

Review file for "Tip dating supports a Middle Ordovician origin for total-group chondrichthyans and a rapid radiation of acanthodian-grade taxa" by Lorenzo Emanuele Morra, published in *Open Palaeontology*.

This file contains the editorial and reviewer comments for the two rounds of review for this manuscript. Confidential comments to the editor and marked up/tracked changes documents are not included.

Round 1

Reviewer #1: Christian Klug

Dear Dr. Morra, dear Juan, dear editors,

I have read the manuscript and came to the conclusion that it is a thorough piece of research.

I must add that my methodological knowledge in the methods used herein is limited and I hope that the other reviewer(s) have a deeper expertise in that regard.

Concerning acanthodians, I am not surprised by the results. I had this impression already from the results of various other published analyses and thus agree with the conclusions.

The only thing that needs attention are the tapeworm sentences. There are several sentences that go on over numerous lines. Such endless phrases tend to contain (and hide) grammatical mistakes. More importantly, they are difficult to understand. In the interest of future readers, please reduce phrase length. In some places, I did this already, but please double-check for this aspect.

The first supplementary figure lacks an indication that the horizontal axis shows age [Ma].

Once this is done (minor revisions), the ms can be published (as long as somebody else has looked into the methodology).

Best regards,

Christian Klug

Reviewer #2: Plamen Andreev

The study provides the first tip-dating phylogenetic reconstruction of early chondrichthyans that incorporates recently discovered taxa from the lower Silurian. As such, it has the potential of improving our understanding of the timing of the origins of major jawed vertebrate clades and supply a hypothesis for the pattern of the initial radiation of chondrichthyans.

I suggest addressing the following issues (see also annotated manuscript for further comments) in order to make this work publishable:

There is no clear explanation as to what type of advancement the applied phylogenetic methodology and results represent in comparison to available time-adjusted trees of early vertebrates (Zhu et al. 2022, Andreev et al. 2022).

The author seems to have overlooked the significance of the origin date of crown gnathostomes in their tip-dated tree, which is c.20 Mya older than previous estimates (Zhu et al. 2022, Andreev et al. 2022). This has a bearing on the radiation pattern of early chondrichthyans and I would like to see it discussed in the text.

Include a results-based hypothesis (e.g. short-, long-fuse, explosive) for the initial diversification of chondrichthyans.

Remove or significantly reduce the second part of the Discussion section which currently is dedicated to explaining the shortcomings of morphology-based trees of extinct taxa.

Editorial decision

Dear Dr. Morra,

Thank you very much for your submission and for your patience while we collected the reviews.

The reviewers have provided constructive feedback on your manuscript. Both reviewers consider that revisions are needed before the paper can be considered for publication, and I agree with this assessment.

In particular, the manuscript should more clearly explain how the methodological approach and/or revised dataset advances our understanding of the phylogenetic relationships and evolutionary history of the study group. The *Discussion* would also benefit from a deeper consideration of the evolutionary patterns in light of your results.

Additionally, please revise the manuscript carefully to improve readability. In the *Methods* and *Results* sections, several paragraphs consist of a single, very long sentence and should be broken up for clarity.

Regarding figures, please note that in **Figure 3** the taxon names appear too small and should be enlarged to ensure legibility.

Kind regards,

Juan Carrillo
Handling Editor

Below you may find the reviewer comments. Additional review files are available in the Review Files section of our submission platform in the files called:

MS+Acanthodii_Morra_Klug_rev.docx

MS+Acanthodii_Andreev_rev.docx

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- a revised editable version of the manuscript with tracked changes,
- a editable 'clean' version of the manuscript (with no tracked changes)
- a 'clean' version of the manuscript (with no tracked changes) as a pdf,
- a point by point explanation of how you have addressed the reviewers' comments,

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Response 1

Dear Dr. Carrillo and dear reviewers,

Thank you for the prompt handling of my manuscript and for the reviews.

I really appreciated comments from both reviewers. I agree with all the points raised and I have addressed all the requests and suggestions. Below is a list of my responses, which are highlighted in blue.

Modifications include an added explanation on the advantages of the applied phylogenetic methodology compared to a posteriori time-scaling approaches, further discussion and comparisons with previous phylogenetic results and divergence age estimates, as well as the inclusion of a results-based hypothesis for the initial diversification of chondrichthyans.

The title and abstract were revised and the second part of the discussion was removed as suggested by reviewer Plamen Andreev.

Furthermore, long sentences were broken up and emended throughout the text as suggested by both Editor and reviewer Christian Klug.

Figure 3 was emended: taxon names were enlarged and some were omitted for clarity. For the same reason, Figure 1 was also slightly modified.

Reviewer #1: Christian Klug

- Dear Dr. Morra, dear Juan, dear editors,

I have read the manuscript and came to the conclusion that it is a thorough piece of research.

I must add that my methodological knowledge in the methods used herein is limited and I hope that the other reviewer(s) have a deeper expertise in that regard.

Concerning acanthodians, I am not surprised by the results. I had this impression already from the results of various other published analyses and thus agree with the conclusions.

I thank the reviewer for the comments that significantly helped improve the MS.

- The only thing that needs attention are the tapeworm sentences. There are several sentences that go on over numerous lines. Such endless phrases tend to contain (and hide) grammatical mistakes. More importantly, they are difficult to understand. In the interest of future readers, please reduce phrase length. In some places, I did this already, but please double-check for this aspect.

I thank the reviewer for the suggestion. I have emended such sentences throughout the text.

- The first supplementary figure lacks an indication that the horizontal axis shows age [Ma].

Indication added.

-Comment at page 1, line 23

Emended to 'Early Devonian' (page 1, line 23 in the revised MS).

-Comments at page 2, lines 51-55

Corrected. Sentences shortened as suggested (page 2, lines 48-54 of the revised MS).

-Comment at page 2, line 63

Corrected (page 2 line 61 of the revised MS).

-Comments at page 3, lines 67, 69, 77

Corrected and citation to Frey et al. (2019) added as suggested by the reviewer (lines 459-461 of the revised MS).

-Comment at page 8, lines 245-246

Corrected. (page 8, line 251 of the revised MS).

-Comments at page 9, lines 274-280 and 282-287

Emended as suggested by the reviewer. Sentences shortened (page 9 lines 301-308 of the revised MS).

-Comments at page 10, lines 296, 303-306, 309-311, 317

Corrected.

-Comment at page 11, line 322

Corrected.

-Comments at page 12, line 352

Corrected.

Reviewer #2: Plamen Andreev

- The study provides the first tip-dating phylogenetic reconstruction of early chondrichthyans that incorporates recently discovered taxa from the lower Silurian. As such, it has the potential of improving our understanding of the timing of the origins of major jawed vertebrate clades and supply a hypothesis for the pattern of the initial radiation of chondrichthyans.

I thank the reviewer for the comments that considerably improved the MS.

- The author seems to have overlooked the significance of the origin date of crown gnathostomes in their tip-dated tree, which is c.20 Mya older than previous estimates (Zhu et al. 2022, Andreev et al. 2022). This has a bearing on the radiation pattern of early chondrichthyans and I would like to see it discussed in the text.

I agree with the reviewer. The following discussion was added to the text at page 9, lines 260-277: "Differently from the time-adjusted parsimony analyses in Andreev et al. (2022a,b) and Zhu et al. (2022), the tip dating analysis presented herein recovered an Early Ordovician (Floian) age for crown gnathostomes, a Middle Ordovician (Darriwilian) age for total-group chondrichthyans and Upper Ordovician dates for the origin of major acanthodian groups. This suggests a long fuse model of diversification, in which all interordinal diversification took place in the Ordovician and most of the intraordinal cladogenesis that produced the Devonian taxonomic diversity of acanthodians occurred in the Silurian. A long fuse diversification model would also imply a relatively low taxonomic diversity in the Middle-Upper Ordovician and for most of the Silurian, consistent with the patchy fossil record of the group in these periods. Older divergence dates recovered herein could be explained by the more complete taxon sample of the present matrix, as well as the different tree reconstruction method used. A Floian age for the origin of crown gnathostomes is ~20 million years older than previous estimates based on morphological data (Andreev et al., 2022b and Zhu et al., 2022) and is possibly supported by Middle Ordovician chondrichthyan-like scales described in Sansom et al. (2012). This seems to lend further support to the hypothesis that the initial diversification of Gnathostomata was part of the Great Ordovician Biodiversification Event, as already discussed in Marjanović (2021) and Andreev et al. (2022b)."

- *Include a results-based hypothesis (e.g. short-, long-fuse, explosive) for the initial diversification of chondrichthyans.*

I thank the reviewer for the suggestion. I added the following text at page 9, lines 264-269: "This suggests a long fuse model of diversification, in which all interordinal diversification took place in the Ordovician and most of the intraordinal cladogenesis that produced the Devonian taxonomic diversity of acanthodians occurred in the Silurian. A long fuse diversification model would also imply a relatively low taxonomic diversity in the Middle-Upper Ordovician and for most of the Silurian, consistent with the patchy fossil record of the group in these periods."

- *Remove or significantly reduce the second part of the Discussion section which currently is dedicated to explaining the shortcomings of morphology-based trees of extinct taxa.*

Done. I removed many of the general comments about morphological phylogenetic inference.

- *There is no clear explanation as to what type of advancement the applied phylogenetic methodology and results represent in comparison to available time-adjusted trees of early vertebrates (Zhu et al. 2022, Andreev et al. 2022).*

I thank the reviewer for the suggestion and agree on the necessity of such an explanation. I added it in the Materials and Methods section, page 4, lines 118-124 of the revised MS. The following text was added: "Tip-dating Bayesian methods are used to simultaneously infer tree topology, branch lengths and divergence dates using morphological and stratigraphic information from the terminal taxa. As a result, topologies obtained by these methods are generally more stratigraphically congruent than trees retrieved by undated Bayesian and parsimony analyses (King, 2021; López-Antoñanzas and Peláez-Campomanes, 2022) and are, hence, preferable to other a posteriori time-scaling methods for inferring divergence dates."

- *The title is a bit counter intuitive. Are you suggesting that there were non-acanthodian chondrichthyan lineages predating the origin of acanthodian-grade taxa? Please revise.*

Title revised as suggested by the reviewer.

- *Comment at page 1, line 20*

Emended.

- *I am not sure what operational means here? It is more pertinent to state what type of taxa are being studied, articulated taxa, organ taxa (e.g. scales, teeth) or a mix of both.*

Page 1, line 21

Changed to 'articulated taxa' as suggested by the reviewer (page 1 line 20-21 of the revised MS).

- *Total-group chondrichthyans? Please apply cladistic terminology consistently throughout the text. Page 1, line 22*

Emended to 'total-group chondrichthyans' throughout the text.

- *Can you be more specific, when did this initial radiation occur according to the tip-dated analyses? Also, is it possible to infer the divergence pattern of the radiation?*

Page 1, line 27

I thank the reviewer for the suggestion. I added more specific age estimates for the initial radiation of total-group Chondrichthyes as inferred by the tip dating analysis

(page 1 line 30 of the revised MS). The exact divergence pattern recovered by the analysis, although poorly supported, is discussed later in the text.

- *This statement is poorly constrained. How is 'morphologically similar' defined here, is it at a species, genus or higher taxonomical level. What constitutes a low rate of evolutionary change, is that determined relative to the morphological clock data shown in Figure 2.*

Page 1, lines 27-30

I added a brief explanation on what rates of morphological divergence mean that could help make the sentence clearer (abstract, page 1 lines 33-34 of the revised MS). A more detailed explanation is in the Discussion section because of the word limit in the abstract.

- *Do you mean explosive radiation? Page 1, line 33*

This part of the abstract was deleted and emended. Nonetheless, throughout the text I use 'ancient rapid radiation' *sensu* Whitfield and Lockhart (2007) and Whitfield and Kjer (2008), that is "where the deeper internal branches of the phylogeny are much shorter than the branch lengths between them and the tips ... In this situation, there might have been little opportunity for evolutionary changes (molecular or morphological) to accumulate in these short internal time spans", and "...diversification in which lineages ... have diverged in rapid succession within a relatively short time span in the ancient past, generating patterns of molecular and morphological change that are difficult to discern phylogenetically. We refer to these patterns as ancient rapid radiations, with no implication that evolutionary change has accelerated in these cases; instead, it is lineage splitting or diversification that has happened rapidly".

-*Comments at pages 1 and 2, lines 33-40*

I emended the abstract according to the reviewer's suggestion; it now has a clearer conclusion with the results and their implications.

-*Comment at page 2, line 45*

Changed 'group' to 'grade' as suggested (page 2 line 43 of the revised MS).

- *Many 'acanthodian' lineages (e.g. climatiids, diplacanthids) also possess pectoral dermal plates. Page 2, lines 50-51*

I thank the reviewer for specifying. I emended the sentence accordingly (page 2 line 48-49 of the revised MS).

-*Comment at page 2, line 51*

Emended, 'probably' was deleted.

-*Comment at page 2, line 52*

Emended, 'morpho-anatomy' was changed with 'anatomy' (page 2, line 52 of the revised MS).

-*Comment at page 2, line 60*

I added the two citations to recent works as suggested by the reviewer.

- *I agree, this is true for these and other (e.g. Frey et al. 2020) chondrichthyan dominated trees. However, more inclusive data matrices (Trinajstic et al. 2022, Brazeau et al. 2023,*

Cui et al. 2025) of early vertebrates return different tree topologies of the chondrichthyan stem, where the climatiids are a derived component of the stem group. Page 2, line 66

I thank the reviewer for the comment, I specified that more inclusive analyses usually retrieve climatiids in a more crownward position as suggested (page 3, line 66-67 of the revised MS).

- Nevertheless, time-correlated trees were provided by Zhu et al. 2022 and Andreev et al. 2022. You need to explain here why the tip-dating approach is better at inferring the timing of divergence events. Page 3, lines 78-80

I added a discussion and references on why a Bayesian tip dating approach is preferable for inferring divergence dates to other methods in the Materials and Methods section, at page 4, lines 118-124 of the revised MS.

-Comment at page 3, line 81

At page 3, lines 79-84 of the revised MS, I specified that 'comprehensive' here refers to data collecting practices and to the 'total evidence' philosophy behind the matrix presented, where all, or almost, of the published informative characters and most of the better known and reasonably complete acanthodian taxa are included.

-Use total group chondrichthyans consistently throughout the text. Page 3, line 81
Changed throughout the text.

-Comment at page 4, line 120

Temperature is a correct parameter, burn-in is specified later in the text and is 0.25.

-Which taxa are included here, do they form a clade? Page 6, lines 174-175

I listed those taxa and specified they don't form a clade. (page 6 line 179-180 of the revised MS).

- It is in agreement with Zhu et al. 2022, suggesting that the resultant topology of the chondrichthyan stem is influenced by the character/taxon selection rather than the use of the tip-dating methods. Page 6, lines 176-180

I agree with the reviewer. I specified this at page 7, lines 200-202 of the revised MS.

- There is precious little in a way of interpretation of the results in this section. Instead of going at lengths about the limitations of morphological characters in fossils, this space could be dedicated to putting forward a hypothesis for the pattern of the initial radiation of early chondrichthyans. Your data seem to suggest that the major acanthodian lineages originated in the Upper Ordovician just prior to the end Ordovician mass extinction event (c. 445 Mya). This fits a radiation model (long fuse?), where the major phase of acanthodian cladogenesis at lower taxonomic levels happens in the Silurian to early Devonian. Page 8, line 241

I agree with the reviewer on the necessity of a more detailed discussion about the differences in the results between prior time-adjusted analyses and the Bayesian analysis in my study, as well as a discussion and hypothesis on the diversification of major acanthodian clades. I added such discussion at page 9, lines 260-277. Further, I agree with the reviewer about my results suggesting a long fuse or quasi-long fuse model of diversification for acanthodians, and I expressed this in the text. Despite this, I still endorse a rapid radiation hypothesis for the earliest radiation of acanthodians, with the initial interordinal diversification happening in a relatively short amount of time

(~8 million years from the common ancestor of total chondrichthyans to the climatiiforms divergence in the Bayesian results). Such a compressed phylogenetic pattern can explain low support values and uncertainty regarding acanthodian orders relationships. Consequently, I have maintained some of the relative parts in the text.

- The apparent low rates of morphological evolution at more basal nodes could be influenced in part by the sparse fossil record of jawed vertebrates in the Upper Ordovician-lower Silurian. The age of Fanjingshania has shifted the origin of climatiids in your analysis to the Katian, and it plausible to assume that the other 'acanthodian' lineages should have comparable origin dates. Therefore, the divergence rates produced by your analysis can not be interpreted without the caveat of potential cryptic morphological diversity in early chondrichthyans caused by preservational bias. Pages 8-9, lines 255-262

I strongly agree with the reviewer on this, and I made it clear in the text. (Page 10, lines 284-287). I added “Comparatively low rates of divergence could be due to the sparse fossil record of jawed vertebrates in the Upper Ordovician and lower Silurian. Cryptic morphological diversity caused by preservational bias could have artificially lowered rates of morphological evolution in this case”.

-Comment at page 9, line 261

I used ‘internode’ as a synonym of ‘internal branch’ throughout the paper, see for example Whitfield and Lockhart (2007).

References

Whitfield, J.B. and Kjer. K.M. 2008. Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology* 53:449-72.
<https://doi.org/10.1146/annurev.ento.53.103106.093304>. PMID: 17877448. 664 665

Whitfield, J.B. and Lockhart, P.J. 2007. Deciphering ancient rapid radiations. *Trends in Ecology & Evolution* 22, 258–265. <https://doi.org/10.1016/j.tree.2007.01.012>

Round 2

Reviewer #2: Plamen Andreev

The author has addressed the main issues that I had with the original submission, which I am really happy to see.

Aside from a few minor changes that I recommend in the annotated manuscript I want to highlight that the proposed early radiation pattern of stem chondrichthyans does not fit a typical long fuse model. Instead, it appears that it is closer to some type of explosive radiation[1], where the branching events at high taxonomic levels largely occurred within a relatively narrow timeframe in the Middle-Upper Ordovician. An argument could be made that the extremely poor fossil record of jawed vertebrates in the Ordovician-lower Silurian could mask a long fuse diversification pattern of early chondrichthyan lineages, but this needs to be made clear in the title and the main text.

1. David M. Grossnickle, Stephanie M. Smith, Gregory P. Wilson. 2019. Untangling the Multiple Ecological Radiations of Early Mammals, *Trends in Ecology & Evolution*, Volume 34, Issue 10