

A key environmental driver of osteichthyan evolution and the fish-tetrapod transition?

H. M. Byrne, J. A. M. Green, S. A. Balbus and P. E. Ahlberg

Article citation details

Proc. R. Soc. A **476**: 20200355.

<http://dx.doi.org/10.1098/rspa.2020.0355>

Review timeline

Original submission: 4 May 2020
Revised submission: 16 September 2020
Final acceptance: 24 September 2020

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

Review History

RSPA-2020-0355.R0 (Original submission)

Review form: Referee 1

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

Good

Is the paper of sufficient general interest?

Excellent

Is the overall quality of the paper suitable?

Good

Can the paper be shortened without overall detriment to the main message?

Yes

Do you think some of the material would be more appropriate as an electronic appendix?

No

Do you have any ethical concerns with this paper?

No

Recommendation?

Accept with minor revision (please list in comments)

Comments to the Author(s)

The contribution is one of the first analyses showing a potential association between palaeotidal dynamics and the early vertebrate evolution during the Siluro-Devonian, more specifically osteichthyans and elpistostegalians. The analysis is sounded in terms of the tidal simulations for the Late Silurian and Early-Upper Devonian. Two different major events of vertebrate evolution are addressed: the diversification of osteichthyans and the origin of tetrapods. Although I'm working on tidal cycles at a micro-temporal scale in Devonian sites, my review will primarily focus on the palaeobiological perspective and the accuracy of the information about the palaeoichthyological sites of interest. The paper is an important contribution and, as mentioned by the authors, this type of analyses "establishing the role of paleotides in influencing major evolutionary events is a field holding great promise."

Review form: Referee 2**Is the manuscript an original and important contribution to its field?**

Excellent

Is the paper of sufficient general interest?

Excellent

Is the overall quality of the paper suitable?

Excellent

Can the paper be shortened without overall detriment to the main message?

Yes

Do you think some of the material would be more appropriate as an electronic appendix?

Yes

Do you have any ethical concerns with this paper?

No

Recommendation?

Accept with minor revision (please list in comments)

Comments to the Author(s)

The authors use a completely new, very innovative approach which is a great enrichment in the debate on the fish-tetrapod transition. It supports the previous hypothesis that the fish-tetrapod transition took place in tidal environments. I enthusiastically support the publication of this manuscript in Proceedings of the Royal Society A, and I have only two minor suggestions:

1) Page 4, lines 54-63. The scenario of the origin of early tetrapods living in a tidal environment and moving from one tidal pond to another was – to my best knowledge – first published by Schultze in 1997 (Reference: Schultze, H. P. (1997). Umweltbedingungen beim Übergang von Fisch zu Tetrapode [Paleoenvironment at the transition from fish to tetrapod]. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 36: 59-77).

2) Page 5, lines 66-69. The authors write that "elpistostegids" were found in deltaic or estuarine environments. This applies to Elpistostege and Panderichthys, but what about Tiktaalik? According to sedimentological data, it lived in a non-marine environment like shallow streams

and swamps (Daeschler et al. 2006). The habitat of “elpistostegids” was obviously diverse; did they evolve in tidal areas, and Tiktaalik is derived in that it lived in a different environment? You definitively should mention Tikaalik in your manuscript.

Decision letter (RSPA-2020-0355.R0)

09-Sep-2020

Dear Miss Byrne,

On behalf of the Editor, I am pleased to inform you that your Manuscript RSPA-2020-0355 entitled "Tides: A key driver of the fish-tetrapod transition?" has been accepted for publication subject to minor revisions in Proceedings A. Please find the referees' comments below.

The reviewer(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the reviewer(s)' comments and revise your manuscript. Please note that we have a strict upper limit of 28 pages for each paper. Please endeavour to incorporate any revisions while keeping the paper within journal limits. Please note that page charges are made on all papers longer than 20 pages. If you cannot pay these charges you must reduce your paper to 20 pages before submitting your revision. Your paper has been ESTIMATED to be 22 pages. We cannot proceed with typesetting your paper without your agreement to meet page charges in full should the paper exceed 20 pages when typeset. If you have any questions, please do get in touch.

It is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let me know in advance of the due date.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/prsa> 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.

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 referee(s) 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 referee(s).

IMPORTANT: Your original files are available to you when you upload your revised manuscript. Please delete any redundant files before completing the submission process.

In addition to addressing all of the reviewers' and editor's comments, your revised manuscript **MUST** contain the following sections before the reference list (for any heading that does not apply to your work, please include a comment to this effect):

- Acknowledgements
- Funding statement

See <https://royalsociety.org/journals/authors/author-guidelines/> for further details.

When uploading your revised files, please make sure that you include the following as we cannot proceed without these:

- 1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".
- 2) A separate electronic file of each figure (tif, eps or print-quality pdf preferred). The format should be produced directly from original creation package, or original software format.
- 3) Electronic Supplementary Material (ESM): all supplementary materials accompanying an accepted article will be treated as in their final form. 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 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://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. Alternatively you may upload a zip folder containing all source files for your manuscript as described above with a PDF as your "Main Document". This should be the full paper as it appears when compiled from the individual files supplied in the zip folder.

Article Funder

Please ensure you fill in the Article Funder question on page 2 to ensure the correct data is collected for FundRef (<http://www.crossref.org/fundref/>).

Media summary

Please ensure you include a short non-technical summary (up to 100 words) of the key findings/importance of your paper. This will be used for to promote your work and marketing purposes (e.g. press releases). The summary should be prepared using the following guidelines:

- *Write simple English: this is intended for the general public. Please explain any essential technical terms in a short and simple manner.
- *Describe (a) the study (b) its key findings and (c) its implications.
- *State why this work is newsworthy, be concise and do not overstate (true 'breakthroughs' are a rarity).
- *Ensure that you include valid contact details for the lead author (institutional address, email address, telephone number).

Cover images

We welcome submissions of images for possible use on the cover of Proceedings A. Images should be square in dimension and please ensure that you obtain all relevant copyright permissions before submitting the image to us. If you would like to submit an image for consideration please send your image to proceedingsa@royalsociety.org

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

Best wishes
Raminder Shergill
proceedingsa@royalsociety.org

Proceedings A

on behalf of
Professor Gregory Ivey
Board Member
Proceedings A

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

The contribution is one of the first analyses showing a potential association between palaeotidal dynamics and the early vertebrate evolution during the Siluro-Devonian, more specifically osteichthyans and elpistostegalians. The analysis is sounded in terms of the tidal simulations for the Late Silurian and Early-Upper Devonian. Two different major events of vertebrate evolution are addressed: the diversification of osteichthyans and the origin of tetrapods. Although I'm working on tidal cycles at a micro-temporal scale in Devonian sites, my review will primarily focus on the palaeobiological perspective and the accuracy of the information about the palaeoichthyological sites of interest. The paper is an important contribution and, as mentioned by the authors, this type of analyses "establishing the role of paleotides in influencing major evolutionary events is a field holding great promise."

Referee: 2

Comments to the Author(s)

The authors use a completely new, very innovative approach which is a great enrichment in the debate on the fish-tetrapod transition. It supports the previous hypothesis that the fish-tetrapod transition took place in tidal environments. I enthusiastically support the publication of this manuscript in Proceedings of the Royal Society A, and I have only two minor suggestions:

1) Page 4, lines 54-63. The scenario of the origin of early tetrapods living in a tidal environment and moving from one tidal pond to another was – to my best knowledge – first published by Schultze in 1997 (Reference: Schultze, H. P. (1997). Umweltbedingungen beim Übergang von Fisch zu Tetrapode [Paleoenvironment at the transition from fish to tetrapod]. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 36: 59-77).

2) Page 5, lines 66-69. The authors write that "elpistostegids" were found in deltaic or estuarine environments. This applies to Elpistostege and Panderichthys, but what about Tiktaalik? According to sedimentological data, it lived in a non-marine environment like shallow streams and swamps (Daeschler et al. 2006). The habitat of "elpistostegids" was obviously diverse; did they evolve in tidal areas, and Tiktaalik is derived in that it lived in a different environment? You definitively should mention Tikaalik in your manuscript.

Author's Response to Decision Letter for (RSPA-2020-0355.R0)

See Appendix A.

Decision letter (RSPA-2020-0355.R1)

24-Sep-2020

Dear Miss Byrne

I am pleased to inform you that your manuscript entitled "Tides: A key environmental driver of osteichthyan evolution and the fish-tetrapod transition?" has been accepted in its final form for publication in Proceedings A.

Our Production Office will be in contact with you in due course. You can expect to receive a proof of your article soon. Please contact the office to let us know if you are likely to be away from e-mail in the near future. If you do not notify us and comments are not received within 5 days of sending the proof, we may publish the paper as it stands.

Open access

You are invited to opt for open access, our author pays publishing model. Payment of open access fees will enable your article to be made freely available via the Royal Society website as soon as it is ready for publication. For more information about open access please visit <https://royalsociety.org/journals/authors/which-journal/open-access/>. The open access fee for this journal is £1700/\$2380/€2040 per article. VAT will be charged where applicable.

Note that if you have opted for open access then payment will be required before the article is published – payment instructions will follow shortly.

If you wish to opt for open access then please inform the editorial office (proceedingsa@royalsociety.org) as soon as possible.

Your article has been estimated as being 20 pages long. Our Production Office will inform you of the exact length at the proof stage.

Proceedings A levies charges for articles which exceed 20 printed pages. (based upon approximately 540 words or 2 figures per page). Articles exceeding this limit will incur page charges of £150 per page or part page, plus VAT (where applicable).

Under the terms of our licence to publish you may post the author generated postprint (ie. your accepted version not the final typeset version) of your manuscript at any time and this can be made freely available. Postprints can be deposited on a personal or institutional website, or a recognised server/repository. Please note however, that the reporting of postprints is subject to a media embargo, and that the status the manuscript should be made clear. Upon publication of the definitive version on the publisher's site, full details and a link should be added.

You can cite the article in advance of publication using its DOI. The DOI will take the form: 10.1098/rspa.XXXX.YYYY, where XXXX and YYYY are the last 8 digits of your manuscript number (eg. if your manuscript number is RSPA-2017-1234 the DOI would be 10.1098/rspa.2017.1234).

For tips on promoting your accepted paper see our blog post: <https://royalsociety.org/blog/2020/07/promoting-your-latest-paper-and-tracking-your-results/>

On behalf of the Editor of Proceedings A, we look forward to your continued contributions to the Journal.

Sincerely,
Raminder Shergill
proceedingsa@royalsociety.org

Appendix A

Response to reviewers

Reviewer one

The contribution is one of the first analyses showing a potential association between palaeotidal dynamics and the early vertebrate evolution during the Siluro-Devonian, more specifically osteichthyans and elpistostegalians. The analysis is sounded in terms of the tidal simulations for the Late Silurian and Early-Upper Devonian. Two different major events of vertebrate evolution are addressed: the diversification of osteichthyans and the origin of tetrapods. Although I'm working on tidal cycles at a micro-temporal scale in Devonian sites, my review will primarily focus on the palaeobiological perspective and the accuracy of the information about the palaeoichthyological sites of interest. The paper is an important contribution and, as mentioned by the authors, this type of analyses "establishing the role of paleotides in influencing major evolutionary events is a field holding great promise."

The authors would like to thank reviewer one for their appraisal of our work and for their thorough review of the manuscript, with valuable and constructive feedback. The Manuscript is stronger from their contributions.

1. The title is attractive but it does not properly reflect the content of the manuscript. This title is inappropriate because it provides a partial and biased view of the richness of the manuscript. Although the question about the fish-tetrapod transition is addressed, the main purpose of the paper is not to test if palaeotidal dynamics is a key driver. In terms of evolutionary biology, a key driver has to be tested and not solely assume as it is in this title (furthermore this expression is not use in their manuscript). The paper does not look only at the origin of tetrapods but also at the origin-diversification of osteichthyans. I strongly suggest to change the title to something that reflects the totality of the results of the research.

We appreciate the opinion of the reviewer; we have therefore amended the title to better represent the scope of the paper.

2. The abstract provides also only a one-sided view of the analysis. As it is the title and the abstract agree, however, both of them do not agree with the remaining parts of the paper. The first sentence addresses the question of the origin of tetrapods, while the paper deals equally (if not more) with the origin-diversification of osteichthyans. Furthermore, the end of the first sentence (line 14) presents one view concerning the timing of the origin of tetrapods. Although there is one hypothesis based on trackways suggesting a ca. 393 Ma origin of tetrapods, all osteological evidences suggest a more recent origin of tetrapods. I considered that the abstract (and subsequently in the introduction and discussion) of this great paper should not be used as a platform to address this issue. Furthermore, the abstract puts a greater emphasis on the palaeobiological association rather than the results and conclusions about Devonian tidal dynamics. As it is, the abstract is highly speculative and does not reflect the strong content of the paper.

We have considered the opinion of the reviewer, and so have re-written the abstract to better reflect the contents of the paper.

3. At the beginning of the introduction (lines 29-30), one more time the ichnological hypothesis is presented as the sole hypothesis, while all anatomical evidences suggest a different timing. I think that both hypotheses should be presented although I understand that one of the coauthors defends this point of view (which I'm not saying that is false but that it is not the most prevalent hypothesis).

The authors welcome the reviewers comment, and have amended the text to include reference to the earliest body fossil evidence for the timing of the origin of tetrapods. We would note here that the trackway evidence (some of which is currently under description by members of this author team) is very robust, but this is really a discussion for another day and another paper.

4. On line 34, the authors refer to the “early radiation of bony fishes,” although we have fairly good evidences that there has been an early diversification, the hypothesis of an early evolutionary radiation has not been tested. I suggest to use the term “diversification” rather than “radiation” as it has been used throughout the text.

The word ‘radiation’ has been changed to ‘diversification’ in the text.

5. I suggest to add a reference at the end of lines 36-38 (references that already have been cited at the end of this paragraph).

The relevant references have now been included at the end of lines 36-38.

6. One more time, on line 46, only the trackway evidences are presented.

Like with comment number three, the authors have now amended the text to include reference to the earliest body fossil evidence for the timing of the origin of tetrapods

7. At the beginning of the second paragraph (line 53), it is presented that the “tides were an important environmental adaptive pressure.” I'm not questioning the pertinence of the importance of tidal dynamics. However, tides, itself, are not necessarily the selective pressure. It could be specific phenomena associated with tides, such as the amplitude of the tides or the environmental fluctuating stability created by the tidal cycles, that are the selective pressures.

We appreciate the view of the reviewer, and agree with them. This is why we include the statement in lines 64-66: While the expanse of estuaries and deltas is largely controlled by long-term sea-level fluctuations, a large tidal range would also help to maintain such regions, which provide an ideal transitory environment for the terrestrialisation of tetrapods.

8. When talking about the selection associated with the appendages and breathing (lines 62-63), I think it would be appropriate to refer to the experimental work of Standen et al. (2014) on the plasticity observed in *Polypterus* under experimental conditions simulating terrestrialisation.

We thank the reviewer for the suggestion to mention this study in the manuscript, and so it has been included with reference to the paper suggested.

9. I would rather use the term elpistostegalians or elpistostegalids than ‘elpistostegids’ (lines 67 and 87)

The words ‘elpistostegids’ has been amended to ‘elpistostegalians’ in both lines

10. On line 68, Cloutier et al. (2011, *Palaeobio. Palaeoenviron.*) is also an appropriate reference for this relation between estuarine and elpistostegalians. On lines 74-75, the authors mentioned the time period between the Late Silurian and Early Devonian for evidence for early osteichthyans and early tetrapods. As I mentioned already, the first “hard evidence”, i.e., anatomical evidence for early tetrapods are Middle-Late Devonian and not Early Devonian (as suggested by trackways).

The suggested reference has been included, and the wording for Early Devonian has been changed to early Late Devonian, to include the period of study observed.

11. On numerous lines (e.g., lines 76, 133-134, 150-151) the authors write Early Middle Devonian and Early Late Devonian; the first capitalized letter could be confusing, I would rather suggest to write “early Middle Devonian” and “early Late Devonian.”

We thank the reviewer for pointing out this error and it has been amended in all cases.

12. On lines 86-87, the authors mention that the first body fossils of ‘elpistostegids’ occur during the Early Frasnian. Subsequently in the paper, the authors use the Escuminac Formation as the locality where *Elpistostege watsoni* occur for such time period. Although Panderichthys is late Givetian-early Frasnian and *Tiktaalik* is early-middle Frasnian, *Elpistostege* is middle Frasnian. On line 242, the authors write that the Escuminac Formation is dated “Early Frasnian” providing in reference Cloutier et al. (1996). However, Cloutier et al. (1996) provided palynological evidence that the Escuminac Formation is middle Frasnian and not early Frasnian. Furthermore, recently, Cloutier et al. (2020) identified *Elpistostege watsoni* as a tetrapod rather than an elpistostegalid fish.

We appreciate the correction from the reviewer on the dating of *Elpistostege watsoni*, and it has been altered in the text in lines 97, 151, 242 and in Table 1.

13. On line 160, “i.e.,” is used rather than “e.g.,” (then no need to use “etc”)

The suggested amendment has been made on line 160.

14. On line 242, it is tetrapodomorph rather than tetrapodamorph. On line 242, it is foordi rather than foordii

The text has been fixed in the text as recommended.

15. On line 243, when referring to the palaeoenvironment of the Escuminac Formation, the reference Hesse & Sawh (1992) is outdated and should be replaced by Cloutier et al. (2011, Palaeobiol. Palaeoenviro.)

This reference has been updated as recommended.

16. On line 267, replace fund by found In the conclusion, the authors mention that their simulations are broadly supportive of the hypothesis that tides were an important environmental and evolutionary impetus for the origin of osteichthyans and tetrapods. Although I consider that they authors have shown a potential relation between these two evolutionary events and the importance of tidal dynamics in the broad regions where fossils occur, a causal link is impossible to identify. Although the estuarine (-tidal) environment could potentially be link to the origin-diversification of these groups, the spatial scale of their study is at a quite different scale than the occurrence of the evolutionary events. Furthermore, without having the prevailing condition prior to the evolutionary events it is difficult to infer if a change in environmental-tidal conditions is truly associated with these events. Nevertheless, I still consider this study to be an important one to look at these evolutionary questions. I suggest to be more cautious in the evolutionary interpretation.

The authors acknowledge the viewpoint of the reviewer. We have made it clear throughout the text that we accept the complexities and uncertainties surrounding the evolution of the osteichthyan and tetrapod lineages, and that we are testing whether large tides occurred in conjunction with this evolution, which is motivated by the hypothesis that tides could have acted as an environmental driver in the origin of lungs and limbs.

17. Table 1: In order to be consistent with the geographic terminology provided for the USA (i.e., state, country), I suggest that a similar terminology be used for China and Canada (e.g., Quebec, Canada). The “Geological period” is in fact the “Geological stage” (or Geological age). The Escuminac Formation is Middle Frasnian.

The authors thank the reviewer for pointing these issue out, and they have been amended with “Geological period” changed to “Geological stage”, and the states/territory names included for China and Canada in Table 1.

Figure 1: The abbreviations for the localities are missing in the caption. In Fig. 1f the Battery Point Formation is identified as a small dot; however, the Battery Point Fm extends for more than 300 km on the eastern coast of the Gaspé Peninsula of Quebec. The positioning of the localities on the maps has not been explained in the Mat & Met (nor the caption); since tidal dynamics is dependent on the position of the localities, I think it could be important to specify.

The authors appreciate this feedback and have included the missing abbreviations. The authors appreciate the reviewer’s comments on the size and positioning of the proxy localities, and the absence of an explanation in the text. The first author was responsible for outlining the proxy locations on the palaeogeographic reconstructions and did so using the same palaeogeographic reconstructions as shown in Figure 1., but which had the addition of present day country outlines superimposed. Exact locations and scales were difficult to ascertain due to the coarse resolution of the reconstructions, so the author admits that the locations are an approximation. This explanation has been included in the Mats&Mets as recommended by the reviewer.

Reviewer 2

The authors use a completely new, very innovative approach which is a great enrichment in the debate on the fish-tetrapod transition. It supports the previous hypothesis that the fish-tetrapod transition took place in tidal environments. I enthusiastically support the publication of this manuscript in Proceedings of the Royal Society A, and I have only two minor suggestions.

The authors would like to thank reviewer two for his appraisal of our work and for his suggested comments. We have implemented them accordingly.

1. Page 4, lines 54-63. The scenario of the origin of early tetrapods living in a tidal environment and moving from one tidal pond to another was – to my best knowledge – first published by Schultze in 1997 (Reference: Schultze, H. P. (1997). Umweltbedingungen beim Übergang von Fisch zu Tetrapode [Paleoenvironment at the transition from fish to tetrapod]. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 36: 59-77).

The authors are aware of Prof Schultze’s hypothesis of a tidal origin for tetrapods, and we have made reference to this on line 55, but we appreciate the information of the original reference to his hypothesis and so have included this one instead.

2) Page 5, lines 66-69. The authors write that “elpistostegids” were found in deltaic or estuarine environments. This applies to *Elpistostege* and *Panderichthys*, but what about *Tiktaalik*? According to sedimentological data, it lived in a non-marine environment like shallow streams and swamps (Daeschler et al. 2006). The habitat of “elpistostegids” was obviously diverse; did they evolve in tidal areas, and *Tiktaalik* is derived in that it lived in a different environment? You definitively should mention *Tiktaalik* in your manuscript.

We acknowledge the point raised by the reviewer. However as we have already made to reference to the complexities and alternative hypotheses surrounding the fish-tetrapod transition, and as we are exploring tidal ranges in relation to the tidal hypothesis in this study, we do not feel it necessary to state the palaeoenvironment of *Tiktaalik*. The important point is that *some* elpistostegalians lived in estuarine/deltaic environments, and that this underscores the potential relevance of tidal environments to our understanding of tetrapod origins; the fact that *Tiktaalik* lived in a fluvial environment is less important, given that this is primarily a paper about tides, not about elpistostegalians as such.