scientific community.

A minor method/results clarity issue – at first I was looking for a reproductive mode variable in Table S1, but in the code “reproductive mode” seems to refer to the infraclass variable (i.e. metatherians vs. eutherians), rather than an actual reproductive mode – I also later found this in the text but it could be easier to understand if “reproductive mode” was replaced with “infraclass”, and perhaps an explanation that the main distinction assumed is between birth maturities.

OUR REPLY: we agree that this point needs to be clarified in the manuscript, we added one sentence in the main manuscript as well as in the supplementary information stating:

“Note that it is assumed in this study that all eutherians give birth to more developed newborns (from altricial to precocial) whereas all metatherians give birth to less developed newborns (highly altricial).”

We also used carefully checked the main manuscript and supplementary material in order to use the word “infraclass” when it was more appropriate to use than “reproductive mode”.

The discussion is also clear and comprehensive.

The roughly page-long passage that raises validity concerns with Martin-Serra and Benson’s paper might need some shortening, it seems out of scope because it deals with broader issues of serial homology and differential constraints in limbs, which this study is not addressing.

OUR REPLY: we agree and shortened this paragraph.

I thought a bit about the differences between the pMANOVA and the PCA morphospace. It sounds like the pMANOVA is done on the whole variation in the dataset whereas the PCA “only” accounts for ~half of the variation. Also, marsupials overlap with placentals on both PCs (but particularly on the much more important PC1). So this suggests that the differences in disparity and evolutionary rates between marsupials and placentals are a much greater point of difference than the actual differences in shape that we see on PC1/2 space. I find that fascinating and perhaps it could be emphasized, but this is just a suggestion.

OUR REPLY: thanks for this pertinent suggestion! We added a sentence to the discussion to highlight it!

P. 4, line 36: comma after “gestation”

OUR REPLY: thanks, we changed it

P. 4, line 46: comma after “evolution”

OUR REPLY: thanks, we changed it

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p. 8, the Procrustes disparity could be explained more clearly as to what the disparity measures (because there are different ways of measuring disparity).

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OUR REPLY: thanks, we changed it.

I would recommend using a more precise term than “functional pressures”, which sounds a bit like evolutionary selection pressure but is here used in the context of the evolution of individual development. Maybe “jaw function”?

OUR REPLY: we agree, we used jaw function as suggested.

Vera Weisbecker